The ammonoids from the Three Forks Shale (Late Devonian) of Montana

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Abstract

The ammonoid fauna from the Late Devonian Three Forks Shale of Montana is revised. Six taxa were recognised, which belong to the genera *Tornoceras*, *Pernoceras*, *Raymondiceras*, *Platyclymenia*, *Pleuroclymenia*, and *Carinoclymenia*. The ammonoid assemblage suggests a stratigraphic position within the middle Famennian, most probably the *Platyclymenia annulata* Zone. The ammonoids display extreme septal crowding in intermediate as well as adult growth stages, which can be regarded as evidence for instable palaeoecological conditions during lifetime of the animals.

Schlüsselwörter: Ammonoidea, Biostratigraphie, Three Forks Shale, Oberdevon, Montana.

Zusammenfassung

Die Ammonoideenfauna aus dem oberdevonischen Three Forks Shale von Montana wird revidiert. Sechs Taxa werden unterschieden; sie gehören zu den Gattungen *Tornoceras*, *Pernoceras*, *Raymondiceras*, *Platyclymenia*, *Pleuroclymenia* und *Carinoclymenia*. Die Ammonoideen-Vergesellschaftung spricht für eine stratigraphische Position im mittleren Famennium, wahrscheinlich in der *Platyclymenia annulata* Zone. Die Ammonoideen zeigen auffällige Drängung der Septen in intermediären und adulten Wachstumsstadien, die als Hinweis auf instabile Lebensbedingungen für die Tiere gewertet werden kann.

Introduction

The ammonoid fauna from the Three Forks Shale of Madison County, Montana, was for a rather long period the only rather rich Famennian assemblage from the New World. It was discovered by Percy E. Raymond, who in three articles (Raymond 1907, 1909, 1912) provided descriptions of his five new species *Tornoceras crebriseptum*, *Tornoceras douglassi*, *Prolobites simplex*, *Platyclymenia americana*, and *Platyclymenia polypleura*. He already attributed the rocks with this fauna to the 'latest Devonian'.

The material, stored in the Carnegie Museum, Pittsburgh was then studied by Schindewolf in 1933. In the following year, he published a discussion of the assemblage and reached the conclusion that the fauna has to be attributed in the '*Prolobites-Platyclymenia*-Stufe' (Schindewolf 1934). His revision included the confirmation of the four species erected by Raymond and the establishment of the new genus *Raymondiceras* for '*Prolobites simplex*', but he was not able to

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assign this remarkably simple-sutured ammonoid to a specific ammonoid group. A relationship with the superficially similar Middle Devonian genus *Subanarcestes* Schindewolf, 1933 was taken into consideration, but also the possibility that *Raymondiceras* derived from cheiloceratids, in possessing a secondarily simplified morphology.

Miller (1938) later revised and re-figured the fauna and discussed its stratigraphy once again. He was also puzzled by the composition of the fauna and not sure about the age of the assemblage, but stated that it "... is almost certainly younger than that of the Canadaway with *Manticoceras*" (Miller 1938, p. 9).

The Three Forks fauna lost its exclusivity, caused mainly by the peculiarly simple morphology of *Raymondiceras*, with the description of the species-rich Famennian ammonoid assemblages from the South Urals by Bogoslovsky (1960, 1971). Bogoslovsky found another species that he treated as *Raymondiceras*, *R. aktubense* (now attributed to *Roinghites* Korn, 2002) from middle Famennian rocks of Kazakhstan. Petersen (1975) added a third species to the genus, *R. inceptum*, from the *Platyclymenia* horizon of Western Australia.

House (1962), who figured some of the species described earlier, contributed the additional new species *Rectoclymenia haynesi* from the Three Forks Shale. In a subsequent article (House 1965), he described *Tornoceras crebriseptum* in detail.

A rich collection of new material from several exposures at Three Forks (Fig. 1) was assembled by A.T. between 1993 and 1995 and serves as the basis for the revision of the ammonoid fauna. It was surprising that, despite of the repeated reports on the ammonoid assemblage from the Three Forks, new data could be gained that allow an update of the knowledge of this occurrence.

Stratigraphy

The Three Forks Formation was named by Peale (1893). Although he did not designate a type section, the Milligan Canyon area west of the town of Three Forks has been used as such by default. The formation as originally defined included all of the clastic and mixed carbonate clastic less resistant strata between the underlying Jefferson Dolomite (Devonian) and the overlying Lodgepole Limestone (Mississippian). Later, the Three Forks Formation was divided by Sandberg (1965) in the type area into, in ascending order, the Logan Gulch, Trident, and Sappington Members. Most of the unit has a Late

Devonian (Fammenian) age, however the upper few meters of the Sappington Member belong unequivocally to the Early Carboniferous (Tournaisian).

The ammonoids described herein all come from the Trident Member, which consists almost entirely of greenish or reddish weathering grey shale with concretions of limonite and siderite. Fossils, including cephalopods are locally abundant. The type section of the Trident Member is only a few kilometers northeast of Milligan Canyon section discussed herein, so correlation of the ammonoid bearing unit there, as well as that of the other locality, is straightforward. Although the lithology of the Trident Member is fairly monotonous, there is a distinct succession of fossils. Small limonitic internal molds of ammonoids, especially tornoceratids, seem more common in the lower part of the studied section. Larger ammonoids and nautiloids, along with a sparse benthic fauna of bivalves and gastropods, become more common upsection, but then disappear, being replaced by a rich brachiopod-bryozoan dominated benthic fauna.

Although the Three Forks Shale is mapped widely in southwestern Montana, good exposures of the ammonoid bearing Trident Shale Member are actually quite uncommon.

The junior author examined two localities during a limited survey of Three Forks Shale outcrops done in the summers of 1990 and 1995, both of which had been reported previously by Sandberg (1965). The first locality is within Milligan Canyon (Fig. 1), just over 8 kilometers west of the town of Three Forks. The Milligan Canyon drainage is classically viewed as the type section for the Three Forks Shale, however, good outcrops of the Trident Member with ammonoid fossils were found to be limited to a rather small area. Exposures are best in the east-center of Sect. 36, T 2 N, R 1 W (Montana Principal Meridian), along a small north trending drainage. The lower contact of the Trident Member with the underlying Logan Gulch Member is not exposed, and the lowest exposed bedrock in the immediate succession is a prominent andesite sill that is pervasive in the area. Just above the hornfels caused by the sill are excellent, generally north-dipping outcrops of the upper portion of the Trident Member and the overlying Sappington-Lodgepole sequence. A measured section was recorded and all Milligan Canyon specimens came from this locality (Fig. 1). Ammonoids generally decrease in abundance upsection, coincident with the appearance of orange
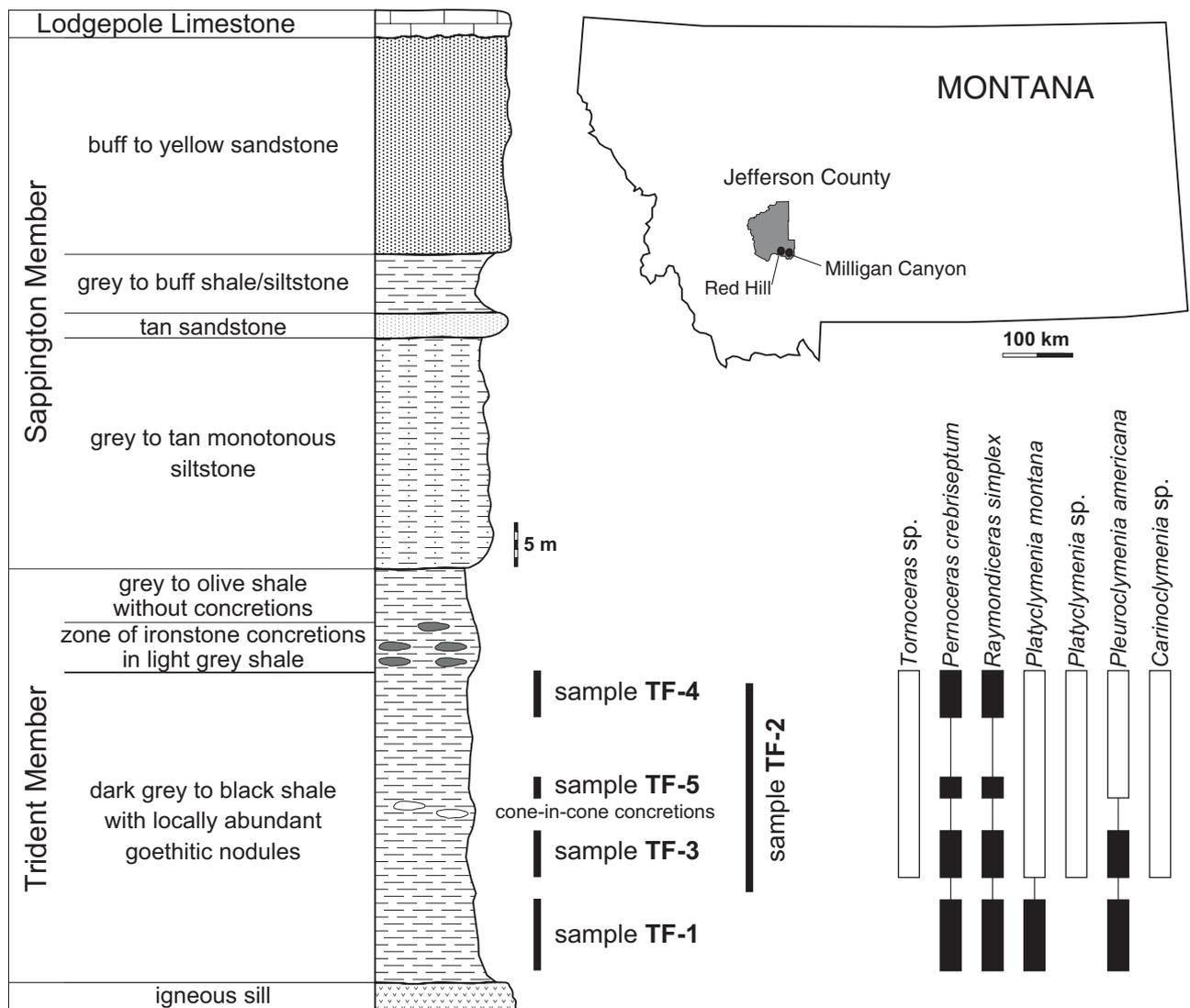
Fig. 1. Geographic position of the Three Forks localities, columnar section of the Milligan Canyon section, and stratigraphic range of the ammonoid species within the section.

and yellow weathering sideritic carbonate concretions and a much more abundant and diverse benthic fauna.

The second locality on Red Hill, is located about 22 kilometers west and slightly north of the Milligan Canyon section in the center of Sect. 22, T.2.N, R.3.W (Fig. 1). Exposures of the middle and upper portions of the Trident Member are better at Red Hill, but the remainder of the section is not as well exposed, and the base of the Trident was not seen. In overall aspect the section is similar to that of the Milligan Canyon area, but is somewhat thicker. Ammonoids were especially common at this locality, indicating the collecting had probably not occurred there for many years. Unfortunately, the nature of the outcrop made collecting with a high degree of stratigraphic control exceedingly difficult.

Palaeontological descriptions

Material

240 specimens are available for study. The majority of these specimens, however, are fragments, and distinct specific interpretation is not always possible. Except for a few individuals, the entire material is preserved as limonite (previously markasite) steinkern specimens that only rarely bear remains of the shell.

Suborder **Tornoceratina** Wedekind, 1918
Family **Tornoceratidae** von Arthaber, 1911

Tornoceras Hyatt, 1884

Tornoceras sp.
Figs 2A, 3A

M a t e r i a l. One specimen (MB.C.9126) from Red Hill.

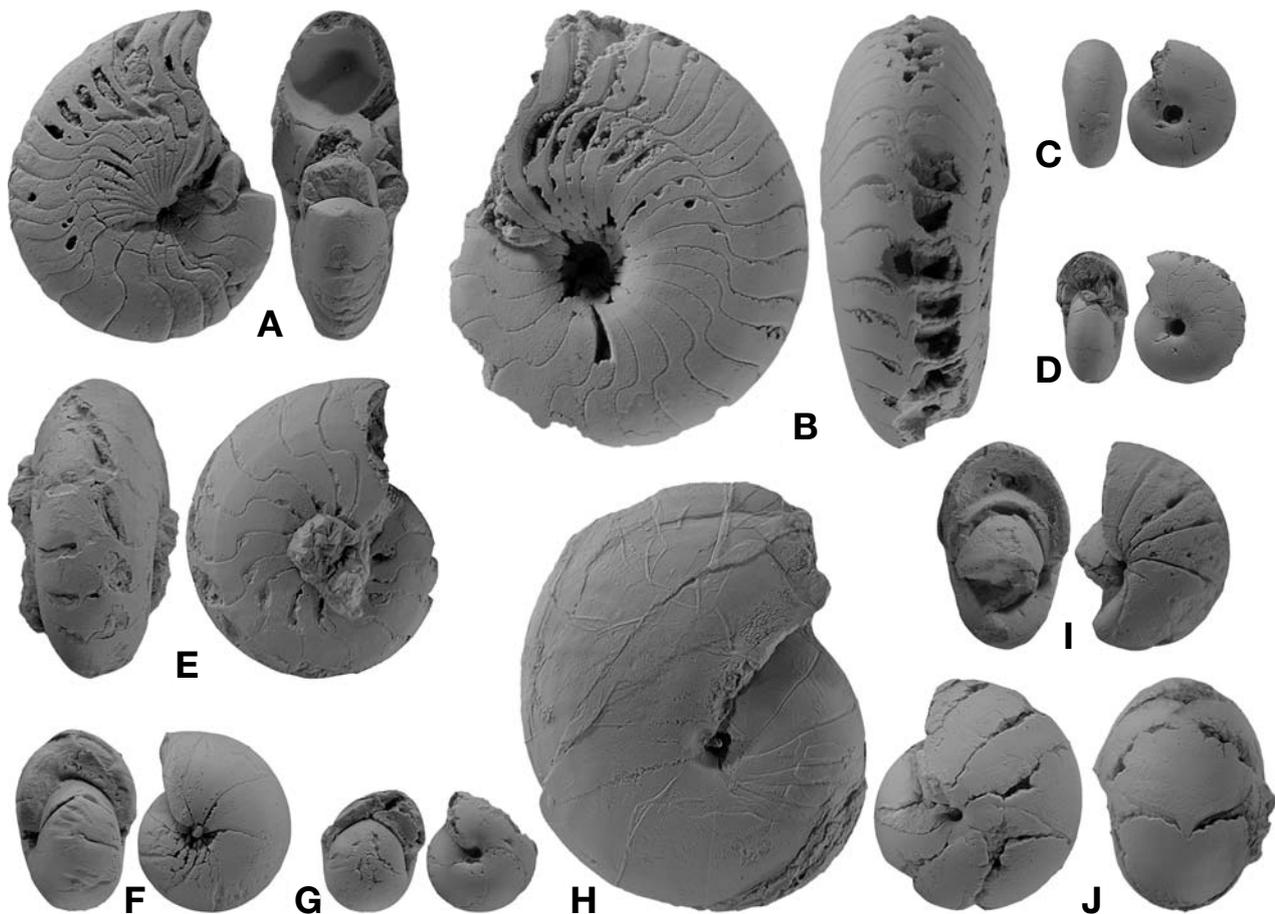D e s c r i p t i o n. Specimen MB.C.9126 has 17.5 mm conch diameter and differs in several

Fig. 2. Tornoceratin ammonoids from the Three Forks Shale of Montana, coll. Titus, all × 2.5. **A** – *Tornoceras* sp., specimen MB.C.9126 from Red Hill, lateral and dorsal views; **B** – *Pernoceras crebriseptum* (Raymond, 1909), specimen MB.C.9140.1 from Milligan Canyon (sample TF-2), lateral and ventral views; **C** – *Pernoceras crebriseptum* (Raymond, 1909), specimen MB.C.9145.1 from Milligan Canyon (sample TF-3), ventral and lateral views; **D** – *Pernoceras crebriseptum* (Raymond, 1909), specimen MB.C.9145.2 from Milligan Canyon (sample TF-3), dorsal and lateral views; **E** – *Pernoceras crebriseptum* (Raymond, 1909), specimen MB.C.9140.2 from Milligan Canyon (sample TF-2), ventral and lateral views; **F** – *Raymondiceras simplex* (Raymond, 1909), specimen MB.C.9134.2 from Red Hill, dorsal and lateral views; **G** – R*aymondiceras simplex* (Raymond, 1909), specimen MB.C.9146.1 from Milligan Canyon (sample TF-3), dorsal and lateral views; **H** – *Raymondiceras simplex* (Raymond, 1909), specimen MB.C.9134.1 from Red Hill, lateral view; **I** – *Raymondiceras simplex* (Raymond, 1909), specimen MB.C.9134.3 from Red Hill, dorsal and lateral views; **J** – *Raymondiceras simplex* (Raymond, 1909), specimen MB.C.9149.1 from Milligan Canyon (sample TF-4), lateral and ventral views.

characters from the co-occurring *Pernoceras crebriseptum* described below. The umbilicus is completely closed in this specimen, and there is not a well-developed umbilical margin. The specimen is fully septate, with strikingly variable septal distances on the last volution. Septal distance at the beginning of the last whorl is about 18–25°, but then there are two septa spaced 10 and 7°, respectively. The next distances are then 14°, 17°, 29°, and 19°. This irregularity, but with lower distances, is maintained toward the end of the phragmocone. The suture line is typical for *Tornoceras* with a shallow, asymmetric adventive lobe and a small external lobe (Fig. 3A).

Discussion. It is surprising that a representative of the genus *Tornoceras* is still present in such a high horizon in the middle Famennian. The morphology of the specimen, however, does not allow any other attribution. It does not possess any traces of ventrolateral grooves, as characteristic for *Phoenixites* Becker, 1993 that would place it into the group of tornoceratids that are more frequent in Fammenian rocks. The shallow adventive lobe is also a criterion that places the specimen in the genus *Tornoceras*, rather than *Phoenixites*.

Pernoceras Schindewolf, 1922

Pernoceras crebriseptum (Raymond, 1909)
Figs 2B–E, 3B–D

1909 *Tornoceras crebriseptum* Raymond: 153, pl. 8: figs 5–7 (only).
1909 *Tornoceras douglassi* Raymond: 155, pl. 8: figs 9–14.
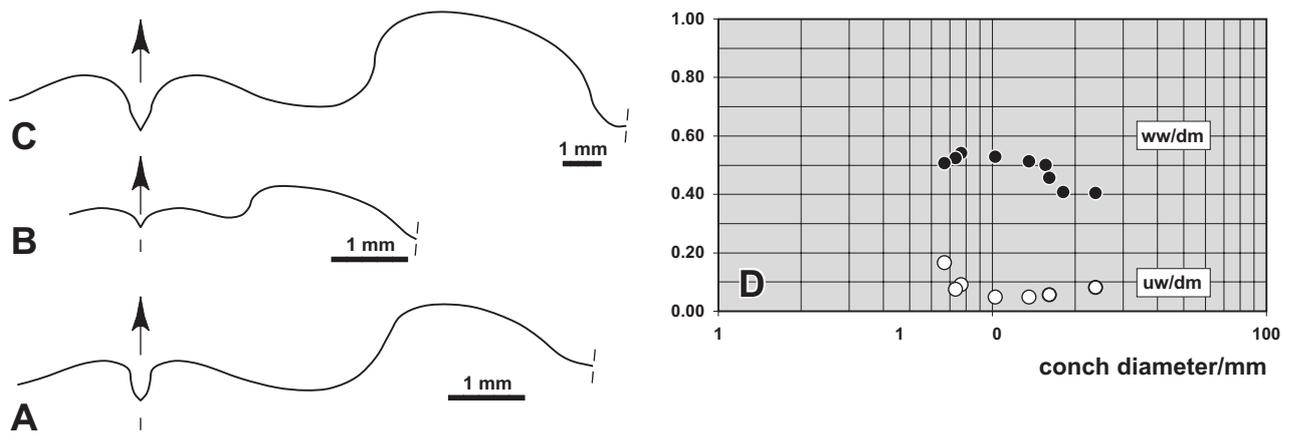1934 *Tornoceras crebriseptum*. – Schindewolf: 331, textfig. 1.

Fig. 3. Suture lines (A–C) and bivariate plots (D) of tornoceratin ammonoids from the Three Forks Shale. **A** – *Tornoceras* sp., specimen MB.C.9126 from Red Hill, at dm = 15.4 mm, ww = 6.1 mm, wh 8.7 mm, × 10; **B** – *Pernoceras crebriseptum* (Raymond, 1909), specimen MB.C.9145.1 from from Milligan Canyon (sample TF-3), at dm = 5.8 mm, ww = 3.3 mm, × 10; **C** – *Pernoceras crebriseptum* (Raymond, 1909), specimen MB.C.9140.1 from from Milligan Canyon (sample TF-2), at dm = 20.9 mm, ww = 9.3 mm, wh = 11.2 mm, × 15; **D** – Ontogenetic development of the whorl width index (ww/dm) and umbilical width index (uw/dm) in *Pernoceras crebriseptum* (Raymond, 1909).

1938 *Tornoceras (Tornoceras) crebriseptum.* – Miller: 149, pl. 38: figs 7–16.
1965 *Tornoceras (Tornoceras) crebriseptum.* – House: 115, pl. 11: figs 117–119.

H o l o t y p e . Specimen 464 (Carnegie Museum, Pittsburgh).

T y p e l o c a l i t y a n d h o r i z o n . Three Forks (Montana); probably basal portion (red shale) of the Trident Member of the Three Forks Shale (probably *Platyclymenia annulata* Zone, middle Famennian).

M a t e r i a l . 38 specimens, which range from 5 to about 35 mm phragmocone diameter from Red Hill and Milligan Canyon. Most of them are fragmentary or somewhat crushed.

D i a g n o s i s . Species of *Pernoceras* with thickly discoid conch at 8 mm dm (ww/dm = 0.50–0.55) and thinly discoid conch at 20 mm dm (ww/dm = 0.35–0.45). Umbilicus funnel-shaped, moderately wide in early juveniles and very narrow between 8 and 20 mm dm (uw/dm = 0.05–0.10). Septa widely spaced in juveniles and closely crowded in the adult stage; suture line with shallow, asymmetric adventive lobe. Steinkern smooth.

D e s c r i p t i o n . Little can be added to the comprehensive descriptions of the species provided by Raymond (1909), Miller (1938), and House (1965). The largest available specimen MB.C.9140.1 is, at 24 mm conch diameter, fully chambered and possesses 24 septa on the last volution, with a tendency towards crowding at the end. It is a discoid conch (ww/dm = 0.41) with a very narrow, funnel-shaped umbilicus. The umbilical wall stands diagonally and is separated from the flanks by a narrowly rounded margin. This is the widest point of the conch; the flanks converge towards the rounded venter (Fig. 2B). The suture line is typical for a tornoceratid ammonoid and possesses an asymmetric, rounded adventive lobe and a small, V-shaped external lobe (Fig. 3C).

The smaller specimens MB.C.9145.1 and MB.C.9145.2 (7 mm dm) closely resemble one another (Fig. 2C, D); they possess 13 and 12 septa, and have a conch morphology that closely resembles the large specimen MB.C.9140.1. They show with a rather conspicuous subangular umbilical margin. The suture line of specimen MB.C.9145.1 has a shallow adventive lobe (Fig. 3B).

D i s c u s s i o n . *Pernoceras crebriseptum* has affinities with species of the genus *Tornoceras* but differs by its open umbilicus from other species of that genus. Furthermore, its characteristic umbilical shape with the pronounced umbilical margin allows a clear separation from the stratigraphically older species. In this respect, it more closely resembles representatives of derived tornoceratids such as *Gundolficeras* Becker, 1995.

P. dorsatum (Wedekind, 1908) is a similar species, but has a slightly wider umbilicus and more flattened flanks.

Family **Prolobitidae** Wedekind, 1913

***Raymondiceras* Schindewolf, 1934**

***Raymondiceras simplex* (Raymond, 1909)**
Figs 2F–J, 4A–D

1909 *Prolobites simplex* Raymond: 152, pl. 7: figs 13, 14, pl. 8: figs 1–3.
1909 *Tornoceras crebriseptum* Raymond: pl. 8: fig. 8 (only).
1934 *Raymondiceras simplex.* – Schindewolf: 336, textfigs 2, 5a, 5b.
1938 *Raymondiceras simplex.* – Miller: 173, pl. 38: figs 1–6.

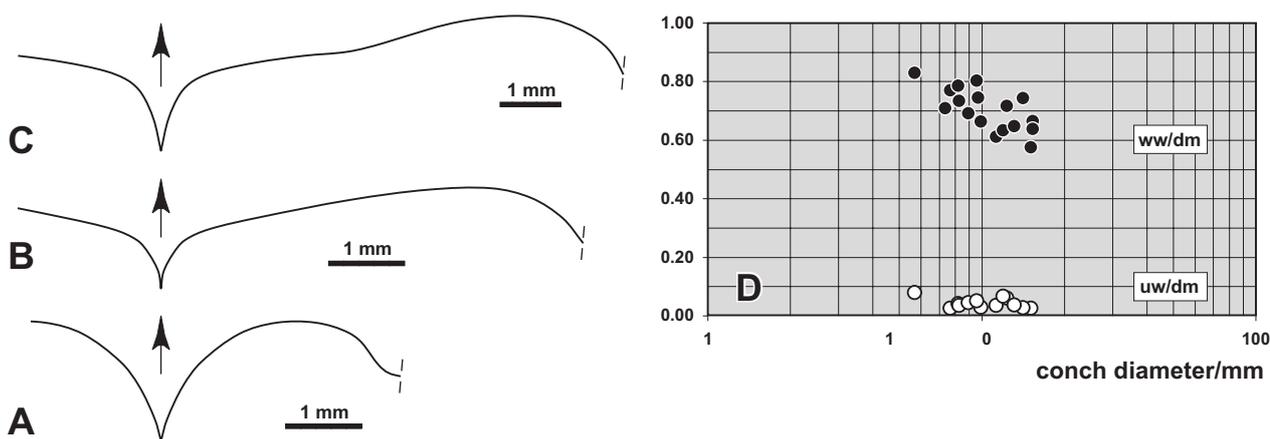T y p e s . Specimens 470 and 471 (Carnegie Museum, Pittsburgh).

Fig. 4. Suture lines (A–C) and bivariate plots (D) of *Raymondiceras simplex* (Raymond, 1909) from the Three Forks Shale. **A** – specimen MB.C.9146.1 from Milligan Canyon (sample TF-3), at dm = 5.2 mm, ww = 5.1 mm, wh = 2.9 mm, × 10; **B** – specimen MB.C.9134.3 from Red Hill, at dm = 10.3 mm, ww = 6.4 mm, wh = 6.2 mm, × 10; **C** – specimen MB.C.9134.1 from Red Hill, at wh = 7.6 mm, × 8; **D** – Ontogenetic development of the whorl width index (ww/dm) and umbilical width index (uw/dm).

Type locality and horizon. Three Forks (Montana); basal portion (red shale) of the Trident Member of the Three Forks Shale (probably *Platyclymenia annulata* Zone, Famennian).

Material. 48 specimens between 5 and 22 mm conch diameter are available from Milligan Canyon and Red Hill. Most of them are fragments of phragmocones.

Diagnosis. Species of *Raymondiceras* with thickly pachyconic conch at 6 mm dm (ww/dm > 0.80) and thinly pachyconic conch at 15 mm dm (ww/dm = 0.55–0.70). Umbilicus very narrow between 6 and 15 mm dm (uw/dm = 0.03–0.10). Septa widely spaced in juveniles and closely crowded in the adult stage; suture line always very simple without or with only barely visible adventive lobe. Ornament in the adult stage with fine spiral lines on the venter.

Description. The largest available specimen MB.C.9134.1 has a conch diameter of 22 mm and is laterally crushed (Fig. 2H). It can be regarded as a mature conch with more or less completely preserved body chamber, indicated by extreme septal crowding in the last segment of the phragmocone. Within an interval of only 60°, the distances of septa are reduced from about 20° to only 2.5°, a distance unique for all known Palaeozoic ammonoids. The course of the outer suture line is simple with a wide and low saddle on the flank and a small external lobe (Fig. 4C). The steinkern surface shows some indications of convex, periodically strengthened growth lines and about 25 spiral lines that are restricted to the outer flanks and the venter.

Several of the smaller specimens are well preserved and can are used for the description of the morphology. Specimen MB.C.9149.1 has a diameter of 12 mm and fully septate with 8 chambers. It is pachyconic (ww/dm = 0.72) with an almost closed umbilicus. The steinkern is smooth, and the suture line extends with a wide and low arch across the flanks (Fig. 2J). Specimen

MB.C.9134.2 (9 mm dm) has a narrower conch (ww/dm = 0.66) and 7 chambers (Fig. 2F), and the small individual MB.C.9146.1 (5.7 mm dm) is thickly pachyconic (ww/dm = 0.82) and possesses only five septa per whorl (Fig. 2G). The suture line of this specimen has a wide saddle on the flank and a V-shaped external lobe (Fig. 4A). There is no modification during ontogeny within these specimens.

Remarks. The species was comprehensively described and discussed by Raymond (1909), Schindewolf (1934), and Miller (1938), but these authors did not solve the phylogenetic relationships of this peculiar species. Miller & Furnish (1957) as well as Petersen (1975) treated *Raymondiceras* as the type of an own subfamily within the cheiloceratids. House (1962) regarded *Raymondiceras simplex* as a close relative to the Middle Devonian homeomorphic genus *Sobolewia* Wedekind, 1918. Later (House 1981), he treated it as a prolobitid ammonoid, as Raymond did, and put the two genera *Sobolewia* and *Raymondiceras* in the family Prolobitidae.

Becker (1993) placed *Raymondiceras simplex*, together with a number of early Famennian homeomorphs, into a subgenus of *Cheiloceras* Frech, 1897, and extended the taxon morphologically and stratigraphically. These cheiloceratids, which differ from typical *Cheiloceras* in the much higher aperture, were then summarised by Korn (in Korn & Ziegler 2002) in the new genus *Nehdenites* Korn, 2002, and *Raymondiceras* was there restricted to forms with a low aperture and convex sutures. At the same time, Korn (2002) described the new genus and species *Roinghites bottkei* from the *Platyclymenia annulata* Zone of

Kattensiepen in the Rhenish Mountains, being the first raymondiceratid from Central Europe. Here it was shown that there are good reasons to follow the interpretation that the taxa under consideration are secondarily simplified prolobitid ammonoids.

Suborder **Clymeniina** Hyatt, 1884
Family **Platyclymeniidae** Wedekind, 1914

Platyclymenia Hyatt, 1884

***Platyclymenia montana* n. sp.**
Figs 5A–D, 6A, B

Derivation of name. After the state of Montana, where the material was collected.

Holotype. Specimen MB.C.9129.1 (coll. Titus); illustrated here in Fig. 5A.

Type locatilty and horizon. Red Hill (Montana); basal portion (red shale) of the Trident Member of the Three Forks Shale (probably *Platyclymenia annulata* Zone, Famennian).

Material. 19 specimens between 15 and 52 mm conch diameter, many of them more or less complete phragmocones from Red Hill and Milligan Canyon. Another 43 fragments are available, but their assignment to the species is not certain.

Diagnosis. Species of *Platyclymenia* with discoid conch (ww/dm = 0.40); whorl width/whorl height ratio (ww/wh) = 1.00–1.25. Whorls rather rapidly expanding (WER = 2.05–2.20). Umbilicus moderately wide (uw/dm = 0.35–0.42). Ornament with 15–23 sharp, slightly concave ribs on the flanks. Growth lines with deep, semicircular ventral sinus. Septa widely spaced in juveniles and closely crowded in the adult stage; suture line with asymmetric, shallow lateral lobe and high external saddle.

Description. The larger specimens (up to 52 mm in conch diameter) of the species are not well preserved, unfortunately, because they are thickly encrusted by markasite aggregates or are somewhat crushed.

The smaller specimens are better preserved. Holotype MB.C.9129.1 is an incomplete specimen but displays the ontogenetic changes of the conch (Fig. 5A). There is a reduction of the whorl width/whorl height ratio from about 1.50 to 1.00 within a growth interval between 4 and 18 mm diameter. At the same time, the umbilical width ratio remains stable with 0.40–0.42. The whorl expansion rate increases from 2.00 at 4 mm dm to more than 2.20 in stages larger than 12 mm dm. The suture line of the specimen has a shallow and wide lateral lobe that occupies the entire flank; it continues into a broadly rounded, raised external saddle (Fig. 6A, B).

Paratype MB.C.9145.2 (Fig. 5B) has 20 mm conch diameter and displays the characteristics of the intermediate stage. The conch is discoid (ww/dm = 0.38) with a moderately wide umbilicus (uw/dm = 0.40). It has 17 ribs on the last whorl; they are strongest on the inner flank, where they almost form elongate nodes, and wedge out towards the venter. They extend in slightly forward direction with a barely visible lateral sinus across the flank. The phragmocone has 19 chambers on the last volution, but towards the aperture, there occurs a significant crowding. The suture line possesses a slightly asymmetric, shallow and wide lateral lobe and a raised external saddle.

Paratypes MB.C.9145.3 and MB.C.9145.4, both with approximately 17 mm conch diameter, are fully septate specimens (Fig. 5C, D). They are ornamented with 18–19 ribs, as in specimen MB.C.9145.2. The suture line of these two specimens also closely resemble that of specimen MB.C.9145.2, but there occur remarkable differences in septal spacing between specimens MB.C.9145.3 (with 22 chambers per whorl) and

▶

Fig. 5. Clymeniid ammonoids from the Three Forks Shale of Montana, all coll. Titus. **A** – *Platyclymenia montana* n. sp., holotype MB.C.9129.1 from Red Hill, ventral and lateral views, × 2; **B** – *Platyclymenia montana* n. sp., paratype MB.C.9145.2 from Red Hill, ventral and lateral views, × 2; **C** – *Platyclymenia montana* n. sp., paratype MB.C.9145.3 from Red Hill, dorsal and lateral views, × 2; **D** – *Platyclymenia montana* n. sp., paratype MB.C.9145.4 from Red Hill, dorsal and lateral views, × 2; **E** – *Platyclymenia* cf. *montana* n. sp., specimen MB.C.9138.1 from Milligan Canyon, lateral and ventral views, × 2; **F** – *Platyclymenia* sp., specimen MB.C.9142 from Milligan Canyon (sample TF-2), dorsal and lateral views, × 2; **G** – *Platyclymenia* sp., specimen MB.C.9130.1 from Red Hill, lateral view, × 1; **H** – *Pleuroclymenia americana* (Raymond, 1907), specimen MB.C.9131.1 from Red Hill, dorsal and lateral views, × 1; **I** – *Pleuroclymenia americana* (Raymond, 1907), specimen MB.C.9131.2 from Red Hill, dorsal and lateral views, × 1; **J** – *Pleuroclymenia americana* (Raymond, 1907), specimen MB.C.9131.4 from Red Hill, dorsal and lateral views, × 1; **K** – *Pleuroclymenia americana* (Raymond, 1907), specimen MB.C.9139.1 from Milligan Canyon, dorsal and lateral views, × 2; **L** – *Pleuroclymenia americana* (Raymond, 1907), specimen MB.C.9131.5 from Red Hill, ventral and lateral views, × 2; **M** – *Pleuroclymenia americana* (Raymond, 1907), specimen MB.C.9131.3 from Red Hill, ventral and lateral views, × 1; **N** – *Pleuroclymenia americana* (Raymond, 1907), specimen MB.C.9147.2 from Milligan Canyon (sample TF-3), lateral and ventral views, × 2; **O** – *Pleuroclymenia americana* (Raymond, 1907), specimen MB.C.9147.1 from Milligan Canyon (sample TF-3), dorsal and lateral views, × 2; **P** – *Carinoclymenia* sp., specimen MB.C.9135 from Red Hill, ventral and lateral views, × 2.
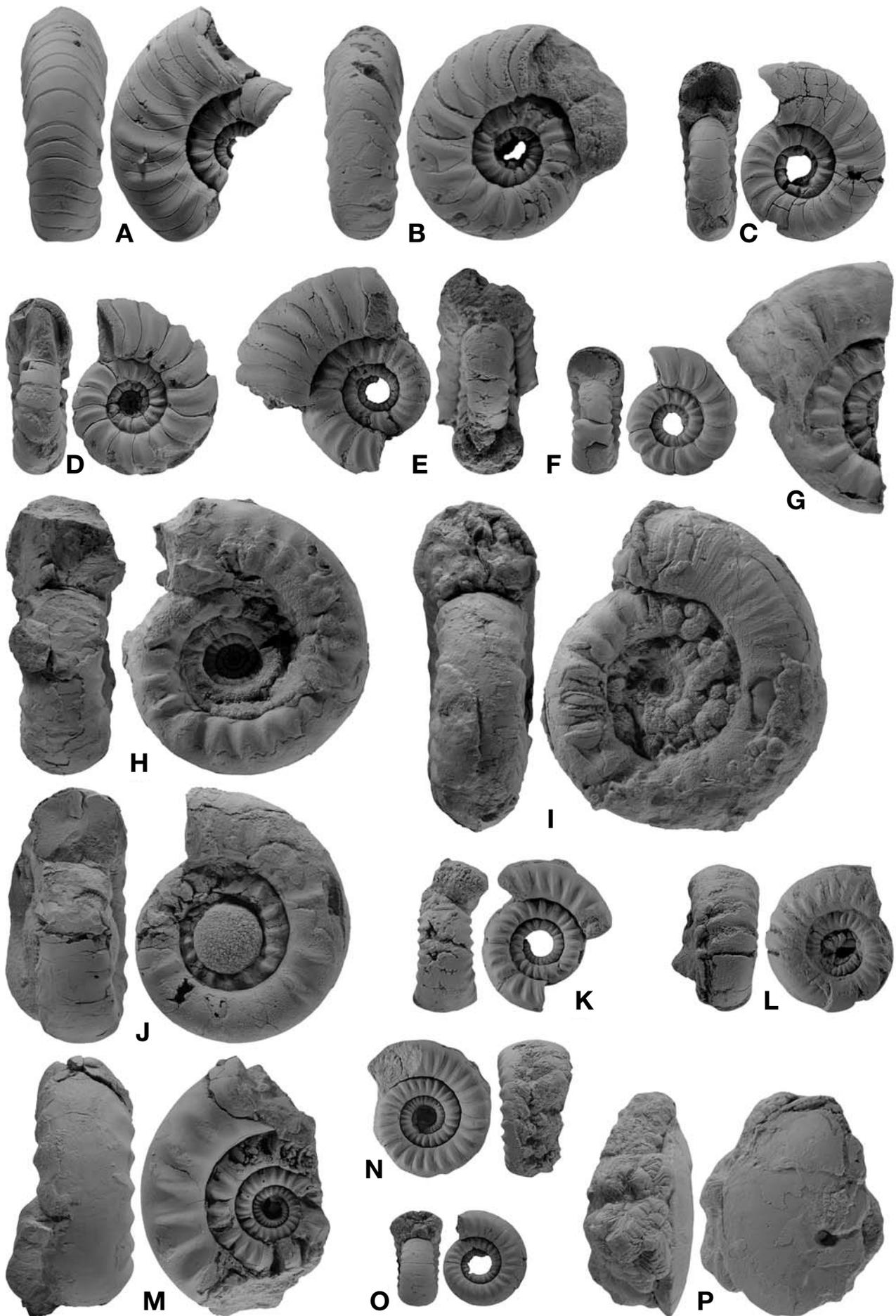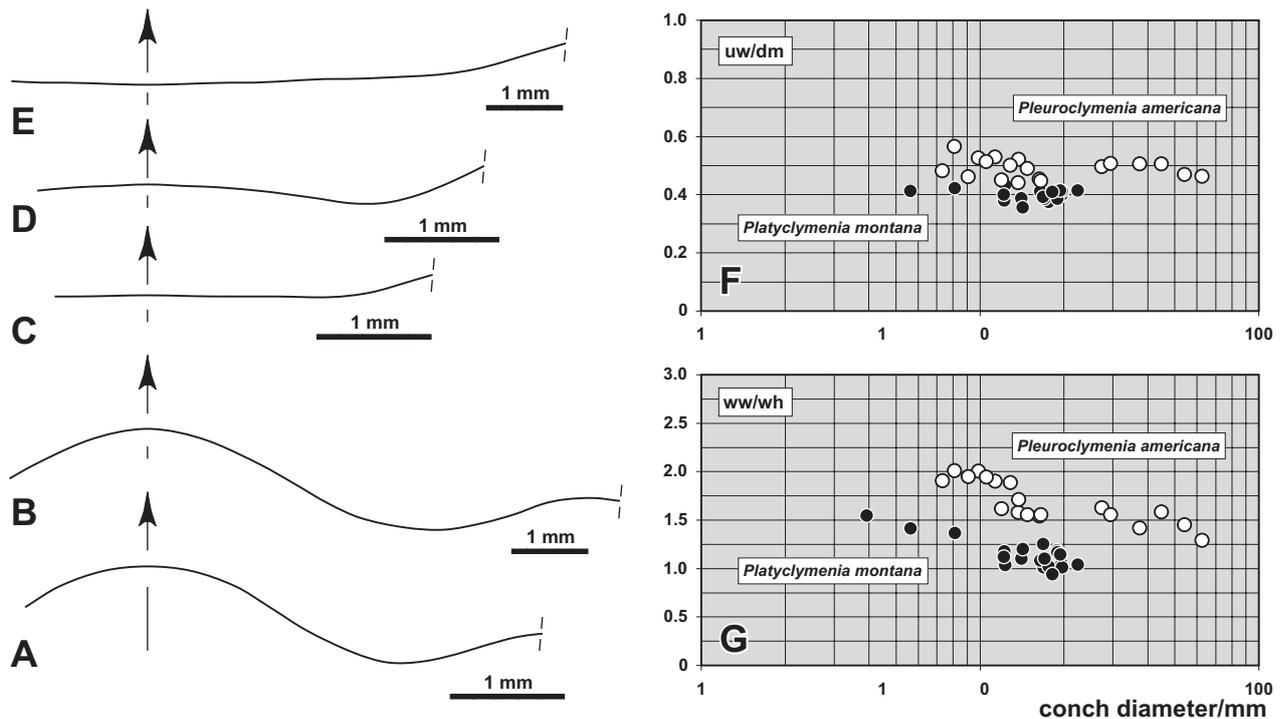

Fig. 6. Suture lines (A–E) and bivariate plots (F, G) of *Platyclymenia montana* n. sp. and *Pleuroclymenia americana* (Raymond, 1907) from the Three Forks Shale. **A** – *Platyclymenia montana* n. sp., holotype MB.C.9129.1 from Red Hill, at dm = 12.8 mm, ww = 4.7 mm, wh = 4.4 mm, × 15; **B** – same specimen, at dm = 12.8 mm, ww = 7.9 mm, wh = 8.2 mm, × 10; **C** – *Pleuroclymenia americana* (Raymond, 1907), specimen MB.C.9147.1 from Milligan Canyon (sample TF-3), at dm = 8.7 mm, ww = 4.5 mm, wh = 2.2 mm, × 15; **D** – *Pleuroclymenia americana* (Raymond, 1907), same specimen MB.C.9139.1 from Milligan Canyon, at dm = 9.9 mm, ww = 5.0 mm, wh = 2.9 mm, × 15; **E** – *Pleuroclymenia americana* (Raymond, 1907), specimen MB.C.9131.4 from Red Hill, at ww = 12.3 mm, wh = 6.9 mm, × 10; **F** – ontogenetic development of the umbilical width index (uw/dm) and differences between *Platyclymenia montana* n. sp. and *Pleuroclymenia americana* (Raymond, 1907); **G** – ontogenetic development of the whorl width index (ww/wh) and differences between *Platyclymenia montana* n. sp. and *Pleuroclymenia americana* (Raymond, 1907).

specimen MB.C.9145.4 (with 14 chambers per whorl).

Specimen MB.C.9138.1 with 20 mm conch diameter is a specimen that possibly belongs to another species (Fig. 5E). It belongs to the more thickly discoid individuals of *Platyclymenia* (ww/wh = 1.35 at 19 mm dm), and has a moderately wide umbilicus (uw/dm = 0.43). It displays significant crowding of septa; the penultimate whorl with 13 mm conch diameter has 10 chambers, and only one quarter of the following whorl has already 10.

Septal crowding is common in many of the specimens. Holotype MB.C.9129.1, for instance, has septa that stand in distances of 15–20° at 12 mm conch diameter. One whorl later, at about 22 mm dm, they have distances of only 5–7°.

Discussion. The new species belongs, with a uw/dm ratio of 0.40, to the more narrowly umbilicate species of the genus. This character, combined with the high aperture (WER = 2.10–2.20), makes the species easily distinguishable from most of the other species. Species with a

similarly narrow umbilicus are, from the Holy Cross Mountains of Poland, *P. inflata* Czarnocki, 1989 with an even narrower umbilicus (uw/dm = 0.35), *P. limata* Czarnocki, 1989 and *P. laxata* Czarnocki, 1989, both insufficiently described and probably with much finer ribbing. *P. nodosa* Gümbel, 1863 and *P. arieticostata* Schindewolf, 1923 from Franconia are similar in the width of the umbilicus, but have a compressed whorl cross section, in contrast to the depressed or circular in the new species. *P. arieticostata* has stronger ribs than *P. montana*, and *P. nodosa* possesses node-like ribs. Finally, the Moroccan *P. ibnsinai* Korn, 1999 resembles the new species in umbilical width and apertural height, but this has also more compressed whorls. The ww/wh ratio is 0.25–0.28 in *P. ibnsinai*, but 0.38–0.42 in *P. montana* at about 22 mm conch diameter.

Platyclymenia montana can easily be separated from the co-occurring *Pleuroclymenia americana* by its laterally compressed whorl section and the much higher external saddle of the suture line.

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Platyclymenia sp.
Fig. 5E–H

M a t e r i a l. One small complete and three larger fragmentary specimens are available from Red Hill and Milligan Canyon. They range between 12 and approximately 60 mm in diameter.

D e s c r i p t i o n. Specimen MB.C.9130.1 (Fig. 5G) is a fragment of a specimen with about 45 mm diameter; it has laterally compressed whorls (ww/dm = 0.90) and a wide umbilicus (uw/dm = 0.47). It bears 9 ribs on the penultimate half whorl; they are restricted to the flanks and reach almost to the umbilical seam.

The small, well preserved specimen MB.C.9142 (Fig. 5F) has 12.5 mm diameter and the conch ratios ww/dm = 0.45, ww/wh = 1.40, uw/dm = 0.45. It therefore does not fall in the range of the other platyclymeniid species from the Three Forks Shale. The whorl cross section is ventrally depressed, oval-shaped and widest near the umbilicus. The last volution possesses 19 sharp ribs; they extend with a shallow concave sinus across the flank and disappear suddenly ventrolaterally. The suture line has a shallow lateral lobe and a raised external saddle.

D i s c u s s i o n. The material is too insufficient to be attributed to a distinct species. It has some similarity with *Platyclymenia annulata* (Münster, 1832), conch shape and ornament.

Pleuroclymenia Schindewolf, 1934

Pleuroclymenia americana (Raymond, 1907)
Figs 5H–O, 6C–E

1907 *Pleuroclymenia americana* Raymond: 118, textfig. 1.
1909 *Pleuroclymenia americana*. – Raymond: 150, pl. 6: fig. 10–13, pl. 7: fig. 2, 3 (only).
1909 *Pleuroclymenia polypleura* Raymond: 151, pl. 7: figs 4–6.
1934 *Platyclymenia* (*Pleuroclymenia*) *americana*. – Schindewolf: 340, textfigs 10, 11.
1934 ?*Platyclymenia* (*Pleuroclymenia*) *polypleura*. – Schindewolf: 344.
1938 *Platyclymenia* (*Pleuroclymenia*) *americana*. – Miller: 196, pl. 39: figs 1–7.
1938 *Platyclymenia* (*Pleuroclymenia*) *polypleura*. – Miller: 196, pl. 39: figs 11–16.
1962 *Platyclymenia* (*Pleuroclymenia*) *americana*. – House: pl. 47: fig. 10.
1962 *Platyclymenia* (*Pleuroclymenia*) *polypleura*. – House: pl. 47: fig. 7.

T y p e s. Four syntypes are stored in the Carnegie Museum at Pittsburgh, Pennsylvania, numbered 456–559. Neither Raymond (1907, 1909) nor Miller (1938), in his revision, designated a lectotype, and hence the largest and most complete specimen (456, the first specimen figured by Raymond and later illustrated by House 1962) of the series is proposed here for the lectotype.

T y p e l o c a l i t y a n d h o r i z o n. Three Forks (Montana); basal portion (red shale) of the Trident Member of the Three Forks Shale (probably *Platyclymenia annulata* Zone, Famennian).

M a t e r i a l. 21 specimens are available from Red Hill and Milligan Canyon; they range in their sizes from a few millimetres up to 55 mm in diameter. Additionally, 70 fragments are available.

D i a g n o s i s. Species of *Pleuroclymenia* with thickly discoid conch at 10 mm dm (ww/dm = 0.50–0.60) and thinly discoid conch at 60 mm dm (ww/dm = 0.35–0.40). Whorls twice as wide as high at 10 mm dm (ww/wh = 1.80–2.10), decreasing to 1.30–1.60 at 25–60 mm dm. Umbilicus wide throughout ontogeny (uw/dm = 0.45–0.55). Ornament with 18–25 sharp, almost linear ribs on the flanks. Growth lines with deep, semicircular ventral sinus. Septa widely spaced in juveniles and closely crowded in the adult stage; suture line always very simple with very shallow lateral lobe.

D e s c r i p t i o n o f n e w m a t e r i a l. Specimen MB.C.9131.1 (Fig. 5H) is the second-largest available specimen; it has a conch diameter of 55 mm and is, apart from some markasite encrustation, well preserved. It is a discoid conch (ww/dm = 0.40) with a wide umbilicus (uw/dm = 0.48) and ventrally depressed, wide whorls (ww/wh = 1.45). The ornament of the last four whorls can be studied, allowing the observation of changes in the shape of the ribs. On these four whorls, the rib number is almost constant, with a slight decrease from 21 to 19. On the inner whorls, however, the ribs are much sharper. The last whorl shows weakened ribs that are strongest on the inner flank and wedge out towards the venter and the umbilical wall. They extend in almost linear course across the flanks. Some remains of the shell are visible on this specimen. There are fine growth lines following the almost linear course of the ribs, and turn back to form a semicircular, rather deep ventral sinus. The inner whorls display ribs, which run concavely in a very shallow sinus across the flanks.

Specimen MB.C.9131.2 (Fig. 5I) is the largest individual with 62 mm diameter. Only portions of the last volution are free from secondary encrustation, and these portions show the transition from the ribbed stage into the adult non-ribbed stage. At the end of the last preserved whorl, there are rough and occasionally strengthened growth lines that run with slightly backward direction across the flank and form a rather deep ventral sinus.

Specimen MB.C.9131.3 (Fig. 5M) shows the pre-adult morphology and ornament of the outer whorl (appr. 48 mm dm). The number of ribs decreases from 26 (appr. 9 mm dm) to about 20 (at 30 mm dm). The fourth rather large specimen MB.C.9131.4 differs in a lower number of

ribs, being 16 on one whorl with a maximum diameter of 36 mm dm.

The small specimens MB.C.9147.1 (9 mm dm) and MB.C.9147.2 (12.8 mm dm) display the juvenile conch morphology that is characterised by strongly depressed whorls with flattened venter and with whorls that are almost twice as wide as high (Fig. 5O, N). They have a trapezoidal cross section and are widest at the transition from the flank to the venter. Both specimens have 24 ribs on the last preserved whorl; these are barely concave towards the aperture and restricted to the flanks. Both specimens show the ventral suture line, which runs almost straight without any lobes and saddles.

The suture lines of specimens MB.C.9147.1 and MB.C.9139.1 show, at 9 and 10 mm conch diameter, a very shallow lateral lobe. This outline with an almost linear course across the venter is also present in the larger specimen MB.C.9131.4 at approximately 25 mm dm (Fig. 6C–E).

Discussion. Raymond (1909, p. 151) as well as Miller (1938, p. 198) separated the two species *P. americana* and *P. polypleura* on the base of the number of ribs, a criterion questioned by Schindewolf (1934). Miller pointed out that there are practically no differences in conch morphology between the two forms. The new material shows that a continuous range in the rib number from about 18 to 30, with most specimens being close to 24. Furthermore, there occurs a more or less well-developed reduction of the number of ribs during ontogeny. The second criterion, i.e., the number of phragmocone chambers per whorl, does not separate two species. Septal spacing has been shown to depend partially on environmental conditions and is highly variable in the material, and it is not possible to find a correlation of number of septa and number of ribs, as stated by Miller (1938, p. 199). As some specimens show, there are even significant differences within the whorls of a single individual.

Many other species of *Pleuroclymenia*, such as *P. ohioensis* House, Gordon & Hlavin, 1986 are usually narrower umbilicate than *P. americana*. The type species *P. costata* (Lange, 1929) resembles the American species in its conch dimensions and ornament, but becomes much earlier unribbed in ontogeny. *P. evoluta* (Czarnocki, 1989) and *P. cyclocostata* (Czarnocki, 1989) are very similar in shape and ornament, but differ in the presence of constrictions.

Family **Carinoclymeniidae** Bogoslovsky, 1975

Carinoclymenia **Bogoslovsky, 1965**

Carinoclymenia **sp.**
Fig. 5P

Material. One fragmentary specimen with approximately 22 mm conch diameter from Red Hill.

Description. The single specimen MB.C.9135 is a flat discoid conch with a sharp venter and a very narrow umbilicus. It is a fragment of the body chamber that is almost smooth and does not show any traces of an ornament. In these characters, it closely resembles *C. beuelensis* (Lange, 1929), but the specimen is too poorly preserved for a distinct attribution.

Septum distances of the ammonoids

A common feature shared by all of the specimens, regardless their attribution to different ammonoid clades, is the striking variability in spacing of the septa. Septal crowding is a character that is usually connected with adultness of specimens and is often used as a criterion for terminal growth. In fact, extreme septal approximation was shown for instance by Bogoslovsky (1969) and Korn et al. (1984) for the mid-Famennian genus *Prolobites* Wedekind, 1913, in which reduction of septal spacing can be linked with adult modifications of the terminal aperture, i.e., the deceleration of accretion of shell material. In this case, it can be assumed that temporal production of new septa is not slowed down; it is only the spaces that became shorter.

It is difficult to tell if such conditions are present in any case of septal approximation in ammonoids. To test of such a hypothesis, extremely well-preserved material has to be examined, which shows septal crowding and also aperture modifications at corresponding diameters. It is likely, however, that septal crowding is, in most of the cases, correlated with slower accretion at the aperture. This provides a proxy for ecological conditions during the life time of the ammonoid individuals.

Septal spacing can best be documented for *Platyclymenia montana* n. sp., of which the specimens MB.C.9145.3, MB.C.9145.4, and MB.C.9142 were analysed (Fig. 7). These three specimens show very different patterns in their septal distances; a common feature is just the general
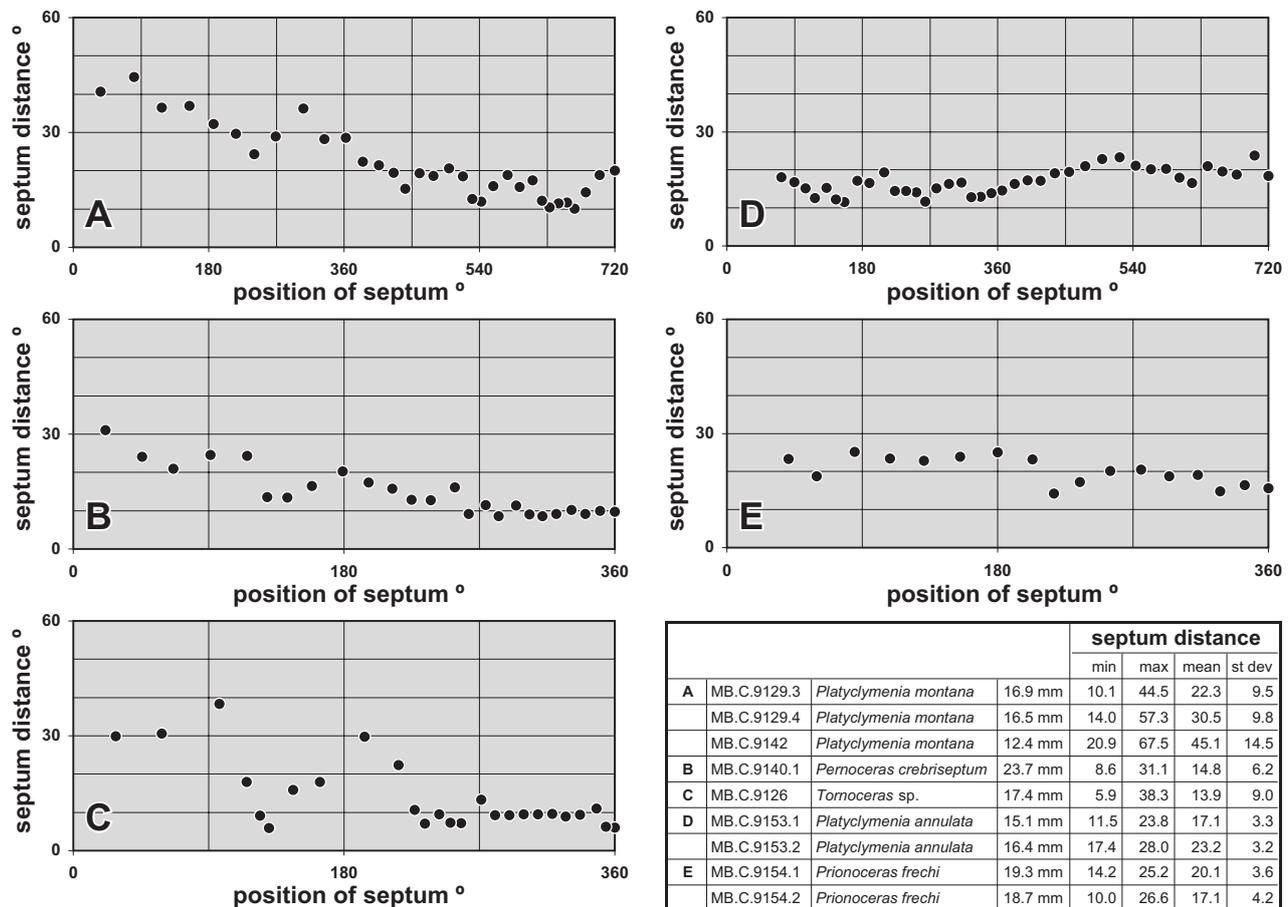
Fig. 7. Septum distances of ammonoids from the Three Forks Shale of Montana and time equivalents from the *Platyclymenia annulata* Zone of Madène el Mrakib (Anti-Atlas, Morocco). **A** – *Platyclymenia montana* n. sp., paratype MB.C.9145.3 from Red Hill; **B** – *Pernoceras crebriseptum* (Raymond, 1909), specimen MB.C.9140.1 from Milligan Canyon; **C** – *Tornoceras* sp., specimen MB.C.9126 from Red Hill; **D** – *Platyclymenia annulata* (Münster, 1832), specimen MB.C.9153.1 from Madène el Mrakib; **E** – *Prionoceras frechi* (Wedekind, 1913), specimen MB.C.9154.1 from Madène el Mrakib.

ontogenetic decrease of spaces between the septa. This decrease can be largely continuous as in specimen MB.C.9145.3 or strikingly irregular as in specimen MB.C.9145.4. In the latter specimen, there occur dramatic fluctuations with discontinuously appearing phases of extreme septal crowding.

Reduction of septal spacing during ontogeny can also be seen in the other species within the assemblage. In all the species, septa are arranged in distances of 10° or even less in the adult stage (Fig. 7B, C). Such a close spacing is very unusual for late Devonian ammonoids.

A comparison with time-equivalent material from other localities demonstrates that the specimens from the Three Forks differ at least markedly from material from Madène el Mrakib (Ma'der, Morocco). Specimens of *Platyclymenia annulata* (Münster, 1832) from that locality may show some irregularities in septal spacing (Fig. 7D), but to a much lower degree than seen in the platyclymeniids from Montana. *Pernoceras*

and *Raymondiceras* are not known from this North African assemblage, but *Prionoceras frechi* (Wedekind, 1913), for instance, does not show septal crowding (Fig. 7E). Variation of septal spacing during one or two volutions can be expressed in the minimum and maximum, as well as the standard deviation. This value ranges between 3.2 and 4.2 in the analysed Moroccan specimens of *Platyclymenia annulata* and *Prionoceras frechi*, but amounts between 6.2 and 14.5 in the specimens of different species from the Three Forks.

Conclusions

The ammonoid fauna of the Three Forks Shale of Montana is one of the most diverse Famennian assemblages in the New World and deserves attention for its stratigraphic position and its genus composition in a palaeobiogeographic context. The co-occurrence of the genera *Platycly-*

menia, *Pleuroclymenia*, and *Carinoclymenia* is a good evidence for a position within the middle Famennian *Platyclymenia annulata* Zone, from which assemblages with morphologically similar species are particularly well known from Central and Eastern Europe and North Africa. On the other hand, the fauna from the Three Forks also contains the genera *Tornoceras* and *Pernoceras*, which are only known from stratigraphically older deposits of the Old World, i.e., the early Famennian. *Raymondiceras* is possibly an endemic genus in North America, but close relatives are already known from time-equivalent horizons of Australia, the South Urals, and the Rhenish Mountains. This pattern in the distribution of the discussed genera speaks for a connection of the shelf regions, and differences of the compositions may largely be caused by ecological reasons.

The Three Forks assemblage appears to be unique in the fact that all ammonoid taxa display significant irregularities in the spacing of the septa, regardless their systematic position. Septal crowding does not only occur as a phenomenon of terminal growth, where it is particularly well known, but also in intermediate stages, followed by phases with wider septal interspaces. Such patterns speak for instable conditions during the lifetime of the ammonoids.

Acknowledgements

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Appendix

Conch dimensions and ratios of ammonoids from the Three Forks Shale (dm, conch diameter; ww, whorl width; wh, whorl height; uw, umbilical width; ah, apertural heigh; WER, whorl expansion rate; IZR, imprint zone rate).

	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZR
Tornoceras sp.										
MB.C.9126	17.4	6.6	10.0	0.0	5.4	0.38	0.66	0.00	2.09	0.47
	12.3	5.5	6.9	0.0	–	0.45	0.80	0.00	–	–
Pernoceras crebriseptum (Raymond, 1909)										
MB.C.9140.1	23.8	9.6	12.6	1.9	7.2	0.41	0.76	0.08	2.06	0.43
MB.C.9145.3	16.1	7.4	9.9	0.9	–	0.46	0.75	0.06	–	–
MB.C.9133.1	13.6	7.0	7.2	0.7	–	0.51	0.97	0.05	–	–
MB.C.9136.3	10.3	5.4	5.9	0.5	–	0.53	0.92	0.05	–	–
MB.C.9136.1	7.7	4.2	4.2	0.7	–	0.54	1.00	0.09	–	–
MB.C.9136.2	7.3	3.9	3.9	0.6	–	0.52	0.98	0.07	–	–
MB.C.9145.2	6.7	3.4	3.3	1.1	–	0.51	1.04	0.17	–	–
Raymondiceras simplex (Raymond, 1909)										
MB.C.9146.4	15.3	9.8	7.9	–	–	0.64	1.24	–	–	–
MB.C.9134.4	15.1	8.7	7.8	0.4	4.1	0.58	1.12	0.03	1.89	0.47
MB.C.9146.5	13.1	8.5	7.4	0.5	–	0.65	1.15	0.04	–	–
MB.C.9149.1	12.3	8.8	6.6	0.8	3.0	0.72	1.33	0.06	1.74	0.55
MB.C.9140.3	11.9	7.6	6.8	0.8	–	0.63	1.12	0.07	–	–
MB.C.9134.3	11.3	6.9	5.6	0.4	2.9	0.61	1.23	0.04	1.80	0.49
MB.C.9134.2	9.9	6.6	5.4	0.3	2.7	0.66	1.22	0.03	1.91	0.49
MB.C.9146.2	9.6	7.7	5.4	0.5	–	0.80	1.44	0.05	–	–
MB.C.9134.7	8.2	6.1	4.9	0.3	–	0.74	1.24	0.04	–	–
MB.C.9146.1	5.7	4.7	–	0.5	–	0.83	–	0.08	–	–
Platyclymenia montana n. sp.										
MB.C.9129.12	22.4	8.8	8.4	9.3	7.2	0.39	1.04	0.42	2.17	0.15
MB.C.9129.13	19.7	7.5	7.4	8.1	–	0.38	1.01	0.41	–	–
MB.C.9129.2	19.6	7.4	7.0	7.9	–	0.38	1.05	0.40	–	–
MB.C.9141.2	19.4	7.6	6.7	8.1	–	0.39	1.14	0.42	–	–
MB.C.9129.11	18.9	7.5	6.3	7.7	5.4	0.40	1.19	0.41	1.98	0.14
MB.C.9129.8	17.6	6.6	6.4	6.6	–	0.37	1.02	0.38	–	–
MB.C.9129.9	17.0	5.9	5.3	6.6	–	0.34	1.10	0.39	–	–
MB.C.9129.3	16.9	6.2	6.1	6.6	5.4	0.37	1.01	0.39	2.14	0.13
MB.C.9129.4	16.5	5.9	5.5	6.8	5.0	0.36	1.08	0.41	2.07	0.08
MB.C.9138.2	16.8	7.2	5.7	6.6	–	0.43	1.26	0.39	–	–
MB.C.9138.4	14.1	5.9	5.3	5.5	–	0.42	1.10	0.39	–	–
MB.C.9129.1	18.1	6.8	7.2	7.4	6.0	0.37	0.94	0.41	2.21	0.18
	12.2	5.0	4.5	4.9	4.1	0.41	1.12	0.40	2.26	0.09
	8.1	3.8	2.8	3.4	2.5	0.46	1.37	0.42	2.08	0.10
	5.6	2.9	2.1	2.3	1.7	0.52	1.42	0.41	2.06	0.17
	3.9	2.2	1.4	–	1.1	0.56	1.55	–	1.97	0.20

	dm	ww	wh	uw	ah	ww/dm	ww/wh	uw/dm	WER	IZW
Pleuroclymenia americana (Raymond, 1907)										
MB.C.9131.2	62.5	22.9	17.7	29.0	–	0.37	1.29	0.46	–	–
MB.C.9131.1	54.1	21.8	15.1	25.5	–	0.40	1.45	0.47	–	–
MB.C.9131.4	37.4	14.7	10.3	18.9	9.3	0.39	1.42	0.51	1.76	0.11
MB.C.9131.3	27.4	13.0	8.0	13.6	–	0.47	1.63	0.50	–	–
MB.C.9147.3	16.5	8.6	5.5	7.4	–	0.52	1.56	0.45	–	–
MB.C.9143.2	16.3	7.2	4.6	7.4	–	0.44	1.54	0.45	–	–
MB.C.9143.5	14.8	6.6	4.3	7.3	–	0.45	1.56	0.49	–	–
MB.C.9131.8	13.8	7.2	4.2	7.2	–	0.52	1.71	0.52	–	–
MB.C.9131.5	13.7	6.7	4.3	6.1	–	0.49	1.58	0.44	–	–
MB.C.9147.2	12.8	6.8	3.6	6.4	3.2	0.53	1.89	0.50	1.77	0.12
MB.C.9143.1	11.3	6.6	3.4	6.0	–	0.58	1.90	0.53	–	–
MB.C.9139.1	9.9	5.0	2.5	5.2	–	0.51	2.01	0.53	–	–
MB.C.9139.2	8.1	4.7	2.3	4.6	–	0.57	2.01	0.57	–	–
MB.C.9147.1	9.1	4.6	2.4	4.2	2.1	0.50	1.95	0.46	1.67	0.13