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Uppermost Devonian ammonoids from Oklahoma and their palaeobiogeographic significance

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ABSTRACT:

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The upper part of the Woodward Shale of southern Oklahoma has yielded the first moderately diverse North American ammonoid fauna from the uppermost Famennian (Upper Devonian VI). It includes six species from three clymeniid and one goniatite family: *Kielcensia vagabunda* sp. nov., *Riphaeoclymenia polygona* sp. nov., *R. pontotocensis* sp. nov., *Cyrtoclymenia* cf. *procera* Czarnocki, 1989, *Spirosporadoceras overi* gen. nov. sp. nov., and a poorly preserved different juvenile sporadoceratid that may represent a second new genus. For comparison, the related *Spirosporadoceras delicatum* sp. nov. from Germany is described. *Kielcensia* specimens from Oklahoma represent the first uncontested record of triangularly coiled wocklumeriids from North America. Together with *Riphaeoclymenia*, the Oklahoma fauna has similarities and strong biogeographical ties with the far distant Holy Cross Mountains of Poland. *Kielcensia* and *Riphaeoclymenia* are missing from the diverse contemporaneous ammonoid faunas of Middle and Southern Europe, which were located between the Oklahoma and the Polish occurrences. Geographically intermediate contemporaneous Moroccan faunas also show a fundamentally different composition but the Afro-Appalachian migration route must have been viable in the uppermost Famennian. Migrations through regions without leaving a trace in available very rich fossil records ("ghost distributions") create a bias for the palaeobiogeographical analysis of nektonic organisms. The faunal composition of the Woodford Shale suggests a control of ammonoid distribution patterns by palaeoecological factors that are not recognizable in the lithofacies.

Key Words: Devonian; Famennian; Clymeniids; Goniatites; Oklahoma; Palaeobiogeography;Palaeoecology.

INTRODUCTION

Famennian ammonoids are rather rare in North America in comparison with the Frasnian and lowermost Carboniferous (Tournaisian). This is especially true for middle to uppermost Famennian faunas with clymeniids (Upper Devonian = UD III to VI; for zonal key see Becker and House 2000 or Ogg *et al*. 2008), which so far have been described or mentioned from Ohio (House 1978; House *et al.* 1986, new unpublished specimen from Ross County), Iowa (House 1962; Glenister in Furnish and Manger 1973; Olempska and Chauffe 1999), Indiana (House *et al.* 1986), New Mexico (Miller and Collinson 1951; House 1962; Cooper and Dutro 1982), Montana (Raymond 1909; Schindewolf 1934; House 1962; Becker 1995; Korn and Titus 2006), Utah (Petersen and Stokes 1983), Nevada (Smith and Ketner 1975; Sandberg *et al.* 1988;

Rolfe and Dzik 2006), California (Anderson *et al.* 1974) Alberta (Warren 1927; Taylor 1958; House and Pedder 1963), and northern Alaska (Sable and Dutro 1961). Currently, twenty-one taxa (not including the report by Morgan, 1924, which is discussed later) have been mentioned or illustrated. The topmost Famennian global Hangenberg Event led to the almost total extinction of clymeniids and goniatites, but the associated transgression allowed a significant, short-termed spread of some Prionoceratidae across the continent (Becker 1993b). In Ohio, a pyritic level near the top of the Cleveland Shale may correlate with the black shale event phase of Europe (Hangenberg Black Shale, holostratigraphic interval 9 of Becker 1996; UD VI-E). Its fauna includes the last cymaclymeniids and sporadoceratids (House et *al.* 1986). The survival of cymaclymeniids into the post-extinction *Acutimitoceras* (*Stockumites*) Genozone (UD VI-F) is also known from Germany (e.g., Schindewolf 1937; Korn 1989, 1991; Becker 1996), Southern France (Kaiser *et al.* 2009), and Morocco (Korn *et al.* 2004), and it has been reported, but not documented, in North America from Utah (Feist and Petersen 1995).

Cephalopod assemblages from just below the mass extinction level or from the main part of the uppermost Famennian (in the sense of Streel 2001 and Streel *et al.* 2006), which roughly equals the German Wocklum Stufe (UD VI, Wocklumian), are almost unknown in North America. In addition to the fauna reported here, there is a questionable occurrence of *Epiwocklumeria* from Rockford, Indiana (House *et al.* 1986) and three species, *Cyrtoclymenia strigata* House, 1962, *Cymaclymenia* aff. *striata* (Münster, 1832), and *?Rectimitoceras opimum* (White and Whitefield 1862), a nomen dubium, are known from the *Chonopectus* Sandstone of southeastern Iowa (House 1962; Furnish and Manger 1973). Over (1992, p. 294) briefly mentioned the discovery of *Wocklumeria* during his detailed investigation of the conodont biostratigraphy of the Woodward Shale of Oklahoma. Since this initial report, a total of fifty identifiable ammonoids belonging to five different genera and six species have been collected and these are described herein. The occurrence of this cephalopod fauna in a region where the stratigraphic interval has not previously produced ammonoids and which was situated close to the southern margin of the North American Devonian outcrop belt is significant. The taxonomic composition of this unique fauna illustrates how incomplete our knowledge of ammonoid palaeobiogeography is despite the well known and richly diverse collections of Europe, China, and North Africa. Especially surprising are close links with far distant clymeniids from the Holy Cross Mountains of Poland. This leads to some general conclusions concerning the distribution patterns of Devonian ammonoids, as a general example of nektonic organisms.

LOCALITY AND FAUNA

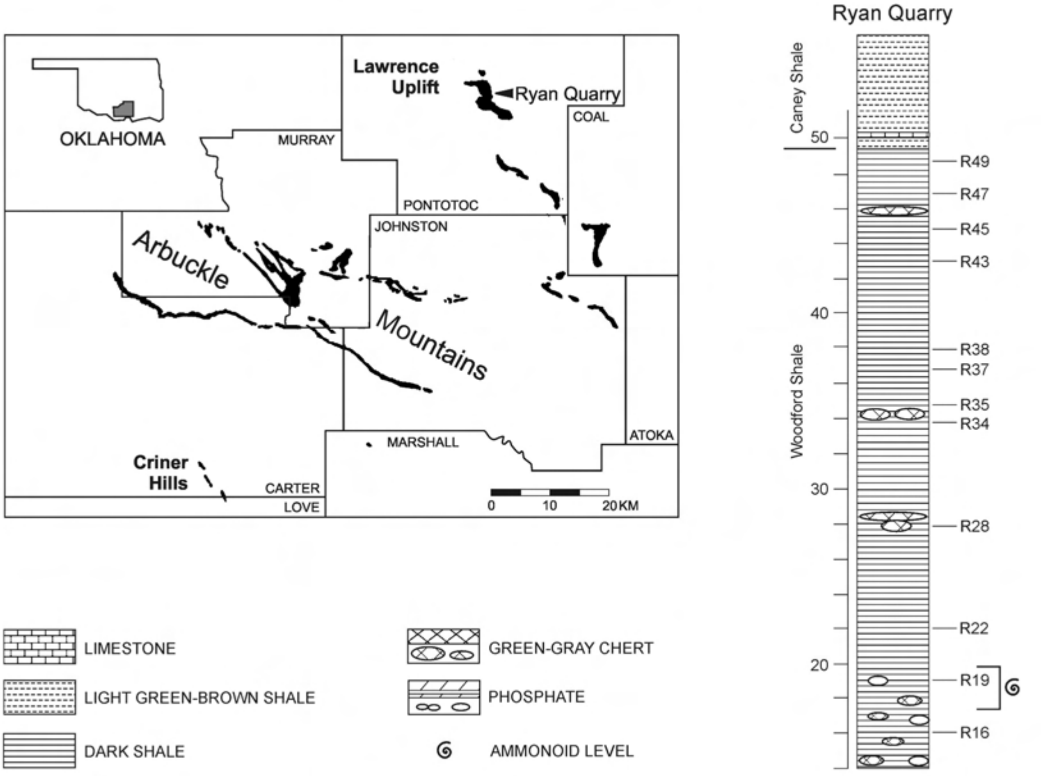
The ammonoids were recovered from the Ryan Quarry (SW1/4, NE1/4, sec. 2, T2N, R6E, Ahloso 7 1/2 minute Quadrangle), south of Ada, Pontotoc County, on the Lawrence Uplift NW of the Arbuckle Mountains in south-central Oklahoma (Text-fig. 1). A lithological log with the position of conodont samples was published by Over (1992, section RSP) and is reillustrated with modification of the ammonoid bearing horizon in Text-fig. 1. All exposed rock in the quarry belongs to the upper part of the Woodford Shale, which consists of pyritic (marcasitic) dark grey shales with beds of phosphate nodules containing pyrite and rare carbonate concretions. Beds in the quarry dip north approximately 5–6°.

The ammonoids reported here were obtained by R.H.M., D.M. Work and Ohio University students in 1986, in the summer of 1990, and in subsequent years to 1999. They are from an area in the southwestern part of the quarry where the shales are exposed at the quarry floor and at the western edge, where quarrying has produced a steep cliff that is several metres high. A single specimen was recovered subsequently during a brief visit to the quarry in 2004 near the base of the cliff, showing that the occurrence has been nearly exhausted in the current outcrop. Fast weathering of exposed specimens to sulphate prevents sampling unless active quarrying creates new outcrop, which is currently not the case. The ammonoids come from ca. 2 meters below to 0.5 m above sample level R19 of Over (1992, RSP section). In this same report on figure 2, and in the figure caption, Over indicated that the ammonoid identified as *Wocklumeria* sp. (here re-assigned to the genus *Kielcensia*) and orthoconic nautiloids occurred at the R28 sample level, which is 21 m below the top of the Woodford Shale; the latter locally coincides with the Devonian/Carboniferous boundary. J. Over did not illustrate or describe any cephalopods in his excellent conodont report, and he did not indicate how he obtained his cephalopod information. His interval is approximately 10 meters above the interval where R.H.M., D.M. Work and Ohio University students recovered the ammonoid fauna reported herein. Since 1992, R.H.M. has made extensive repeated trips to the Ryan Quarry to attempt to recover additional ammonoids and other fauna, and no specimens or traces of specimens of ammonoids or orthoconic nautiloids have been found at interval R28. Therefore, we assume that all Ryan Quarry ammonoids are from around level R19. They belong to the following species:

Kielcensia vagabunda sp. nov.
Riphaeoclymenia polygona sp. nov.
Riphaeoclymenia pontotocensis sp. nov.
Cyrtoclymenia cf. *procera* Czarnocki, 1989
Spirosporadoceras overi gen. nov. sp. nov.
Sporadoceratidae ?gen. nov. sp. nov.

The ammonoid fauna is associated with poorly preserved orthoconic nautiloids, isolated patches of lingulids, conulariids, plant remains of *Callixylon* (some associated with crinoid ossicles, as described by Klug *et al.* 2003 for Famennian wood from Morocco), palynomorphs, conodonts (Over 1992), remains of larger vertebrates (sharks and other fish), and isolated, pyritized monaxon (very rarely tetraxon) spicules of hexactinellid sponges. Many faunal elements are associated with patch-like occurrences on shale bedding planes. These peculiar patchy areas of slightly different lithology contain a mixture of fossils, which is not a common occurrence in the quarry. This condition was only observed in the interval that yielded the ammonoids. We suspect that these concentrations of disarticulated fossil remains are the regurgitation or defecation products of sharks or other fish. Additional faunal elements usually associated with the phosphate concretions include some relatively complete arthropods (Cooper 1932; F. Schram and R. Feldmann, personal communications to R.H.M.).

Previous reports on ammonoids from the Woodford Shale in the North American Midcontinent are limited to the single occurrence of "*Probeloceras*? *lutheri*", an early Middle Frasnian species, reported by Morgan (1924). This specimen is without a suture, ornament, or exposed siphuncle. It was found isolated without other associated faunal elements, and the precise stratigraphic position in the shale that contained the specimen is unknown. Identification of this ammonoid is presently impossible. Other cephalopod debris recovered from the formation includes mandibles (Cooper 1932). Evaluation of all the Devonian cephalopod mandible occurrences in North America was made by Frye and Feldmann (1991), including those from the Woodford Formation. Their analysis showed that the Oklahoma specimens, which usually occur in phos-



Text-fig. 1. Geographical position of Ryan Quarry (arrow) within the Lawrence Uplift of Pontotoc County, Oklahoma, U.S.A., and its lithostratigraphy, showing conodont sample numbers and the interval of ammonoid occurrences (updated from Over 1992, figs 1–2). Black areas = Woodword Shale outcrops phate concretions, are essentially identical to those from Ohio, except that the Ohio specimens are all flattened, and the Oklahoma specimens are more three-dimensional. It is unfortunate that mandibles have not yet been recovered *in situ* in the ammonoids from the Devonian of Oklahoma as some of those described and illustrated by Cooper (1932) probably fit with the goniatites and clymeniids that are described herein.

Almost all of the ammonoids from the Woodford Shale at Ryan Quarry are crushed, incomplete and distorted, with both the test and the phragmocone replaced by rapidly oxidizing marcasite. Internal mould and test features, therefore, can be observed on different specimens and the varying preservation and distortion leads to a false impression of variability. The largest identifiable fragment (MB.C.2842) is bigger than 90 mm; however, rotten pieces of ammonoids over 180 mm diameter were observed but not collected because of their poor condition. The recovery of the ammonoid specimens was best when the shale was freshly excavated for road fill. After one year, because of the rapid breakdown of the marcasite in the shale by surface weathering, there were no traces of ammonoids or other fossils except for phosphatized specimens and plant material. The holotype and one paratype of *Kielcensia vagabunda* sp. nov. differ in their preservation from the rest of the material by partial replacement with phosphate and pyrite of large parts of one shell side. Apart from these two specimens, there is only one juvenile sporadoceratid (MB.C.2833) that is partly preserved three-dimensionally as a phosphatic internal mould. The incomplete preservation prevents the preparation of useful cross-sections and precise measurements of conch parameters in most specimens. Estimates are given where possible.

BIOSTRATIGRAPHY

Since the majority of ammonoid species of the Oklahoma fauna are new and, at least to current knowledge, endemic, a careful age assessment is required. Zonal abbreviations used here follow Becker and House (2000), with updates in Becker *et al.* (2002). *Cyrtoclymenia procera* was described from the upper part of the *Wocklumeria* Stufe (UD VI-C/D) of Kowala in the Holy Cross Mountains (Czarnocki 1989). All dated members of the Wocklumeriidae, including *Kielcensia*, are restricted to the *Parawocklumeria paradoxa* (UD VI-C2) and *Wocklumeria sphaeroides* zones (UD VI-D). New collections from southern Morocco from 2003/2004 (Bou Tlidat, Maider) proved that *Synwocklumeria* is restricted regionally to the upper part of UD VI-C (regional *Mayneoceras nucleus* Zone, Becker *et al.* 2002), and this most probably is also the level of *Kielcensia ingeniens* Becker, 2000b. The holotype of the latter was found loose, but the preservation is identical with *Synwocklumeria mapesi* Becker, 2000b from the same collection and different from the *Wocklumeria* material from higher levels (UD VI-D). At Kowala (Holy Cross Mountains, Poland), *Kielcensia* was first described (Czarnocki 1989) from a thick unit that also yielded *W. sphaeroides* (Richter 1848) and *Epiwocklumeria applanata* (Wedekind, 1908), suggesting an UD VI-D age. Dzik (2006), however, questioned this age assignment and proposed a level below *Wocklumeria* and *Epiwocklumeria*. The precise level of Polish *Kielcensia* needs to be re-assessed when the Kowala quarry produces new specimens.

substage	ammonoid zones	zonal key	
UPPERMOST FAMENNIAN (WOCKLUMIAN)	***Acutimitoceras (Stockumites) prorsum***	**VI-F**	
	Postclymenia evoluta	**VI-E**	**HANGEN-BERG EXTINCTION** ←
	Epiwocklumeria applanata	**VI-D2**	
	Wocklumeria sphaeroides	**VI-D1**	
	Parawocklumeria paradoxa	**VI-C2**	← **Ryan Quarry Fauna**
	Kamptoclymenia endogona	**VI-C1**	
	Effenbergia lens	**VI-B**	
	Muessenbiaergia bisulcata ***Muessenbiaergia parundulata***	**VI-A2**	
	Linguaclymenia similis ***Muessenbiaergia sublaevis***	**VI-A1**	

Text-fig. 2. Uppermost Famennian (Wocklumian, UD VI) ammonoid biostratigraphy (updated from Becker and House 2000 and Becker *et al.* 2002), with the position of the new Oklahoma fauna and of the mass extinction level of the Hangenberg Event. The subdivision of UD VI-D into two subzones is so far limited to the northern Rhenish Massif and, perhaps, Holy Cross Mountains

The age of the type species of *Riphaeoclymenia* from the Kiya Section at the Russian–Kazakh boundary in the South Urals is not known with certainty. Nikolaeva and Bogoslovskiy (2005b) suggest that the unique specimen may have come from the regional *Mayneoceras nucleus* Zone that correlates with UD VI-C2. At Kowala, three species of the genus (originally assigned to *Dimeroclymenia*) were found together with open umbilicate parawocklumeriids, suggesting an UD VI-C1 (*Kamptoclymenia endogona* Zone) age. The data in Dzik (2006) support a stratigraphical range below the onset of *Wocklumeria*. At the Ryan Quarry, *Riphaeoclymenia* and *Kielcensia* occur around the R19 level, so this association most likely falls in UD VI-C2 (Text-fig. 2).

The Woodford Shale represents a very long period of time, starting low in the Frasnian (Hass and Huddle 1965) and reaching into the basal Carboniferous (Over 1992). Conodonts from the ammonoid level in its uppermost part (around R19) occur in the coprolite or regurgitation masses and consist predominantly of ramiform elements. This suggests the absence of hydraulic sorting of apparatus elements and is in accordance with the interpretation of a predation-control of preservation. Pa-elements consist of *Bispathodus stabilis*, *Branmehla inornata,* and very rare *Polygnathus* cf. *symmetricus*. All are long-ranging species that form the *Bispathodus/Branmehla* assemblage of Over (1992), which is regarded to represent a typical deeper-water, outer shelf and pelagic association. However, his sample from level R19 was unproductive and the next lower level also produced only zonally undiagnostic conodonts. No undoubted *Siphonodella* has been recovered from the shales of the Ryan Quarry, but wocklumeriids are not known to occur below the (Lower) *Si. praesulcata* Zone elsewhere (Becker 1996, Becker and House 2000). It is remarkable that the common palmatolepids, polygnathids, pseudopolygnathids, and advanced bispathodids, which are associated with latest Famennian ammonoids in the micritic cephalopod limestones of Europe (e.g., Kaiser *et al.* 2009) and South China, are lacking locally. This documents a significant palaeoecological difference.

SYSTEMATIC PALAEONTOLOGY

(R. Thomas Becker)

All material is housed in the Museum für Naturkunde, Berlin, under numbers MB.C.2821 to 2857. Abbreviations of shell parameters (given in mm) are as follows: dm = diameter, wh = whorl height, ww = whorl width, ah = apertural height, uw = umbilical width, WER = whorl expansion rate. The suture terminology follows the classical German phylogenetic and ontogenetic definitions of Wedekind (1913), with E for ventral lobes, A for adventitious flank lobes, L for the lateral lobe (either on the flank, near or at the umbilical seam), U for umbilical lobes, and I for dorsal lobes. Summaries of the systematics and phylogeny of Devonian ammonoids were published by Becker and Kullmann (1996) and Korn and Klug (2002).

Order Clymeniida Wedekind, 1914
Suborder Wocklumeriina Becker, 1997a

DIAGNOSIS: See Becker (2000b).

INCLUDED SUPERFAMILIES: Glatziellaceae Schindewolf, 1928, Wocklumeriaceae Schindewolf, 1937, Biloclymeniaceae Bogoslovskiy, 1955.

DISCUSSION: Becker (2000b) documented in detail the probable early separation of clymeniids into two major groups, one with very slowly expanding, longidomic whorls and with primarily very wide and shallow dorsal and ventral lobes (suborder Wocklumeriina), and the second one with faster expanding, mesodomic whorls and narrow dorsal lobe (suborder Clymeniina). The traditional distinction of two main groups, the two suborders Gonioclymeniina and Clymeniina (e.g., Schindewolf 1923; Ruzhencev 1957; Bogoslovskiy 1981; repeated in Nikolaeva and Bogoslovskiy 2005c), was shown to be a polyphyletic grouping, since ventral lobes, including true lobes with septal fold, were re-introduced iteratively at least twice in clymeniid evolution: at the transition from the *Platyclymenia* to the *Clymenia* Stufe (UD IV/V) in the lineage from the Platyclymeniidae (*Nodosoclymenia*) to the descendent first Gonioclymeniaceae (Costaclymennidae: *Endosiphonites*), and in the uppermost Famennian *Wocklumeria* Stufe (UD VI) in the lineage from the Parawocklumeriidae to the Wocklumeriidae (within the Wocklumeriaceae).

This phylogenetic model was supported by the systematics in Korn and Klug (2002), who, however, included the Wocklumeriina within the suborder Clymeniina. They introduced a new suborder, the Cyrtoclymeniina, for goniatite-like clymeniid groups with moderately fast expanding, convolute shells. It is agreed that there was an early separation of the Cyrtoclymeniidae and their descendents from the more evolute Platyclymeniidae, the oldest family of the Clymeniina. But both share the mesodomic shells and moderately deep to very deep and pointed dorsal lobe of their tornoceratid goniatite ancestors. Longidomic whorls probably did not develop independently in several descendent clymeniid lineages since changes in whorl expansion and body chamber length reflect much more fundamental palaeobiological changes (e.g., controlling shell orientation, swimming capacities, and feeding strategies; e.g., Trueman 1941; Jacobs and Chamberlain 1996) than variations in umbilical widths. The change from mesodomic tornoceratid-type shells to longidomic coiling is thought to represent an important apomorphic novelty in clymeniid evolution, which deserves recognition at high taxonomic rank. The early evolutionary separation of the convolute cyrtoclymeniid branch is well expressed in the recognition of superfamily Cyrtoclymeniaceae within the Clymeniina (see systematics in Korn 1992a). Thus, establishment of the taxonomic rank as a distinctive suborder is not warranted.

Superfamily Wocklumeriaceae Schindewolf, 1937
Family Wocklumeriidae Schindewolf, 1937

Genus *Kielcensia* Czarnocki, 1989

1989 *Kielcensia* gen. n.; J. Czarnocki, pp. 44–45.
2000b *Kielcensia*; R.T. Becker, pp. 45–46.
2002 *Kielcensia*; D. Korn and C. Klug, pp. 261–262
part 2006 *Epiwocklumeria*; J. Dzik, p. 301
part 2007 *Synwocklumeria*; V. Ebbighausen and D. Korn, p. 34

TYPE SPECIES: *Kielcensia bohdanoviczi* Czarnocki, 1989.

OTHER SPECIES/SUBSPECIES: *K. bohdanoviczi inaequilobata* Czarnocki, 1989, *K. pusilla* Czarnocki, 1989, *K. ingeniens* Becker, 2000b, *K. vagabunda* sp. nov.

DIAGNOSIS: Shell markedly biform, with involute, open umbilicate, subglobular, constricted, triangularly coiled inner whorls that abruptly change into mature, subevolute to evolute, compressed, normally or triangularly coiled whorls; longidomic, with low WER (ca. 1.45–1.65). Growth lines linear to slightly concave. Sutures with small, rounded ventral lobe, high and arched ventral saddle, narrow, deep, lingulate or pointed adventitious lobe on mid-flank, high inner flank saddle, small, rounded, subumbilical outer lateral lobe, and (based on Czarnocki 1989) three internal lobes. Sutural formula: $EAL_e:L_iI_1I_2$.

DISCUSSION: Dzik (2006) regarded *Kielcensia* as a synonym of *Epiwocklumeria* but this opinion was not explained and not based on any new data. The unique convolute to evolute adult shell morphology rules out that *Kielcensia* occupies an intermediate phylogenetic position between *Parawocklumeria* and *Epiwocklumeria*, as suggested by Dzik.

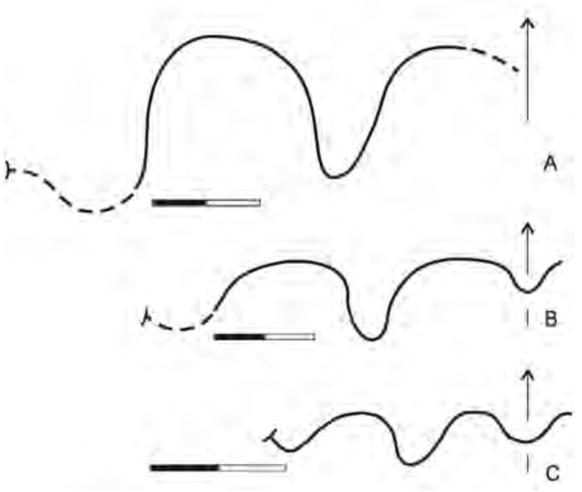
OCCURRENCE: Uppermost Famennian (probably UD VI-C2) of Poland, southern Morocco, and Oklahoma.

Kielcensia vagabunda sp. nov.
Text-fig. 3A–C, 4A–B

ETYMOLOGY: From the Latin *vagabundus* (= randomly travelling), due to the unexpected geographical occurrence in North America.

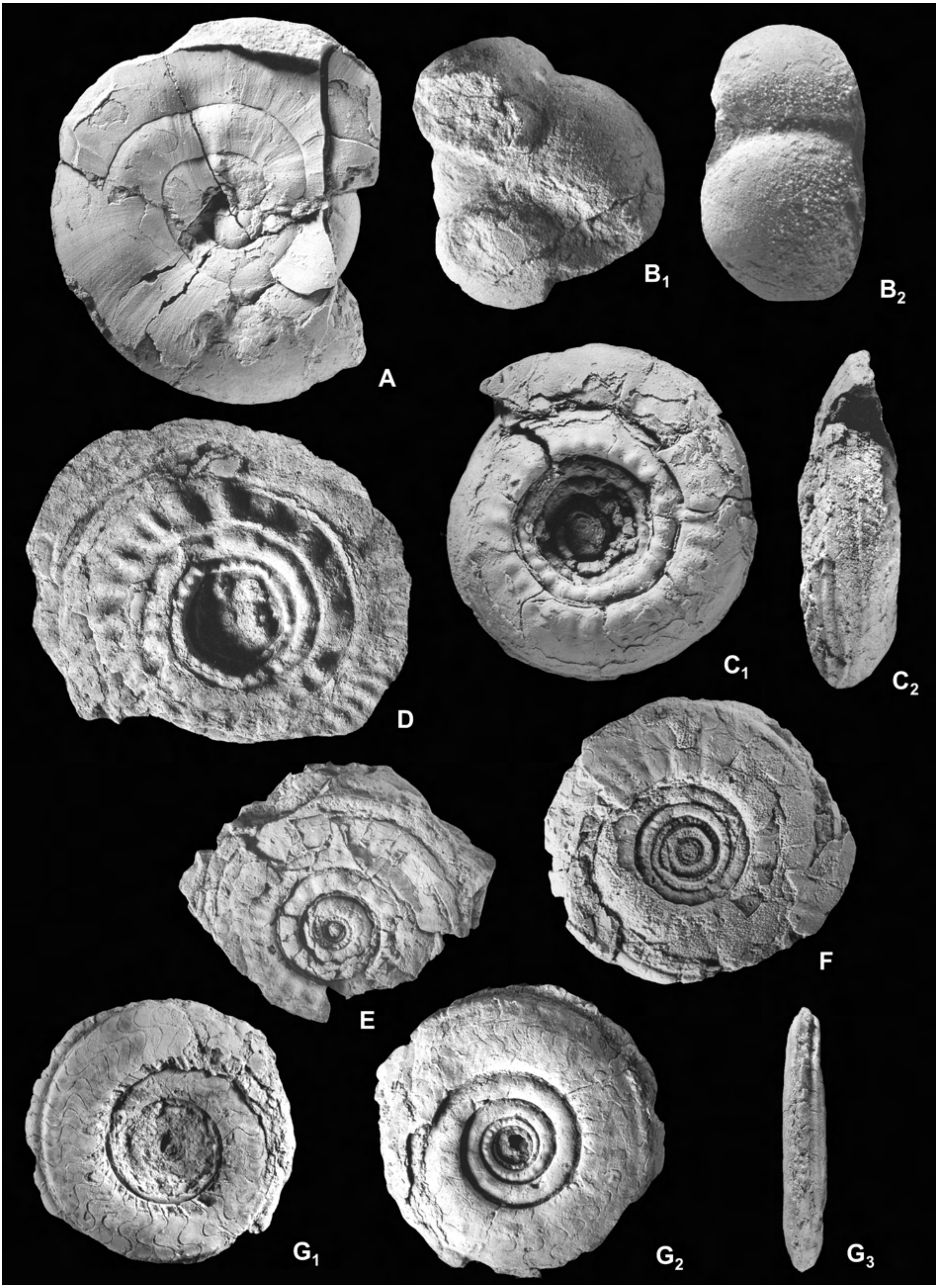
MATERIAL: The holotype (MB.C.2840, Text-fig. 3A, 4A), a partially phosphatic and well-preserved mature specimen showing shell form, ornament and parts of the suture, and two juvenile paratypes, MB.C.2838-2839 (Text-fig. 3B–C, 4B), preserved as marcasitic moulds with some phosphate.

TYPE LOCALITY, HORIZON, AND AGE: Ryan Quarry, south of Ada, Oklahoma, uppermost Woodford Shale, upper *Wocklumeria* Stufe, probably UD VI-C2 (upper *Parawocklumeria* Genozone).



Text-fig. 3. Sutures of *Kielcensia vagabunda* sp. nov. **A** – Holotype, MB.C.2840, at 10 mm wh. **B** – Juvenile paratype, MB.C.2839, at 4.3 mm wh (reversed for comparison), **C** – Juvenile paratype, MB.C.2838, at 2.5 mm wh; scale bars = 2 mm

Text-fig. 4. Clymeniids from the Woodword Shale of Oklahoma. **A** – *Kielcensia vagabunda* sp. nov., holotype, MB.C.2840, lateral view, × 2. **B_1, B_2** – *K. vagabunda* sp. nov., juvenile paratype, MB.C.2838, lateral and ventral views, showing the strong shell trilobation, × 6. **C_1, C_2** – *Riphaeoclymenia polygona* sp. nov., holotype, MB.C.2822, lateral and adoral views, × 4. **D** – *R. polygona* sp. nov., paratype, MB.C.2823, lateral view, showing the polygonal coiling of early whorls, × 1.9. **E** – *R. pontotocensis* sp. nov., paratype, MB.C.2850, lateral view, × 1. **F** – *R. pontotocensis* sp. nov., paratype, MB.C.2845, lateral view, × 1.5. **G_1, G_2, G_3** – *R. pontotocensis* sp. nov., holotype, MB.C.2846, two lateral views with sutures and ventral view showing the distinctive keel, × 1.5


A
B1
B2
C1
C2
D
E
F
G1
G2
G3

DIAGNOSIS: Early stages strongly involute, with low whorls (WER = ca. 1.65), subcircular in cross-section, and with three deep constrictions per whorl causing a strong trilobation. Adult stage widely evolute (uw/dm = ca. 50 %), compressed, with rounded triangular coiling, lacking constrictions. Growth lines very fine, straight to slightly concave and rectiradiate. Outer suture with two equally shaped flank saddles, narrow, angular A-lobe, and narrow, rounded and small ventral lobe.

DESCRIPTION: Only one side of the holotype is preserved, which shows that the last 2½ whorls are widely evolute, markedly subtriangular in coiling, and that they overlap ca. half of the preceding whorl. The radial and slightly concave growth lines are very fine (ca. 8 per mm) and two or three of them often form one bundle. There is no evidence of a ventral sinus, and there are no growth lirae. At ca. 31 mm dm, uw is ca. 15 mm but ww cannot be measured. WER is ca. 1.55, which, based on figures in Czarnocki (1989, pl. 45), is in the scale of adult *K. bohdanoviczi*. The flanks are very gently rounded and suggest that ww did not increase much during mature growth. Sutures with two equally high flank saddles and a pointed, somewhat v-shaped, adventitious flank lobe are visible at ca. 30 mm dm. The subumbilical outer lateral (L_e) lobe is also angular. Paratype MB.C.2839 shows sutures at 3.7 mm wh that resemble the adult, *Synwocklumeria*-type course but the lobes are still rounded (lingulate) and the ventral saddle is lower than the mid-flank saddle. At 7.5 mm dm, ww is ca. 5 mm. Paratype MB.C.2839 shows a suture with rounded lobes and equally high flank saddles at 7.7 mm wh and a subcircular whorl cross-section. At 8 mm dm, wh is 5 mm, ww ca. 6 mm, and ah ca. 1.7–1.8 mm, giving a low WER rate in the range of longidomic ammonoids. The umbilicus is very small in both juvenile paratypes but MB.C.2839 shows how the coiling suddenly changes at ca. 7 mm wh, by reducing the whorl overlap during a still deeply constricted ontogenetic stage. Czarnocki (1989, pl. 45, fig. 1) illustrated a similar sudden break in ontogeny towards evolute mature whorls in Polish forms of the genus.

DISCUSSION: *K. vagabunda* sp. nov. differs by its triangular and more evolute adult stages from the Polish *K. bohdanoviczi* Czarnocki, 1989. The rare Moroccan *K. ingeniens* Becker, 2000b is smaller, much more involute, less triangular and keeps constrictions throughout its ontogeny. Ebbighausen and Korn (2007) recently suggested that *K. ingeniens* is a synonym of *Synwocklumeria mapesi*. As shown in the re-illustration of Ebbighausen and Korn, the holotypes of both species are equally sized and display a very different shape of the last whorl. Only the type of *K. ingeniens* shows the diagnostic sudden uncoiling of *Kielcensia*. The suggestion that both forms are variants of a single, variable species is not supported by new additional material of *S. mapesi* from the type area, but small specimens are inconclusive.

OCCURRENCE: The new species is known only from the type locality and the type level.

Superfamily Biloclymeniaceae Bogoslovskiy, 1955 (nom. transl. Becker 1997a)

DIAGNOSIS: Mesodomic to longidomic, early stages depressed, subevolute to widely evolute, mature whorls weakly compressed, very slowly to moderately fast expanding, subinvolute to evolute, venter rounded, keeled or suboxyconic; sometimes with constrictions, ventrolateral furrows, weak ribs or subumbilical nodes. Growth lines weakly to strongly biconvex. Sutures simple and with wide dorsal and ventral lobes or with divided ventral lobe, up to two adventitious lobes, lateral lobe out- or inside the umbilical seam, and narrow dorsal lobe. Suture formulas: EAI (*Uraloclymenia*) – EAL:I (*Pachyclymenia*) – (E_1E_1)A:LI (*Kiaclymenia* and *Riphaeoclymenia*) – $E_2E_1A_1A_2$:LI (*Biloclymenia*).

INCLUDED FAMILIES: Pachyclymeniidae Korn, 1992a and Biloclymeniidae Bogoslovskiy, 1955.

DISCUSSION: The ancestry and taxonomic position of the Biloclymeniaceae are subject to controversial interpretation (Bogoslovskiy 1981; Becker 2000b; Korn and Klug 2002). Typical Biloclymeniidae have rather complex sutures but intermediate forms (*Kiaclymenia*, *Pachyclymenia*) link advanced genera with the simple-lobed and older *Uraloclymenia* of the Pachyclymeniidae (see phylogenetic reconstruction in Becker 2000b, fig. 12). Inclusion of the superfamily Biloclymeniaceae in the suborder Wocklumeriina, despite their biconvex growth lines, higher whorl expansion rates and slightly mesodomic body chamber, can be justified by morphological and stratigraphical links with *Pleuroclymenia* and other members of the Hexaclymeniidae (see Bogoslovskiy 1981), the ancestral, stratigraphically oldest family of the Wocklumeriina: 1. significant shell similarity between oldest species of *Uraloclymenia* and smooth pleuroclymeniids; 2. identical wide primary ventral and dorsal lobes in *Uraloclymenia* and in all typical members of the Hexaclymeniidae; 3. development of characteristic constrictions in all Pachyclymeniidae and in *Pleuroclymenia* s. str.; 4. occurrence both of *Uraloclymenia* and smooth pleuroclymeniids in Kazakhstan, as a potential evolutionary center; 5. the considerable length of the septal necks in all studied Biloclymeniaceae, Hexaclymeniidae, and in wocklumeriids (Bogoslovskiy 1976, 1981), probably a significant synapomorphy. Currently there is no evidence for transitional forms between cyrtoclymeniids, which have the shortest septal necks of all clymeniids, and *Uraloclymenia*, which could justify the placing of the Biloclymeniaceae in the suborder Clymeniina (or the Cyrtoclymeniina of Korn and Klug 2002). Similarities of shell form between some contemporaneous biloclymeniids and cymaclymeniids (Cyrtoclymeniaceae) are here regarded as a case of homeomorphy. The extremely slowly expanding whorls of juvenile *Riphaeoclymenia* strongly resemble similarly sized and ribbed stages of hexaclymeniid genera, such as *Pleuroclymenia* and *Borisiclymenia* (see also Dzik 2006, p. 297), which gives further support for phylogenetic relationships.

Becker (2000b) emphasized that the primary flank lobe of all clymeniids originated from the A-lobe of their tornoceratid ancestors. This requires different sutural formulas than given by Korn and Klug (2002). *Uraloclymenia* has only three lobes. The lobe at or near the umbilical seam in *Pachyclymenia* is a re-appearing lateral lobe that migrates internally in the descendent Biloclymeniidae. Consequently, the small outer subumbilical lobe of *Biloclymenia* appears in an A-L-saddle and has to be called a small A_2-lobe.

Family Biloclymeniidae Bogoslovskiy, 1955

Genus *Riphaeoclymenia* Bogoslovskiy, 1981

* 1981. *Riphaeoclymenia* gen. nov.; B.I. Bogoslovskiy, p. 67.
* 1989. *Dimeroclymenia* gen. n.; J. Czarnocki, pp. 36–37.
* 1989. *Liroclymenia* gen. n.; J. Czarnocki, p. 47.
1997b. *Rhiphaeoclymenia*; R.T. Becker, p. 35.
2002. *Riphaeoclymenia*; D. Korn and C. Klug, p. 230.
2002. *Dimeroclymenia*; D. Korn and C. Klug, p. 230.
2002. *Liroclymenia*; D. Korn and C. Klug, p. 246.
part 2006. *Biloclymenia*; J. Dzik, p. 281.
2006. *Riphaeoclymenia*; J. Dzik, p. 297.

TYPE SPECIES*: Riphaeoclymenia canaliculata* Bogoslovskiy, 1981.

OTHER SPECIES: *Dimeroclymenia pristina* Czarnocki, 1989, *D. semicostata* Czarnocki, 1989, *D. subacuta* Czarnocki, 1989, *Liroclymenia fundifera* Czarnocki, 1989, *R. polygona* sp. nov., *R. pontotocensis* sp. nov.

DIAGNOSIS: Longidomic, early whorls depressed and widely evolute to evolute, slowly or very slowly increasing, mature whorls compressed and subevolute to evolute, slowly to moderately increasing (WER ca. 1.5–1.8), with or without ribs and ventrolateral furrows; venter keeled, rounded or suboxyconic. Growth lines strongly biconvex with projecting ventrolateral salient. Sutures with low saddle at umbilical seam, asymmetrically rounded A-lobe on lower flanks, high mid-flank saddle, rounded or subangular, narrow or wide, deep E-lobe, and wide, low to high median saddle on the venter. Sutural formula: (E_1E_1)A:LI.

DISCUSSION: Becker (1997b, 2000b) argued that *Dimeroclymenia* Czarnocki, 1989 and *Liroclymenia* Czarnocki, 1989 from Poland should be regarded as subjective junior synonyms of *Riphaeoclymenia*, which was based on a single fragment from the famous Kiya section of the southern Urals. The synonymy of *Liroclymenia* with *Riphaeoclymenia* was not accepted by Korn and Klug (2002), but it was supported by Dzik (2006). The latter regarded *Dimeroclymenia* as a synonym of *Biloclymenia*, which, however, has more complex sutures. There is some homoeomorphy of *Riphaeoclymenia* with the keeled *Glatziella* but the latter genus is smaller-sized and typical species do not develop compressed adult whorls. Therefore, the placing of *Riphaeoclymenia* in the Glatziellidae by Dzik (2006) is rejected.

Based on the presence or absence of a second spiral groove and on differences of umbilical width, Korn and Klug (2002) kept a generic distinction between *Riphaeoclymenia* and *Dimeroclymenia*. This, however, seems to interrupt artificially a subevolute to evolute species group in which there are intermediate forms without, with weak, and with strong spiral furrows. The type species of *Riphaeoclymenia, R. canaliculata*, has double furrows and is rather evolute (uw > 50% dm). A single furrow is present in the type species of the evolute (uw > 50% dm) *Liroclymenia, L. fundifera* Czarnocki, 1989. The type-species of *Dimeroclymenia, D. pristina*, lacks furrows and is subevolute (uw = 40–45% dm). *Dimeroclymenia semicostata* and *D. subacuta* have weak ventrolateral furrows and are more strongly subevolute (uw = 33–45% dm), but there is rather large umbilical variation in *D. semicostata,* with higher uw/dm ratios of early whorls. The Oklahoma assemblage includes *R. polygona* sp. nov. with double furrows bordered by longitudinal ridges and *R. pontotocensis* sp. nov. with a strong ventrolateral furrow and with traces of a shallow second furrow in some specimens. The umbilical width changes during ontogeny from very evolute to moderately evolute (ca. 47–50% dm) in the first and to widely subevolute (ca. 41–45% dm) in the second. The transitional morphology of *R. pontotocensis* sp.nov. shows that a clear boundary between the contemporaneous genera *Riphaeoclymenia* and *Dimeroclymenia* cannot be established.

OCCURRENCE: Upper *Wocklumeria* Stufe (UD VI-C) of the Urals, Poland and Oklahoma.

Riphaeoclymenia polygona sp. nov.

Text-fig. 4C–D, 5B.

ETYMOLOGY: After the polygonal coiling of early whorls.

TYPE LOCALITY, HORIZON, AND AGE: Ryan Quarry, south of Ada, Oklahoma, uppermost Woodford Shale, upper *Wocklumeria* Stufe, probably UD VI-C2 (upper *Parawocklumeria* Genozone).

MATERIAL: Holotype MB.C.2822 (Text-fig. 4C), a small-sized specimen showing the typical coiling, shell form, ornament and parts of the suture, and paratypes MB.C.2821 and MB.C.2823-2827.

DIAGNOSIS: Early stages, variably up to 12-20 mm dm, widely evolute (uw/dm > 0.6), depressed, with rounded polygonal coiling, and with strong nodose ribbing; later normally coiled, with uw/dm = ca. 47–50%, and with coarse or dense, straight to slightly concave and prorsiradiate ribs that terminate at a short umbilical wall, and with three keels separated by marked spiral furrows. Sutures with subumbilical, wide and rounded A-lobe, asymmetric and raised flank saddle, with asymmetrically rounded ventral lobe and low and wide median ventral saddle.

DESCRIPTION: The holotype exposes rounded polygonal coiling, especially of the umbilical spiral, and strong nodose ornament until 12–13 mm dm. The nodes end on the crest of the short umbilical wall. There are 25 nodes on the last whorl at 12 mm dm. Two marked ventrolateral furrows border a sharp and narrow spiral ridge and a ventral keel. Sutures are partly covered by marcasitic shell material but a rounded subumbilical lobe and a raised mid-flank saddle are visible. The umbilical width amounts to 50% dm at 13 mm dm but exceeds 60% in earlier whorls. At 2.8 mm wh, ww was larger than 4 mm, giving a very depressed whorl profile. At the end of the last preserved whorl (ca. 14.3 mm dm), ah measures only ca. 2.2 mm, which gives a very low WER in the range of 1.4. All paratypes suggest a very slow whorl expansion at small size, which implies longidomic body chambers. All measurements are interpolations since the specimens are partly crushed.

Paratype MB.C.2821 also displays the deep double furrows and a nodose early whorl as well as a rounded ventral lobe that passes into a low ventral saddle at the margin. In paratype MB.C.2823, the polygonal and nodose stage is expanded, lasting at least until 20 mm dm. It is followed by a mature stage with different ornament, consisting of alternating more or less straight ribs and of impressed interspaces that do not cross the umbilical wall. Crowding of ribs is indicated in the youngest preserved whorl parts; the last whorl before 30 mm dm possesses 20 ribs. Two other paratypes, MB.C.2824 and 2885, have a polygonal and nodose stage that lasts ca. until 12 mm dm. The mature umbilical width in MB.C.2824 is ca. 47% dm. Both specimens show prorsiradiate ribbing of the compressed mature whorls. The poorly preserved, mostly squashed MB.C.2827 indicates that the species reached a maximum size of ca. 50 mm dm, with ribbing disappearing at ca. 40 mm dm.

DISCUSSION: Triangular coiling of early whorls in clymeniids is long known and has been the focus of the classical study of Schindewolf (1937). This is the first evidence for early ontogenetic polygonal coiling during a stage of extreme shell evolution. Becker (2000b) drew attention to a slight polygonal coiling in the early whorls of a similarly evolute *Trochoclymenia* illustrated by Czarnocki (1989, pl. 38, fig. 2). This feature reflects periodic small shifts in apertural orientation during growth. During episodes of more straight growth direction, the aperture orientation became slightly more vertical, reducing the apertural angle, since the distance between the centre of buoyancy and centre of gravity increased (see Trueman 1941). This is in accordance with supposed seafloor feeding of longidomic taxa, whose apertures were oriented towards the substrate (Saunders and Shapiro 1986). The episodic change of shell orientation would be stronger in triangularly coiled shells. Polygonal coiling and aperture shifts offer no functional advantage in mesodomic or brevidomic taxa, whose apertures pointed upwards. The lack of polygonal or trigonal coiling in all known meso- to brevidomic taxa, including the convolute Biloclymeniidae, is consistant with such a functional morphological interpretation.

The strongly nodose and polygonal early stages as well as the strong double furrows, forming a tricarinate venter, separate *Riphaeocymenia polygona* sp. nov. from the other known species of the genus. *Riphaeocymenia canaliculata* Bogoslovskiy, 1981 is similarly evolute but not ribbed and has weaker double furrows. In the evolute and keeled *R. fundifera* (Czarnocki, 1989) from the Holy Cross Mountains, the ribs are almost falcate; this species is morphologically closest within the genus. It is not likely, as suggested by Dzik (2006), that *R. canaliculata* and *R. fundifera* are conspecific.

OCCURRENCE: The new species is known only from the type locality and the type level.

Riphaeoclymenia pontotocensis sp. nov.
Text-fig. 4E–G, 5A.

ETYMOLOGY: After Pontotoc County in Oklahoma, which is the region where the types were collected.

TYPE LOCALITY, HORIZON, AND AGE: Ryan Quarry, south of Ada, Oklahoma, uppermost Woodford Shale, upper *Wocklumeria* Stufe, probably UD VI-C2 (upper *Parawocklumeria* Genozone).

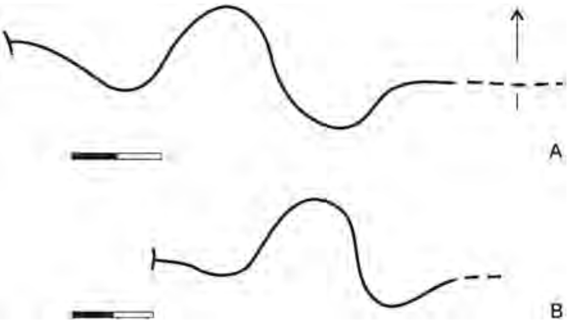
MATERIAL: Holotype MB.C.2846 (Text-fig. 4G), an almost mature, but still fully septate marcasitic mould, two marcasitic paratypes, MB.C.2845 and 2850, and two rather poorly preserved further specimens, MB.C.2847-88.

DIAGNOSIS: Early stages before ca. 10 mm dm widely evolute and with dense nodose ribs, later stages smooth or with undulose low ribs, with short, well rounded umbilical wall, flat flanks, compressed, and widely subevolute (uw = 41–45% dm). Mature stage also with a strong keel, bordered by deep spiral furrows and sometimes by a very faint second spiral depression. Sutures posses a subumbilical wide and subangular A-lobe, an asymmetric and high mid-flank saddle, an asymmetrically rounded, relative wide E-lobe, and a wide ventral saddle that is lower than the flank saddle.

DESCRIPTION: The holotype is slightly crushed and flattened but shows all diagnostic characters. At 8 mm dm, the last widely evolute and depressed whorl possesses 27 nodose flank ribs. The last node lies at ca. 10 mm dm; afterwards there are only gently undulose rib traces. Whorls soon become compressed and the umbilicus narrows. It is 15 mm wide at 34 mm dm (wh 10.2 mm, ww = ca. 5.5 mm, giving a wh/ww ratio of ca. 1.85). The last septate whorl has 30 chambers with some indication of septal crowding and advent of presumed maturity in the last quarter of the whorl. The body chamber and growth ornament are not preserved. The ventrolateral furrows are pronounced on the last whorl and produce a very distinctive narrow keel. Paratype MB.C.2845 has a somewhat more extended evolute stage and shows some indications of polygonal coiling. Nodose ribbing persists until ca. 13 mm dm, and adult whorls also are weakly ribbed. Sutures are identical as in the holotype. The umbilical width is ca. 41% at 34 mm dm. The squashed paratype MB.C.2850 has a shorter nodose stage but also adult ribs. Its adult umbilical width lies at ca. 45% at ca. 45 mm dm.

DISCUSSION: *R. pontotocensis* sp. nov. differs from *R. polygona* sp. nov. by the lack of the additional ventrolateral keel pair and by smoother adult stages. Polygonal coiling is also less distinctive and the umbilicus is slightly narrower. It is, therefore, assumed that there were two *Riphaeoclymenia* species living in the same environment. Within the genus, *R. pristina* from Poland is morphologically closest to *R. pontotocensis* sp. nov. and has similar sutures but is smooth and lacks a ventral keel. Ventrolateral furrows are rather weak in the suboxyconic *R. semicostata* and *R. subacuta*, and both have narrow E-lobes; the latter species is also more involute (uw = 33–35 % dm). Dzik (2006) considered the possibility that the three Polish species originally described as *Dimeroclymenia* are variants of just one species. This possibility does not effect the clear distinction of the Oklahoma species. Both *R. fundifera* and *R. canaliculata* remain very evolute (uw > 50% dm) at maturity.

OCCURRENCE: The new species is known only from the type locality and the type level.



Text-fig. 5. Sutures of *Riphaeoclymenia* from the Woodford Shale of Oklahoma. **A** – *R. pontotocensis* sp. nov. holotype, MB.C.2846, at mm 11.5 wh. **B** – *R. polygona* sp. nov., paratype MB.C.2821, at 7 mm wh; scale bars = 2 mm

Suborder Clymeniina Hyatt, 1884
Superfamily Cyrtoclymeniaceae Hyatt, 1884

INCLUDED FAMILIES: Cyrtoclymeniidae Hyatt, 1884, Cymaclymeniidae Hyatt, 1884, Rectoclymeniidae Schindewolf, 1923, and Carinoclymeniidae Bogoslovskiy, 1975. Contrary to Korn and Klug (2002), the Hexaclymeniidae are excluded (see discussion above).

Family Cyrtoclymeniidae Hyatt, 1884

INCLUDED GENERA: *Cyrtoclymenia* Hyatt, 1884, *Protactoclymenia* Wedekind, 1908, *Pricella* Korn in Clausen *et al.*, 1989, and several new, still unnamed genera. Evolute taxa, such as *Praeflexiclymenia* Czarnocki, 1989 and the late Famennian *"Cyrto." acuta* Group, are here excluded from the family.

Genus *Cyrtoclymenia* Hyatt 1884

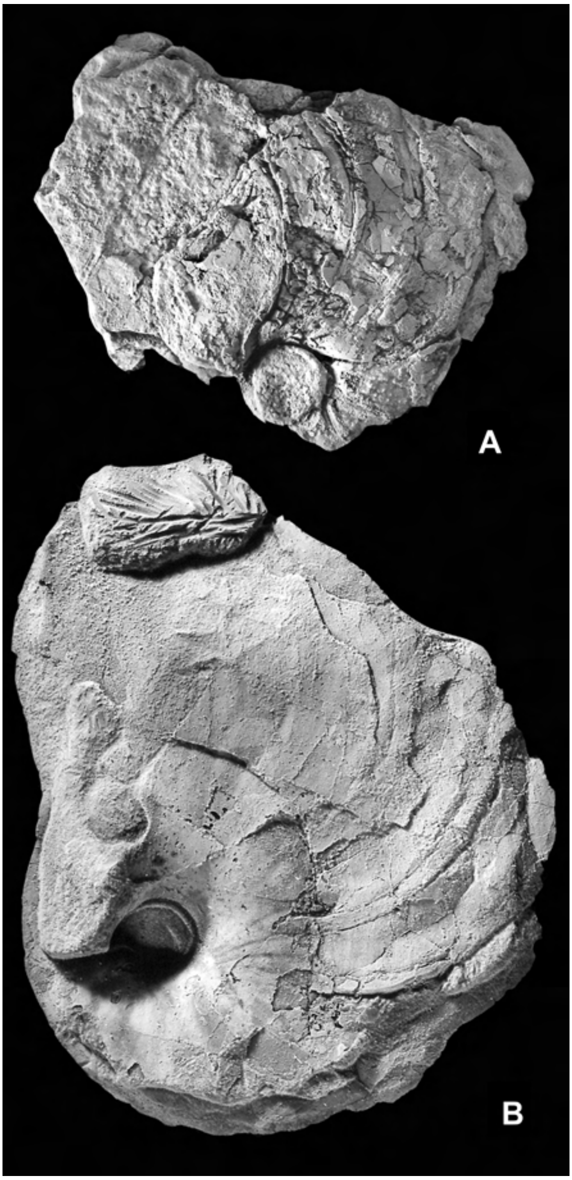
Cyrtoclymenia cf. *procera* Czarnocki, 1989
Text-fig. 6A–B.

*cf. 1989. *Cyrtoclymenia procera* sp. n.; J. Czarnocki, p. 50, pl. 15, figs 8, 10, pl. 46, figs 2a–d, 3

cf. 2006. *Cyrtoclymenia? procera*; J. Dzik; p. 285, fig. 208D (not 208E as indicated in text)

MATERIAL: Five fragments, MB.C.2841-2844 and MB.C.2849.

DESCRIPTION: MB.C.2841 is a squashed phragmocone fragment that shows the deep curvature of the single adventitious flank lobe. The last three septa have approximately the same height and give no evidence for septal crowding or maturity at almost 50 mm wh. MB.C.2842 is a partly squashed body chamber fragment that displays a pronounced projecting ventrolateral salient of the growth lines. The growth ornament forms slight bundles of 2.0 to 2.5 mm width. The reconstructed wh must have been in the scale of 100 mm. In MB.C.2843 equally spaced septa and the ornament of the rounded umbilical wall are visible at almost 50 mm wh. Growth line bundles start from the umbilical seam in a well-rounded sinus and seem to form a very low, short salient on the inner flank. In MB.C.2844, the most complete fragment, sutures, a well-rounded umbilical wall and the lateral sinus of the growth lines are visible. At ca. 65 mm wh, the umbilical width was less than 9 mm, suggesting an uw/dm ratio of less than 10 %. MB.C.2849 is very poorly preserved and adds no new morphological details.



Text-fig. 6. *Cyrtoclymenia* cf. *procera* Czarnocki, 1989 from the Woodford Shale of Oklahoma. **A** – MB.C.2841, × 1. **B** – MB.C.2844, showing the deeply curved flank lobe and traces of growth ornament, × 1

DISCUSSION: The Oklahoma specimens belong to a rather large sized clymeniid that reached between 15 and 20 cm in diameter. Shell form and ornament are very similar as in the Polish types of *Cyrtoclymenia procera*, but preservation is too incomplete for an unequivocal identification; hence a cf. is added. There is no reason to question the cyrtoclymeniid nature of such specimens, as suggested by Dzik (2006). The also large-sized and involute *Cyrto. strigata* House, 1962 from the uppermost Famennian of Iowa differs in its ornament with a much lower ventrolateral salient. Re-examination of its holotype at the University of

Iowa fossil repository (SUI 8041) and of two additional specimens in the same collection (SUI 51148, and SUI 46915) showed that small specimens have rounded, adult shells, such as the holotype (see House 1962, pl. 48, fig. 4), and a concave umbilical wall. The fragmentary *Cyrto*. aff. *strigata* Petersen and Stoakes, 1983 from Utah is also rather similar but lacks preservation of growth lines, which prevents further comparison. There are compressed and involute but much smaller-sized cyrtoclymeniids both in the Wocklum Stufe (UD VI) of South China (*Cyrto. perinvoluta* Sun and Chen, 1965 and *Cyrto. subinvoluta* Ruan, 1981) and of the Rhenish Massif of Germany (the poorly known *Cyrto. gracilis* Schmidt, 1924 and undocumented close relatives of *Cyrto. perinvoluta*). The uppermost Famennian *Cyrto. patera* Nikolaeva and Bogoslovskiy, 2005a from the Northern Caucasus is suboxyconic and probably represents an endemic side-branch of the Cyrtoclymeniidae.

OCCURRENCE: Uppermost Famennian of the Holy Cross Mountains and (cf.) of Oklahoma.

Order Goniatitida Hyatt, 1884
Suborder Tornoceratina Wedekind, 1914
Superfamily Praeglyphioceratacea Ruzhencev, 1957

DIAGNOSIS: See Becker (1993b).

FAMILIES INCLUDED: Sporadoceratidae Miller and Furnish in Miller *et al.* (1957) and Praeglyphioceratidae Ruzhencev, 1957.

DISCUSSION: Becker (1993a) discussed the subdivision of the Tornoceratina into superfamilies and argued that the Praeglyphioceratidae and Sporadoceratidae are so close in terms of morphology and phylogeny that separation into different superfamilies or even different suborders (Ruzhencev 1957) is not justified. Consequently, all descendents of the Cheiloceratidae with at least two adventitious lobes were included in an emended and monophyletic superfamily Praeglyphioceratacea. Korn and Klug (2002) included both families in the Prionocerataceae, but this produces a morphologically and stratigraphically rather heterogeneous, large systematic unit, which, in its proposed content, is probably polyphyletic. Whilst the evolutionary transition from cheiloceratids (*Puncticeras lagowiense*) to oldest Sporadoceratidae (*Maeneceras meridionale nuntio*) has been established by Becker (1993a; see also phylogenetic tree in Bockwinkel *et al.* 2002, text-fig. 5), the much younger origin of the Prionoceratidae at the base of UD IV is still unsolved. Most likely, however, and as proposed long ago by Wedekind (1913b), *Prionoceras* was derived by very early ontogenetic changes from the Prolobitidae, which Korn and Klug (2002) placed in an own superfamily. The Prolobitidae are the only and stratigraphically immediately preceding Middle Famennian goniatite group with shell constrictions that are so typical for *Prionoceras*. Morphologically somewhat intermediate prionoceratids from the basal UD IV of Morocco with widely open umbilicate early whorls as in prolobitids (Nawrath 2009) support this phylogenetic model. The separation of the Praeglyphioceratacea and Prionocerataceae, adopted by Furnish *et al.* (2009) in the revised Ammonoid Treatise, should be maintained within the Tornoceratina.

Family Sporadoceratidae Miller and Furnish, 1957 (in Miller *et al.* 1957)
Subfamily Sporadoceratinae Miller and Furnish, 1957 (nom. transl. Korn and Klug, 2002)

DIAGNOSIS (emend.): Sporadoceratidae with two angular A-lobes, with or without spiral ornament. Growth lines convex, concavo-convex or biconvex.

DISCUSSION: Bockwinkel *et al.* (2002) gave an overview of sporadoceratid evolution and pointed out that there were several unnamed genera. Some of these were formally established soon afterwards (Becker *et al.* 2002: *Umbosporadoceras* and *Enkebergoceras*; Becker 2002: *Maideroceras* and *Selwoodites*; Korn 2002: *Felisporadoceras* and *Xenosporadoceras*). Korn and Klug (2002) placed genera with rounded A_2-lobe, spiral ornament and biconvex growth lines in their new subfamily Xenosporadoceratinae, including species from UD IV and V. Becker (2002), however, showed that biconvex growth lines developed independently and earlier (UD III-C) in the paedomorphic *Maideroceras*, and spiral ornament occurs also in the much younger (UD VI) *Selwoodites* and in N. Gen. IV of Bockwinkel *et al.* 2002, which is here named as *Spirosporadoceras* gen. nov. Previously, Perna (1914) mentioned very fine spiral ornament in the Russian *Sp. denticulatum* of UD III-C, which was later illustrated by Bogoslovskiy (1971). Therefore, the subdivision into subfamilies requires an emendation. The major division in sporadoceratid evolution was the sharpening of the second adventitious lobe at the transition from *Maeneceras* to *Sp. teicherti*, the oldest species of *Sporadoceras* s. str. Shell and ornament changes, such as evolution of inner and outer whorls, the introduction of an ocular sinus and of spiral lirae, occurred iteratively within descendents of both genera. Consequently, the Xenosporadoceratinae are here re-defined to include all genera with rounded A_2-lobe (*Iranoceras, Maeneceras, Umbosporadoceras,* ?N. Gen. II Bockwinkel *et al.*, 2002*, Erfoudites, Felisporadoceras*, and *Xenosporadoceras*), whilst the Sporadoceratinae include the genera with angular A_2 (*Sporadoceras, Enkebergoceras, Araneites*, *Nothosporadoceras, Maideroceras, Spirosporadoceras* gen. nov.), and, rarely, with incipient A_3 (N. Gen. V Bockwinkel *et al.*, 2002, *Selwoodites*). There is currently no morphologic or stratigraphic evidence that angular A_2-lobes originated twice within the family. Middle to upper Famennian spirally ornamented Xenosporadoceratinae retain a rather small A_2.

Spirosporadoceras gen. nov.

TYPE SPECIES: *Spirosporadoceras overi* sp. nov.

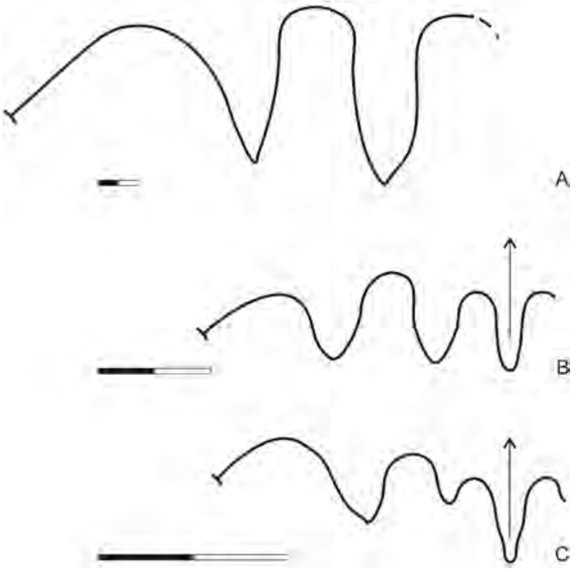
OTHER INCLUDED SPECIES: *Spiro. delicatum* sp. nov., *?Spiro. denticulatum* (Perna, 1914).

DIAGNOSIS: Conch always involute, with closed umbilicus; cross-section compressed and with rounded venter; ornament with very fine, convex and bundled growth-lines, and with fine spiral striae that may offset the growth lines. Sutures as in *Sporadoceras*, with two deep, narrow and pointed adventitious lobes. Sutural formula: EA_2A_1LUI.

DISCUSSION: The new genus differs from *Sporadoceras* by its fine spiral ornament, as in *Erfoudites* or in *Xenosporadoceras*, which both, however, have small and rounded A_2-lobes. Since the shell surface is not well known in all sporadoceratids, it is possible that some previously described forms also belong to the new genus. For example, Lange (1929) reported a specimen of *Sp. orbiculare* from UD V of Dasberg with spiral ornament, but material of that species with preserved shell from Morocco does not confirm Lange´s observation. Within the Sporadoceratinae, *Enkebergoceras* differs by its evolute early and mostly low whorls (low WER), *Araneites* by its adult keel, *Nothosporadoceras* by its open umbilicus at maturity, and *Maideroceras* by its markedly biconvex growth lines. The still unnamed *Selwoodites* species from the Rhenish Massif also displays spiral striae but has concavo-convex growth lines and an incipient A_3-lobe (see Becker 2002). The reticulate ornament of the enigmatic *"Sp." reticulatum* Nalivkina, 1953, which represents a different and rather early (UD III-C) sporadoceratid group with small A_3-lobe (N. Gen. V of Bockwinkel *et al.* 2002), seems to be based on the wrinkle layer.

The very fine (ca. 5 per mm) spiral striae of *Sp. denticulatum* Perna, 1914 would justify placing it in *Spirosporadoceras* gen. nov. However, Perna's species possesses a rather unique triangular ventral saddle that is different from the ventral saddles of the two new species of the genus described here, and *Sp. denticulatum* is also much older.

OCCURRENCE: Upper to uppermost Famennian (UD V/VI) of North America (Oklahoma) and Europe (Germany), questionably also in the middle Famennian (UD III-C) of the Southern Urals.



Text-fig. 7. Sutures of sporadoceratids from the Woodford Shale of Oklahoma. **A** – *Spirosporadoceras overi* gen. nov. sp. nov., paratype MB.C.2837, at ca. 22 mm wh. **B** – *Spiro. overi* gen. nov. sp. nov., juvenile paratype MB.C.2833, at 3.8 mm wh. **C** – Sporadoceratidae ?gen. nov. sp. nov., juvenile, MB.C.2856, at ca. 2 mm wh; scale bars = 2 mm

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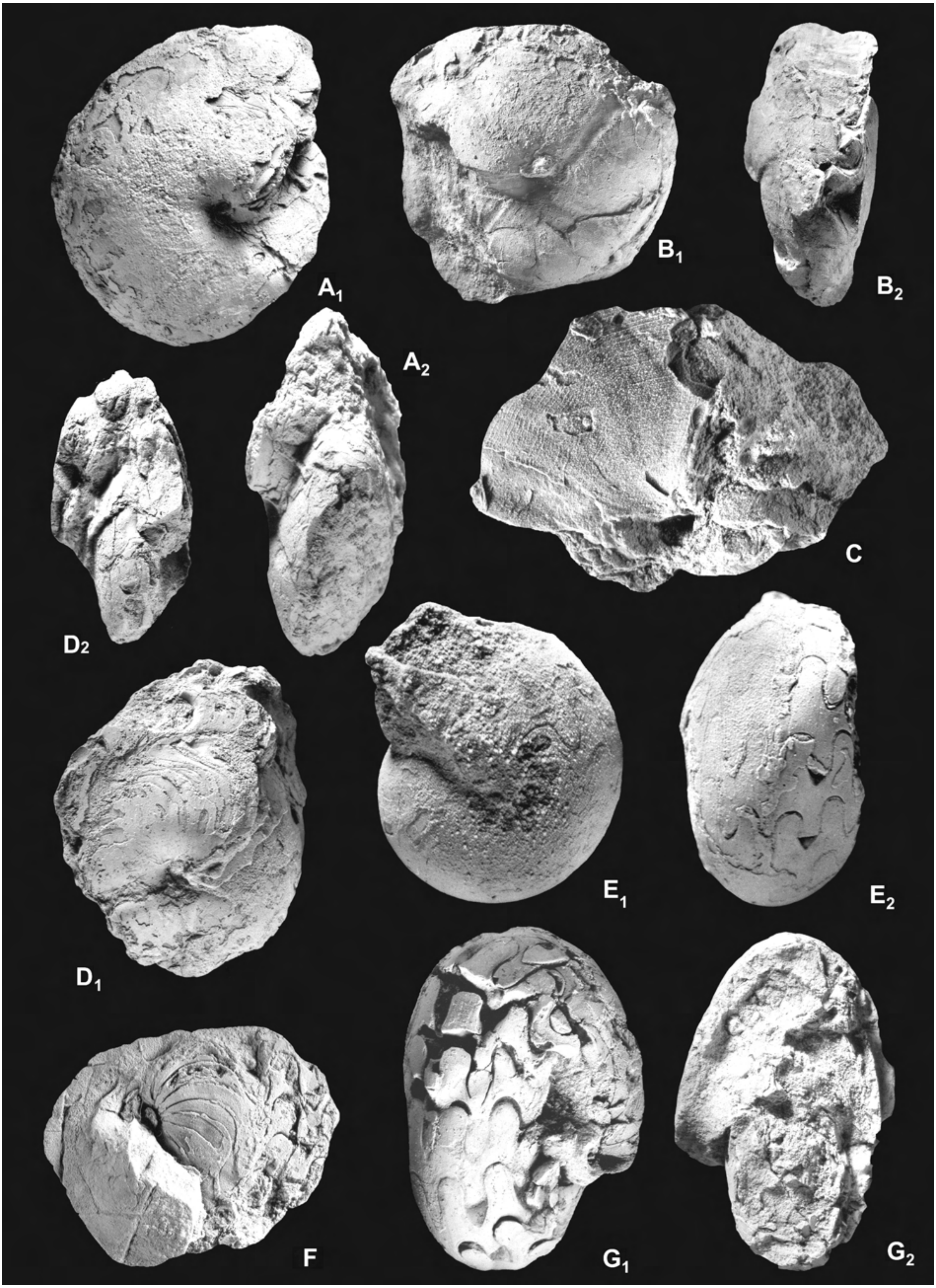
Text-fig. 8. *Spirosporadoceras overi* gen. nov. sp. nov. from the Woodford Shale of Oklahoma. **A_1, A_2** – Holotype, MB.C.2831, lateral view and adoral view showing the compressed cross-section, × 2. **B_1, B_2** – Paratype, MB.C.2828, lateral view showing mould constrictions and ventral view, × 2.5. **C** – Small paratype, MB.C.2832, lateral view showing the spider web-type shell ornament, × 4. **D_1, D_2** – paratype, MB.C.2834, lateral view showing sutures and adoral view, × 1.5. **E_1, E_2** – phosphatized juvenile paratype, MB.C.2833, lateral and ventral views, showing subglobular early ontogenetic shell form and sutures. **F** – paratype, MB.C.2830, lateral view showing the lanceolate adventitious flank lobes, × 1.5. **G_1, G_2** – paratype, MB.C.2854, specimen that was squashed oblique to the bedding surface, ventral view, showing the deep ventral lobe, and adoral view, × 1.5


A1
B1
B2
A2
C
D2
E1
E2
D1
F
G1
G2

Spirosporadoceras overi sp. nov.
Text-fig. 7A–B, 8A–G.

ETYMOLOGY: In honour of Dr. J. Over (Geneseo) for his important contributions to the understanding of the Oklahoma Devonian.

TYPES: Holotype MB.C.2831 (Text-fig. 8A), a marcasitic specimen showing shell form, ornament, and parts of the suture, and paratypes MB.C.2828-2830 and MB.C.2832-2837. There are fourteen additional but poorly preserved specimens (MB.C.2851.1-9. MB.C.2852.1-3).

TYPE LOCALITY, HORIZON, AND AGE: Ryan Quarry, south of Ada, Oklahoma, uppermost Woodford Shale, upper *Wocklumeria* Stufe, probably UD VI-C2 (upper *Parawocklumeria* Genozone).

DIAGNOSIS: Involute throughout ontogeny, with compressed (wh > ww), moderately rapidly (WER = ca. 1.9) expanding whorl profile; flanks converge towards the rounded venter; internal mould with shallow, convex constrictions. Ornament consists of convex growth lines that offset fine spiral lirae (3–4/mm) on the flanks and probably also on the venter. Sutures with high and arched inner flank saddle, deep and lanceolate A_1-lobe, narrow and high mid-flank saddle, deep and lanceolate A_2-lobe, which is slightly deeper than A_1 at maturity, and with high and narrow ventral saddle.

DESCRIPTION: The holotype displays four weak constrictions on the last whorl, which extend more or less straight across the flank and deepen slightly towards a ventral sinus. Not all of the paratypes show these internal shell thickenings but this mostly rests on the quality of preservation. The venter of the holotype is corroded, as in all paratypes apart from the juvenile MB.C.2833, but a compressed cross-section, with gently rounded flanks narrowing towards the venter, is visible. At ca. 30 mm dm, ww may have been 15 mm (50 %) and wh is almost 17 mm, giving a wh/ww ratio of ca. 1.1. The reconstructed WER was ca. 1.9. Sutures with two lanceolate adventitious lobes are more visible in paratypes MB.C.2829, 2830, and 2837. Paratype MB.C.2828 has rather marked constrictions and also shows the typical whorl form with the maximum whorl thickness lying close to the umbilical wall. Pseudosutures are visible in several specimens (e.g., MB.C.2829) and follow the normal course of sutures. A spider-web like delicate ornament is best preserved in the rather fragmentary paratype MB.C.2832. There are 3 or 4 spiral lirae per mm but they are offset by growth ornament. A magnified view shows that the growth lines are made of scale-like, very small (0.1 mm) structures that are only partially organized in radial patterns. The same scale structures are also preserved in phosphatized shell parts of MB.C.2836.4. This supports the conclusion that the scales are not a diagenetic product of marcasite mineralization, but are a previously unknown fine growth structure created by the animal. They suggest that shell mineralization took place in discrete units within the secreting cephalic mantle. Spiral striae are also preserved in MB.C.2828 and MB.C.2836.3, but not in the majority of specimens that lack preservation of outermost shell layers. The wrinkle layer with irregular and branching wrinkles that are oblique to growth lines is preserved on paratype MB.C.2835.

Three specimens, MB.C.2853-55, were originally thought to belong to a different and rather subglobular sporadoceratid species, such as *Sporadoceras orbiculare* (Münster, 1832). Closer examination proved that the three specimens are the only ones that were deformed by pressure on the ventral side, preserving the ventral sutures but creating wider cross-sections. This distortion was probably caused by having been embedded in the sediment at a oblique to near vertical angle to the sea floor. Most specimens are compressed laterally and do not display ventral lobes. MB.C.2854 shows that the ventral lobe was lanceolate, but not as deep as the adventitious flank lobes.

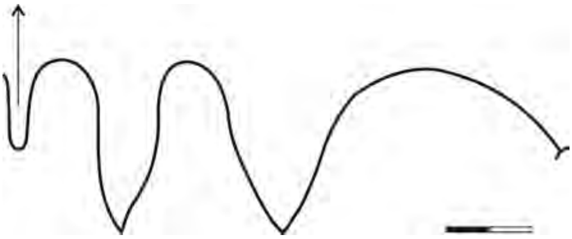
DISCUSSION: The new species cannot be confused with any other described sporadoceratid. Sutures and cross-section resemble the older *Sporadoceras angustisellatum* Wedekind, 1908, which, however, lacks spiral lirae and mould constrictions on the flanks. *Sp. orbiculare* (Münster, 1832) and *Sp. muensteri* (V. Buch, 1832) have thicker whorls and somewhat more bell-shaped adventitious lobes (e.g., Becker *et al.* 2002). The latter is especially true for the Upper Famennian *Sp. kiense* Bogoslovskiy, 1971, including undescribed relatives from Germany.

OCCURRENCE: The new species is known only from the type locality and the type level.

Spirosporadoceras delicatum sp. nov.
Text-fig. 9, 10A–B.

ETYMOLOGY*:* From the Latin *delicatus*; after its rather delicate ornament.

TYPES*:* Only the holotype, MB.C.2857.



Text-fig. 9. Suture of *Spirosporadoceras delicatum* gen. nov. sp. nov., holotype, MB.C.2857, at 22 mm wh; scale bar = 2 mm

TYPE LOCALITY, HORIZON, AND AGE: Dasberg Formation at Beul, near Eisborn (northern Rhenish Massif), precise level unknown but probably from the *Clymenia* Stufe (UD V).

DIAGNOSIS: Flanks and venter well-rounded, subdiscoidal, with wh > ww at maturity; WER = ca. 2.3; mould constrictions are lacking. Growth lines slightly biconvex, with very shallow lateral sinus; spiral ornament very fine, 4–5/mm. Sutures with arched inner flank saddle, moderately wide, v-shaped A_1, narrow mid-flank saddle, narrow and lanceolate A_2 that is as deep as A_1, and narrowly rounded ventral saddle that is slightly lower than the A_1–A_2-saddle.

DESCRIPTION: The holotype and single available specimen is preserved in reddish, yellowish weathering micrite. It is reasonably well preserved and shows all features of shell form, ornament and sutures. The delicate spiral striae are visible from the umbilicus to the venter on one side whilst abrasion of the shell for suture preparation on the other side proves the absence of internal shell thickenings. The shell parameters are as follows: dm = 59 mm, wh = 34 mm, ww = 30 mm, ah = ca. 20 mm, WER = ca. 2.3.

DISCUSSION: The different ornament, lack of constrictions, and the course of sutures allow an easy distinction from *Spiro. overi* sp. nov. The sutures of *Spiro. delicatum* sp. nov. resemble those in the older (UD III) *Sp. equalis* (figured in Petersen 1975, text-fig. 21D) but the ventral saddle and the A_2-lobe are somewhat narrower. The equal depths of both adventitious lobes, however, leave the possibility that *Spirosporadoceras* gen. nov. separated rather early from *Sporadoceras*, which may support the inclusion of *Sp. denticulatum* Perna, 1914 in the new genus. The relatively rapid whorl expansion is higher than in most *Sporadoceras,* but not as high as in *Maideroceras* (Becker 2002). Even if preserved as a mould, confusion with all other known contemporaneous sporadoceratids is impossible.

OCCURRENCE: The new species is known only from the type locality and the type level.

Sporadoceratidae ?gen. nov. sp. nov.
Text-fig. 7C.

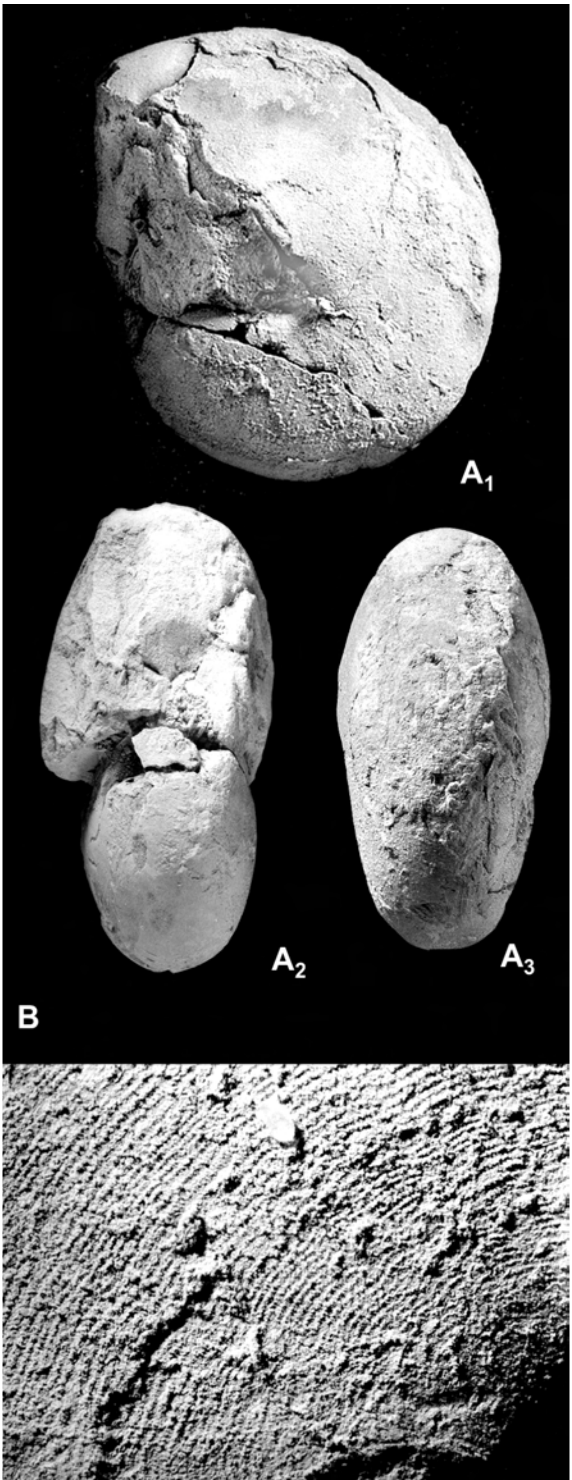
DESCRIPTION: A single juvenile sporadoceratid, MB.C.2856, differs in shell form and sutures significantly from *Spirosporadoceras overi* gen. nov. sp. nov. The specimen is rather poorly preserved and partly sheared but some remarkable features are distinct. At 7 to 8 mm dm, the shell was subglobular with well-rounded flanks and venter, the umbilicus appears to have been widely open (uw/dm > 30 %). Sutures are much less advanced than in typical Sporadoceratinae and the small and rounded A_2 lobe resembles *Maeneceras* or *Erfoudites*. The ventral saddle is lower than the A_1–A_2 saddle.

DISCUSSION: There is no described similar sporadoceratid from the uppermost Famennian. Open umbilicate early whorls are only known from the much older (UD III) *Enkebergoceras* and *Xenosporadoceras* (UD III to IV-A). The first is characterized by deep constrictions, which are lacking in MB.C.2856, and a somewhat deeper A_2 lobe at a comparable size; the second differs by spiral ornament, for which there is no evidence on the preserved whorl parts. The Oklahoma specimen may represent an unknown, new open umbilicate sporadoceratid genus, and certainly a new species, but the poor quality of the only available specimen prevents any formal naming.

PALAEOBIOGEOGRAPHIC ASPECTS

Clymeniids

Rich and diverse uppermost Famennian ammonoid faunas have been known for a long time from various areas of Germany and are characterized by the sudden appearance of triangular coiled clymeniids, the Wocklumeriaceae (extensive reviews in Becker 2000b and Ebbighausen and Korn 2007). Assemblages from other European regions, such as SW England (Selwood 1960), northern France (Péneau 1929), the Montagne Noire of Southern France (Becker and Weyer 2004; Ebbighausen and Korn 2007), and the Carnic Alps (Gaertner 1931; Korn 1992b, 1998; Kaiser *et al*. 2009) point to a rather homogenous biochore of the Western Prototethys (see biogeographic review in Becker 1993b). It extended into North Africa (Petter 1959, 1960; Korn 1999; Becker *et*



Text-fig. 10. *Spirosporadoceras delicatum* gen. nov. sp. nov. from the upper Famennian of Beul, Rhenish Massif, holotype, MB.C.2857. **A_1, A_2, A_3** – Lateral, adoral and ventral views, × 1. **B** – Enlarged part of the flank, showing the delicate spiral ornament, × 6

al. 2002; Ebbighausen and Korn 2007) where, however, various European groups (Glatziellidae, Kamptoclymeniidae, *Epiwocklumeria*) are lacking in very extensive and diverse collections, perhaps due to the higher latitude. A slight southward decreasing gradient of seawater temperatures has recently been recognized in oxygen isotopic values of uppermost Famennian conodont phosphate from Germany to the Carnic Alps but Moroccan isotopic values are considered abnormal (Kaiser *et al.* 2004a), giving much too high reconstructed palaeotemperatures. Rich ammonoid assemblages from South China were described by Sun and Chen (1965) and Ruan (1981) and also proved to be rather similar, despite the large longitudinal distance within the Prototethys. Faunas from the southern parts of the Ural Ocean (e.g., Bogoslovskiy 1981; updated by Nikolaeva and Bogoslovskiy 2005b) and Caucasus (Nikolaeva and Bogoslovskiy 2005a) also showed similarities, but produced some different genera, such as *Synwocklumeria* and the very rare *Riphaeoclymenia*.

The posthumous publication of the important stratigraphic work of Czarnocki (1989) in the Holy Cross Mountains of Poland included a new and very distinctive genus of triangular clymeniids, *Kielcensia*. The Czarnocki data also show that *Riphaeoclymenia*, described under the generic names *Dimeroclymenia* and *Liroclymenia*, is well represented in Polish faunas, and that *R. fundifera* is rather closely related to *R. canaliculata* (see Dzik 2006). This can be interpreted as a faunal influx from the East, resembling the probably current-controlled immigration of a few Upper Famennian "exotic" Ural Ocean conodonts into parts of Silesia (Belka 1998). But, there is no known uppermost Famennian biogeographical or plate tectonic barrier that would have restricted a further migration or spread of the supposedly endemic *Kielcensia* with the westward flowing palaeocurrents (palaeogeography after Paproth *et al.* 1986, see also Text-fig. 11) to the German basins. This is well supported by the discovery of some other clymeniid genera in the Famennian of Germany, such as *Flexiclymenia* and *Nodosoclymenia* (Korn and Klug 2002, new records) that first were thought to be endemic to Poland. The very similar clymeiid-bearing pelagic nodular limestones of the Holy Cross Mountains and Germany represent identical litho- and biofacies and speak against a facies control on ammonoid distribution.

The discovery of rare *Synwocklumeria* and *Kielcensia* in southern Morocco by Becker (2000b) added to the biogeographic enigma. The British *Epiwocklumeria dunhevedensis* Selwood, 1960 was re-assigned by Becker (2000b) to *Synwocklumeria*, extending the range of that genus far westwards. Since the

Carpathian and Bohemian Highs bordered and blocked the Polish Basins in Famennian time to the South, both *Synwocklumeria* and *Kielcensia* must have migrated through the Central European areas from East to West and Southwest, but without leaving a trace in an overwhelmingly rich fossil record, especially of the Rhenish Massif and Saxothuringica. The new *Kielcensia* and *Riphaeoclymenia* species from Oklahoma further deepen the mystery. Even if a distinction of *Riphaeoclymenia* and *Dimeroclymenia* is kept, morphologically close relatives of *R. polygona* sp. nov. and *R. pontotocensis* sp. nov. are so far only known from the Holy Cross Mountains. The Oklahoma fauna occurs in a black shale facies that is not too different from the hypoxic shales of the Maider Basin of southern Morocco. Its taxonomic composition, however, is utterly different from the European–North Africa biochore where *Cymaclymenia*, kosmoclymeniids, mimimitoceratids, Balviinae, the *Cyrtoclymenia angustiseptata* Group, *Parawocklumeria*, and *Wocklumeria* dominate the latest Famennian faunas. This suggests a very selective faunal exchange between southern North America and Europe/Morocco in the uppermost Famennian.

Goniatites

The summary of Lange (1929) showed that the acme of sporadoceratid evolution lay in the Middle Famennian (UD II-G to IV), with only two groups, species now included in *Erfoudites* and close relatives of *Sp. orbiculare*, continuing rather frequently into UD V. The latter is the only species that has been reported repeatedly, but as a rare form, from the uppermost Famennian (UD VI) of the Rhenish Massif, Thuringia, and Silesia. To this sporadoceratid evolution pattern, the rare genus *Selwoodites* has been added by Becker (2002). *Sp. posthumum* Wedekind, 1918 and relatives are not sporadoceratids but fall within *Posttornoceras* (Tornocerataceae, Korn 1999; Becker, 2002). A variety of *Sp. orbiculare* with more narrow lobes is known from UD VI of Cornwall (Selwood 1960). Specimens from Kowala (Holy Cross Mountains) and Dzikowiec (Silesia) were assigned by Dzik (2006) to *Sp. terminus*, which probably falls in the intraspecific variability of *Sp. orbiculare*. Sporadoceratids are so far lacking in the uppermost Famennian of Morocco (Becker *et al.* 2002). *Sp. longilobatum* Petter, 1959 from UD VI of the Saoura Valley of Algeria should be re-assigned as a subspecies to *Sp. orbiculare*. Specimens from UD VI of South China assigned by Sun and Chen (1965) to *Sp. muensteri* need to be re-studied and most likely do not belong to that species. In the South Urals (Bogoslovskiy 1971), the endemic *Sp. kiense* is the only well documented species from UD V, but UD VI sporadoceratids are lacking. Very poorly known are the uppermost Famennian sporadoceratids from the top of the Cleveland Shale and from the basal Bedford Shale of Ohio (Herrick 1893; House *et al.* 1986). They have equally deep adventitious lobes and lack spiral striae. The illustrated lobes of the suture line do not show the typical bell-shape of *Sp. orbiculare*, and the whorls seem to expand rather slowly. This suggests that a different North American lineage of sporadoceratids ranged in parallel with *Spirosporadoceras* gen. nov., and even into the Hangenberg Event interval. Their early stages are still unknown, which prevents any comparison with the juvenile specimen from Oklahoma described in open nomenclature.

This summary of upper and uppermost Famennian sporadoceratid distribution shows that there are no equivalents of *Spirosporadoceras overi* gen. nov. sp. nov. in the UD VI of the Prototethys and Ural Ocean areas, although the Oklahoma form may have had European roots (*Spiro. delicatum* gen. nov. sp. nov.). With respect to the biogeographic links of the clymeniid taxa, this endemism is rather remarkable.

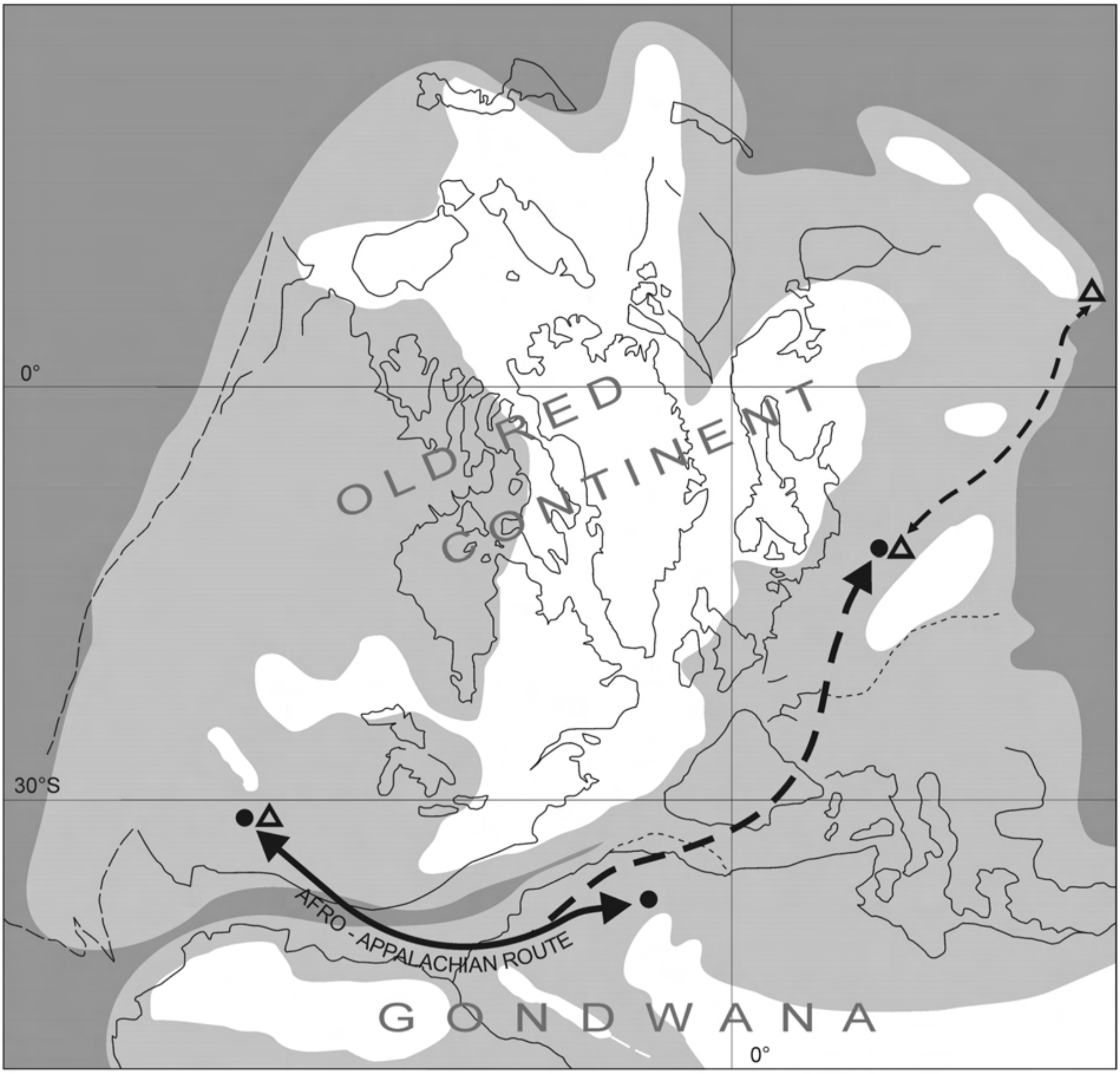
CONCLUSIONS

The new Oklahoma fauna, with its unexpected Polish affinities of clymeniids, leads to four conclusions: (1) A pelagic seaway from Europe to southern Morocco, through the Tindouf Basin and Mauritania and around the Appalachians (within the “Proto-Atlantic”) into the pelagic bay southwest of the Transcontinental Arch of North America, was open in the uppermost Famennian; (2) this seaway allowed specific ammonoid genera to pass from one area to another and barred some of the most common European and North African genera from migrating; (3) ammonoid taxa were capable of migrating through basins without leaving traces in very rich fossil records; and (4) the observable ammonoid distribution patterns were strongly controlled by biofacies factors that leave no easily recognizable signature in the sediments.

(1) Faunal migration from Europe via North Africa into the Appalachian fore-deep has long been recognized and named as the “Afro-Appalachian link” by House (1973). However, there is no faunal evidence from North America that this route was open to ammonoids in the upper Famennian (UD V). An open route for migrating pelagic faunas in the uppermost Famennian, as indicated by the Oklahoma fauna, has not yet been substantiated by the discovery of UD VI clymeniid fau-

nas in SW Morocco, including former Spanish Sahara, or in Mauritania. The uppermost Famennian of the western Dra Valley was deposited in very shallow water with rich neritic brachiopod faunas (Kaiser *et al.* 2004b), lacking any ammonoids, and must have lain to the West of the migration route. The postulated uppermost Famennian pelagic beds of the Tindouf Basin may have been completely eroded subsequently or may not crop out at the surface. The Himalayan-style Appalachian Mountains prevented any other alternative route of migration at the time (Text-fig. 11). It needs to be stressed that the Oklahoma Famennian is known to continue eastwards into Arkansas and westwards to western Texas and western New Mexico (Over and Ruppel 2009) but there are no Devonian outcrops to the South that could provide evidence of a closer link with North Africa.

(2) The second conclusion has to be modified by the records of cymaclymeniids from Ohio (here re-assigned to *Postclymenia*) and Utah, which show that the reconstructed seaway was also open to that genus at some time in the uppermost Famennian. Becker (1993b) suggested that cymaclymeniids spread to North America with the main transgressive pulse of the Hangenberg Event (UD VI-E). It is very intriguing that *Cymaclymenia*, as the most widespread of all clymeniid genera, is missing in Oklahoma.



Text-fig. 11. Famennian plate tectonic reconstruction showing the distribution of *Kielcensia* (dots) and *Riphaeoclymenia* (triangles) in the southern Urals, Holy Cross Mountains, southern Morocco, and Oklahoma, and probable migration routes. White areas = terrestrial regions, light grey areas = epicontinental shelf seas, dark grey areas = open and deep oceanic regions

(3) The third conclusion is confirmed by other recent exotic discoveries of Famennian ammonoids, named as “Spot Taxa” (Becker 2000a), based on their contemporaneous spotty occurrences in widely separate sedimentary basins. The Frasnian goniatite genus *Prochorites* occurs abundantly in eastern North America and in Western Australia, on the opposite side of the Devonian globe, but not in the rich Prototethys faunas between both distant areas. Other examples are findings of *Karaclymenia*, first described from the southern tip of the Urals (Aktyubinsk region, Kazakhstan, Bogoslovskiy 1983), in southern Morocco (Becker *et al.* 2002), or of various Polish goniatite taxa (several cheiloceratids, *Tornia*) in NW Australia (Becker and House 2009). Such records are partly based on rather rare species or on faunas from very thin, easily overlooked strata (e.g., *Cycloclymenia* Bed of Australia, Becker 2000a; Becker and House 2009).

(4) The fourth conclusion is the only explanation for the distinctive faunal composition at Ryan Quarry. Upper to uppermost Famennian black shales of Germany and Morocco have yielded many other goniatite and clymeniid taxa, as well as lingulids, plant and fish remains, and nautiloids. The composition of the conodont faunas cannot be compared since European and North African black shales cannot be processed easily for conodonts. Attempts should be made to detect geochemical differences between black shales with different pelagic faunal communities. The Oklahoma fauna underlines the significance of pelagic assemblage studies for facies discrimination in the vast Middle Palaeozoic outer shelf settings.

As a general summary it needs to be stressed that caution is advised in the interpretation of Devonian ammonoid biogeographic data because continuing research has proven numerous times in the last decade that the spatial distribution of many supposedly endemic taxa was much wider than originally presumed. The results of this study raise some doubts about the value of quantitative analytical methods commonly used for nektonic organisms of the open marine realm, since they bring to question the quality of available databases. As an equivalent for “Lazarus Taxa” in time range analysis, the existing term “Spot Taxa” can be expanded to taxa that must have migrated through a region but without leaving an available trace in rich regional fossil records between spot occurrences. As there are “Ghost Ranges” in time based on phylogenetic and stratigraphical data, “Spot Taxa” allow the reconstruction of “Ghost Distributions” if plate tectonic settings and migrational paths are well established. The “Ghost Distribution” of *Kielcensia* and *Riphaeoclymenia* includes more sedimentary basins (e.g., Saxothuringia, Rhenish Massif, northern France, southern France, Moroccan Meseta, Tindouf Basin, Spanish Sahara/Mauritania, Arkansas/SE North America) than there are regions with an actual fossil record of these forms.

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