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Biostratigraphy and *Inoceramus* survival across the Cenomanian–Turonian (Cretaceous) boundary in the Ram River section, Alberta, Canada

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ABSTRACT:

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The biostratigraphy of the uppermost Cenomanian – Lower Turonian succession in the lower part of the Blackstone Formation exposed in the Ram River (Alberta, Canada), is interpreted in terms of the standard inoceramid/ammonite zonation of the interval. Four successive inoceramid zones are recognized, those of *Inoceramus pictus*, *Mytiloides puebloensis*, *M. kossmati*, and *M. mytiloides*, as established in the stratotype section at Pueblo, Colorado. Their correlation to Pueblo is confirmed by ammonite data.

The mid-Early Turonian zone of *M. kossmati* yielded an assemblage of *Inoceramus*, with species showing close affinity to the latest Cenomanian lineages. This multi-species sample proves the survival of *Inoceramus* lineages into the otherwise *Mytiloides*-dominated Early Turonian, and indicates that their disappearance from the record of the North American Western Interior was not because of their extinction. It is suggested that the apparent lack of *Inoceramus* in Lower Turonian strata is due to an extremely low population abundance in the Early Turonian sea.

Key words: Cenomanian–Turonian boundary; Mytiloides; Ammonites; *Inoceramus* survival; Biostratigraphy; Western Interior Basin; Canada.

INTRODUCTION

There is a simple succession of Inoceramidae across the Cenomanian–Turonian boundary at the genus level in the North American Western Interior (and in at least the entire Euramerican region; following the biogeographic classification of Kauffman 1973). At the end of the Cenomanian, the genus *Inoceramus* disappeared (Tröger 1981, 1989), and all its Cenomanian species were regarded as victims of the Cenomanian/Turonian boundary extinction(s) (e.g., Kauffman *et al*. 1978, 1993; Elder 1989, 1991; Harries 1993; Kauffman and Harries 1996) although rare records of *I. pictus* are known from the earliest Turonian (e.g., Gale et al. 2005; Ifrim and Stinnesbeck 2008). At the beginning of the Turonian, *Inoceramus* was replaced by the rapidlyevolving *Mytiloides* clade, which dominated the Lower Turonian inoceramid record. The genus *Inoceramus* re-enters the record in the Euramerican region in the latest Early Turonian, and once more becomes the dominant genus-level taxon of the family (Tröger 1989; Kauffman *et al*. 1993; Voigt 1995). *Inoceramus* appears to be absent from the Early Turonian for a span of about 0.7 Myr (based on ages in Ogg and Hinnov 2012; see also Harries 1993). In its Early Turonian history, *Inoceramus* therefore behaves as a classic Lazarus taxon (Jablonski 1986; Harries 1996; Wignall and Benton 1999), although what happened to the genus during its apparent hiatal time remains unclear (see discussion in Harries 1993; Kauffman and Harries 1996): Did it survive in a refugium; is the absence due to the poor quality of the fossil record; did it thrive in such small populations that the chance of finding them in the fossil record is extremely low? Other questions appear when this problem is considered at the species level: Did only one, or numerous *Inoceramus* lineages survive; when did the speciation (or pseudospeciation) take place; do the events observed in the North American Western Interior extend beyond that region? Finally, to what extent is the disappearance of the Cenomanian *Inoceramus* species due to extinction?

This report describes and discusses the significance of a mid-Early Turonian sample of the genus *Inoceramus* that was found in the mid-Lower Turonian part of the Cenomanian–Turonian boundary succession exposed in the Ram River, west-central Alberta, Canada. This discussion is preceded by a biostratigraphic analysis of the sequence, based on the *Mytiloides* and ammonites recovered from the succession. This is the first recognition of the precise inoceramid zonation across the Cenomanian–Turonian boundary in the Canadian part of the Western Interior. The location of the succession in the context of the geodynamic model for the western Alberta foredeep is discussed below.

GEOLOGICAL SETTING

During the Cretaceous, westward migration of the North American Plate relative to the oceanic Farallon Plate led to the obduction of exotic terranes onto the continental margin above an east-dipping subduction zone. The resulting compressive stress led to crustal shortening and thickening, and to uplift of the Rocky Mountain Cordillera (e.g. Price 1973, 1994; Evenchick *et al*. 2007). Isostatic subsidence of the lithosphere in response to the load of the thickened crust produced an elongate, retro-arc foreland basin that extended the length of North America. The foreland basin was of the order of 300–500 km wide between the deformation front and the crest of the forebulge (e.g. Beaumont 1981; Plint *et al*. 2012b). The fold-and-thrust belt to the west provided an abundant supply of clastic sediment, derived from uplifted Precambrian and Paleozoic rocks of the former passive continental margin, as well as from up-thrust metamorphic and igneous rocks from lower crustal levels.

Numerical modelling of the relationship between foreland basin subsidence, sea-level and facies distributions (Jordan and Flemings 1991), has shown, in marine basins, that episodes of rapid subsidence resulted in the trapping of sand and gravel in the proximal foredeep, resulting in the vertical stacking of nearshore sandstone bodies close to the orogen. Only muddy sediment was transported, mainly through storm-related processes, to the more offshore part of the basin. When the rate of flexural subsidence was reduced, the rate of sediment supply was then able to match or exceed the accommodation rate allowing a thin sheet of nearshore sandstone to prograde far into the basin. The predictions of these numerical models have been substantiated through detailed stratigraphic studies (e.g. Varban and Plint 2008a, b; Plint *et al.* 2012b; Buckley *et al*. 2015), that show that units of marine mudstone have a pronounced wedge-shape, indicative of rapid syn-depositional subsidence, whereas shallow-marine and strandplain sandstones have a much more tabular geometry, indicative of deposition during periods of lower subsidence rate. The Blackstone Formation (and coeval Kaskapau Formation further north), is therefore interpreted as a syntectonic wedge deposited during a phase of relatively rapid flexural subsidence. Nevertheless, the rocks preserve a continuous record of shallow-marine deposition across a very low-gradient, wave-graded ramp and it is therefore inferred that the rates of sediment supply and subsidence were closely balanced during Late Cenomanian to Early- to Middle Turonian time, and that water depth was never very great. Recent estimates suggest storm wave base may have lain at about 50-70 m (Varban and Plint 2008a; Plint *et al*. 2012a; Plint 2014).

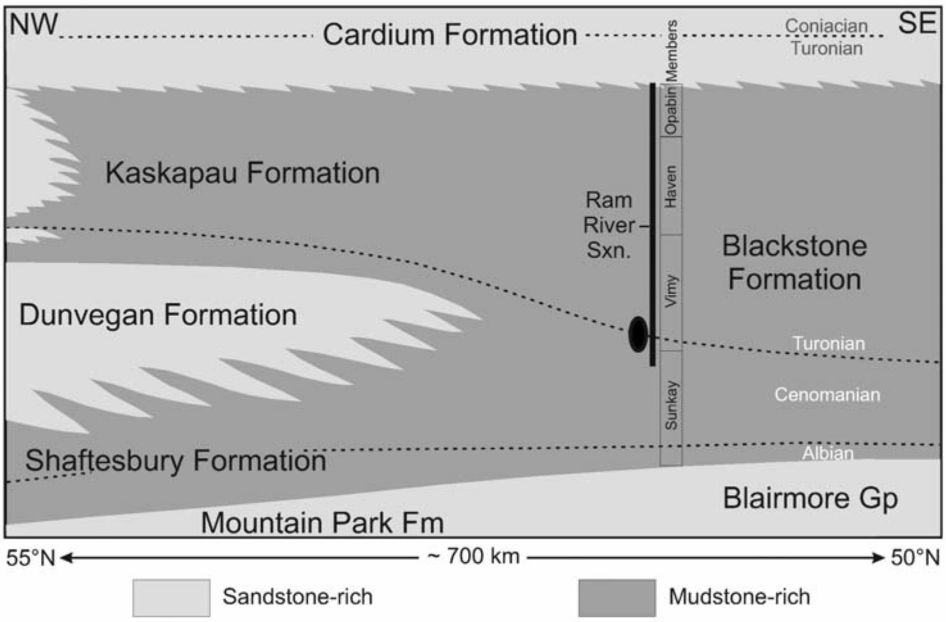
THE RAM RIVER SECTION

The latest Cenomanian – Early Turonian inoceramid and ammonite faunas that are the subject of this study are from a near-complete section through the Late Albian to Middle Turonian Blackstone Formation exposed on the South Ram River in the Rocky Mountain Foothills in central Alberta (Text-figs 1, 2). Malloch (1911) introduced the term Blackstone Formation to describe Cretaceous marine shales from the central Alberta Foothills. Malloch described a 320 m (1,050 ft.) thick section of the Blackstone Formation as "Calcareous shales, dark grey in colour with bands of concretions but apparently no fossils". Subsequent study showed that the Blackstone shales contained a rather sparse and poorly-preserved molluscan fauna, and Warren and Rutherford (1928) recognized a lower 'Barren Zone", overlain by a zone with abundant *Inoceramus labiatus*, and an overlying zone with *Prionotropis* (*Collignoniceras*) *woollgari* below sandstones of the 'Bighorn Formation' (now called the Cardium Formation). Webb and Hertlein (1934), summarized biostratigraphic work, noting the rare presence of the ammonite *'Acanthoceras'* (*Dunveganoceras*) *albertense* in the 'Barren Zone' of Warren and Rutherford. Warren and Stelck (1940) subsequently realized that *D. albertense* was of Late Cenomanian age and that the Blackstone Formation must span the Cenomanian-Turonian boundary.

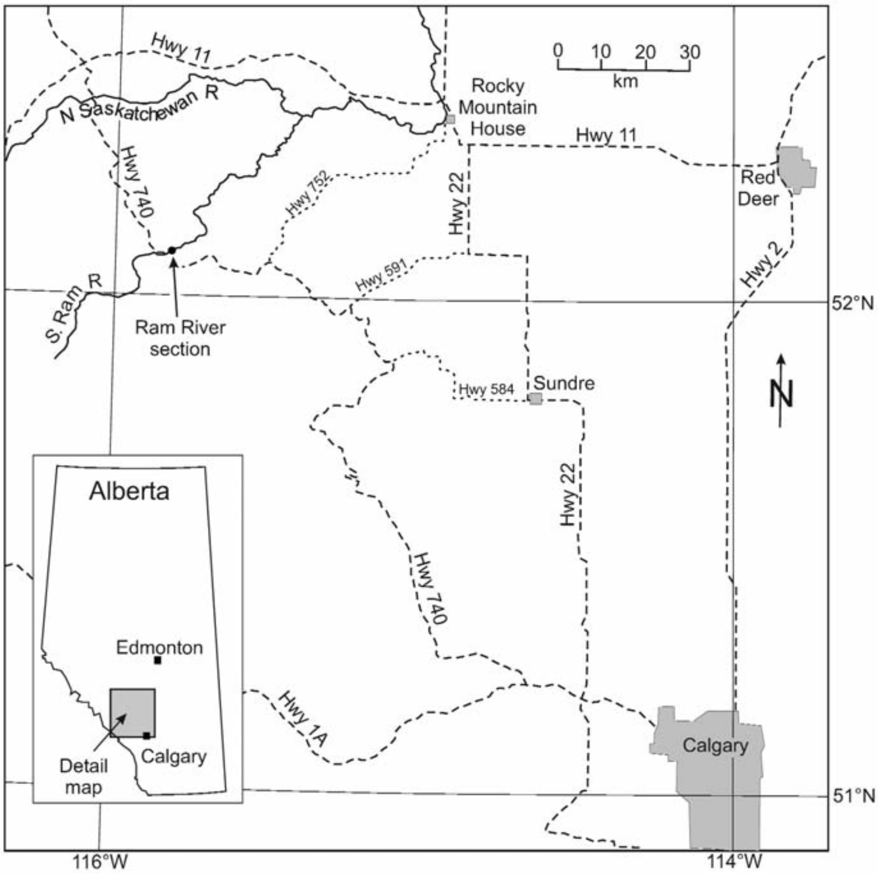
In a comprehensive regional summary of Cretaceous stratigraphy in the Rocky Mountain Foothills, Stott (1963, 1967) established four lithostratigraphic members for the Blackstone Formation in both Alberta and British Columbia. The lowest, Sunkay Member of Stott corresponded to the 'Barren Zone', with a Late Cenomanian fauna, whereas the base of the succeeding Vimy Member was defined at a distinctive lithological change from rusty-weathering to grey-weathering calcareous shales, near the base of which the Early Turonian *Inoceramus labiatus* fauna appeared. Stott (1963) reported *'Prionocyclus*' cf. *woollgari* (Mantell, 1822), *Inoceramus corpulentus* McLearn, 1926, *Inoceramus fragilis* Hall and Meek,1856 and *I. lamarcki* Parkinson, 1819 from the overlying Haven Member of the Blackstone Formation. Stott (1963) also noted that the ammonite '*P.*' *woollgari* was reported from the Vimy, Haven and Opabin members of the Blackstone Formation, and hence provided only a low level of biostratigraphic resolution.

The Blackstone Formation is a mudstone-dominated, north-eastward thinning wedge up to ~ 500 m thick, that occupies the foredeep of central and southern Alberta (Stott 1963, 1967; Tyagi 2009; Plint *et al*. 2012b). Sandy, deltaic strata of the Dunvegan Formation inter-finger south-eastward with silty mudstones of the Sunkay Member of the Blackstone Formation (Stott 1963, 1967; Plint 2000; Text-fig. 1). Grey-weathering mudstones of the Vimy Member record a major transgressive event, reflected in the broadly finer grain-size of the member, relative to the underlying Sunkay.

The faunas described herein were collected from the uppermost part of the Sunkay Member and from the lower Vimy Member (Text-fig. 1; Stott 1963). The Sunkay Member consists of millimetre to centimeter-scale interbeds of silty clay, siltstone and very fine-grained sandstone, many of which show low-amplitude combined-flow or oscillation ripples. These lithologies are typically organized in siltier- and sandier-upward successions, metres to tens of metres thick, although intervals characterized by random interbeds are



Text-fig. 1. Simplified representation of the main Cenomanian and Turonian lithostratigraphic units in the western foredeep of the Alberta foreland basin (based on Stott 1963, 1967). The Ram River section is located seaward of sandy, nearshore deposits of Cenomanian and Lower to Middle Turonian age, and is dominated by mudstone deposited in an offshore, low-gradient ramp environment. The sampled part of the section is indicated by the black ellipse



Text-fig. 2. Map of west-central Alberta showing the location of the studied section on the Ram River, exposed in the fold-and-thrust belt of the Rocky Mountain Foothills, about 150 km NW of Calgary

also present. The intensity of bioturbation is generally low with a bioturbation index of 0 to 1 (e.g. Taylor *et al*. 2003; Bann *et al*. 2008). Nodules of siderite, typically concentrated in discrete horizons, are present throughout the formation. The Sunkay Member contains abundant diffuse pyrite and weathers a rusty orange, with white sulphate efflorescence.

A few bentonite beds are present in the succession, the most prominent of which is the Bighorn River Bentonite (Tyagi *et al*. 2007), which at the Ram River is about 30 cm thick. This bentonite has been traced from Alberta to New Mexico (Stott, 1963, 1967; Elder, 1988; Tyagi *et al*. 2007), and was dated to 94.29± 0.13 Ma by Barker *et al*. (2011) using the U/Pb method on single zircon crystals.

Throughout the Alberta Foothills, the Blackstone Formation consists of mudstones and thinly-bedded siltstones and very fine-grained sandstones deposited in an offshore environment. Only when the formation is traced north-westward into the equivalent Kaskapau Formation in British Columbia are marginal-marine sandy facies preserved (Varban and Plint 2005, 2008a, b; Text fig. 1). In that basin-margin region, sandstone-rich shoreface and inner shelf facies are stacked vertically, forming the principal lithology through ~ 550 m of strata in the most westerly part of the basin (Varban and Plint 2005).

PALEONTOLOGICAL RECORD

Inoceramids

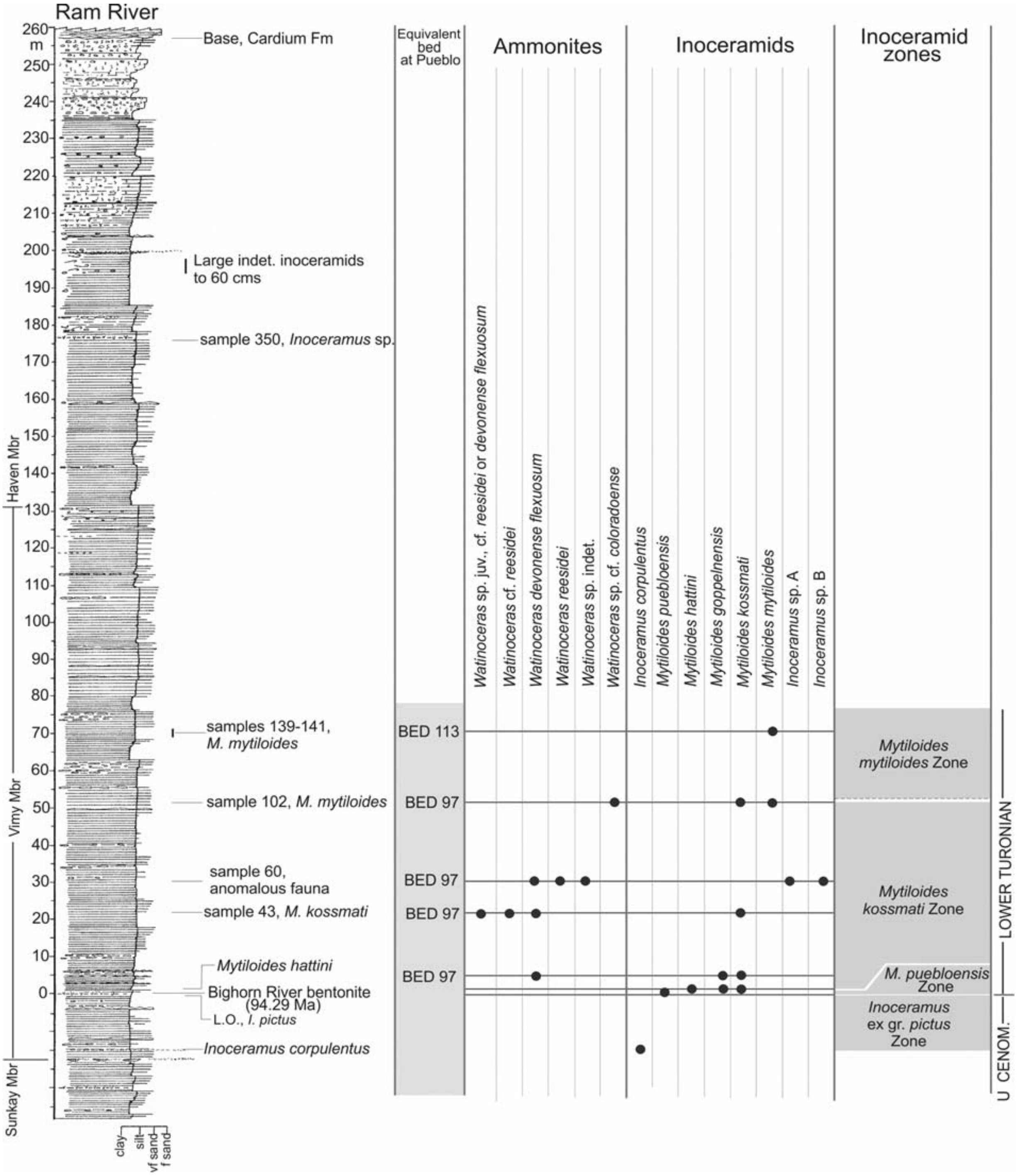
Inoceramids are common in the lower to middle parts of the Lower Turonian interval of the Ram River succession, forming a series of acme horizons (Text-figs 3-7).

Upper Cenomanian

Inoceramids occur only rarely in the uppermost part of the Upper Cenomanian. However, the ledge-forming sandstone bed with scattered calcite-cemented concretions, at about 15 metres below the Bighorn River bentonite, yielded numerous small-sized *Inoceramus* species, that can be confidently referred to *Inoceramus corpulentus* McLearn, 1926. The bed, which consists of tightly-packed, articulated shells, probably represents a storm-winnowed accumulation.

Lower Turonian

Inoceramid shell fragments occur immediately above the Bighorn River Bentonite. The oldest identifiable specimens are from a level 0.45–0.65 m above the bentonite, and are referred to *Mytiloides puebloensis* Walaszczyk

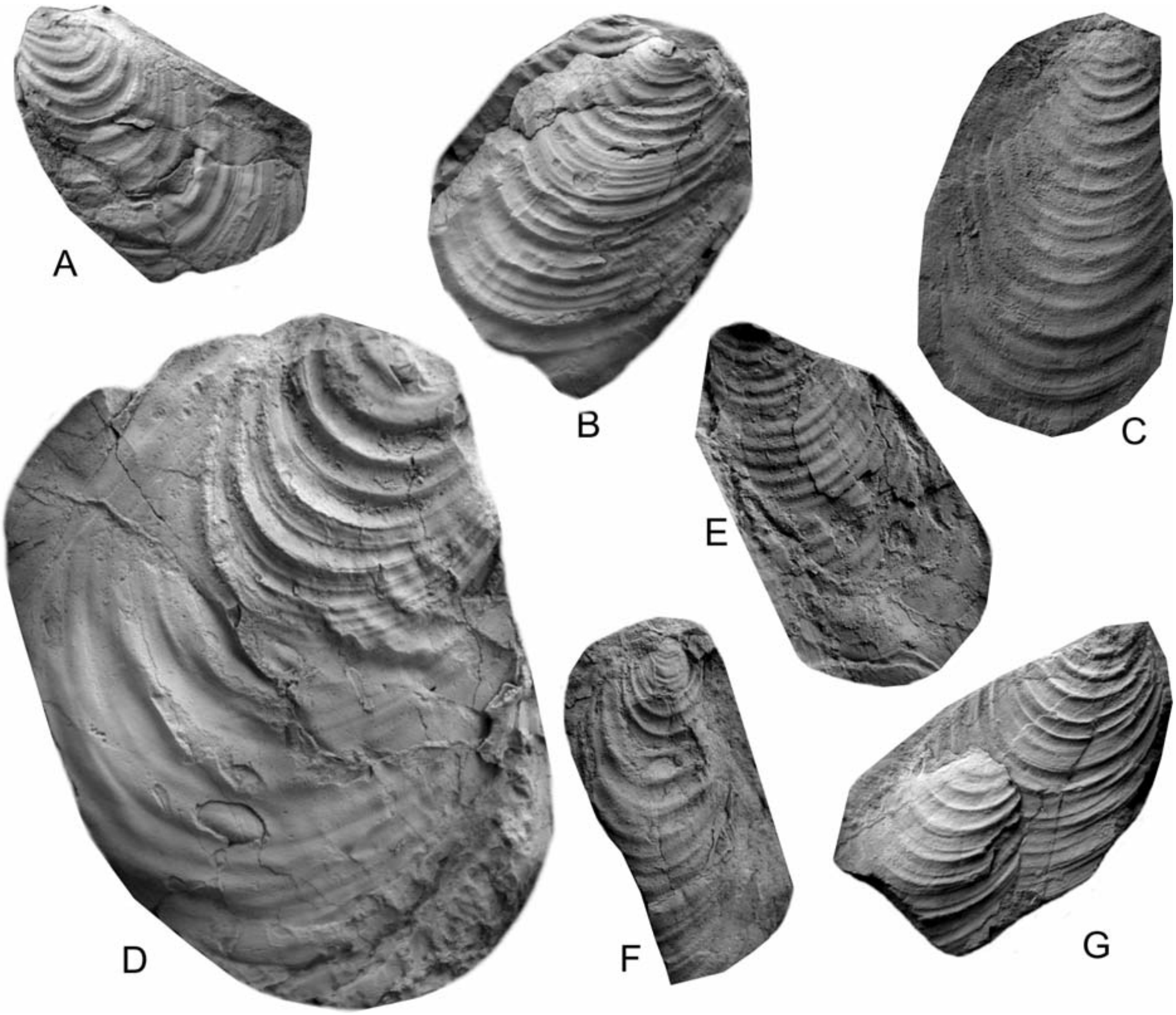


Text-fig. 3. Stratigraphic log and stratigraphic distribution of inoceramids and ammonites for the uppermost Sunkay, Vimy, and Haven members exposed in the canyon of the Ram River immediately below Ram Falls and Cobban, 2000 and to *Mytiloides* cf. *hattini* Elder, 1991. The first *Mytiloides kossmati* (Heinz 1930) and *Mytiloides goppelnensis* (Badillet and Sornay, 1980) are from a slightly higher horizon. They start at 1 m and range up to c. 51 m (sample 102) above the Bighorn River Bentonite. Some abundance horizons of *Mytiloides*, at 6.5 m (sample 13), 22 and 30 m (samples 43 and 60 respectively), and at 51 m (sample 102) above the Bighorn River Bentonite were recognized (Text-fig. 3).

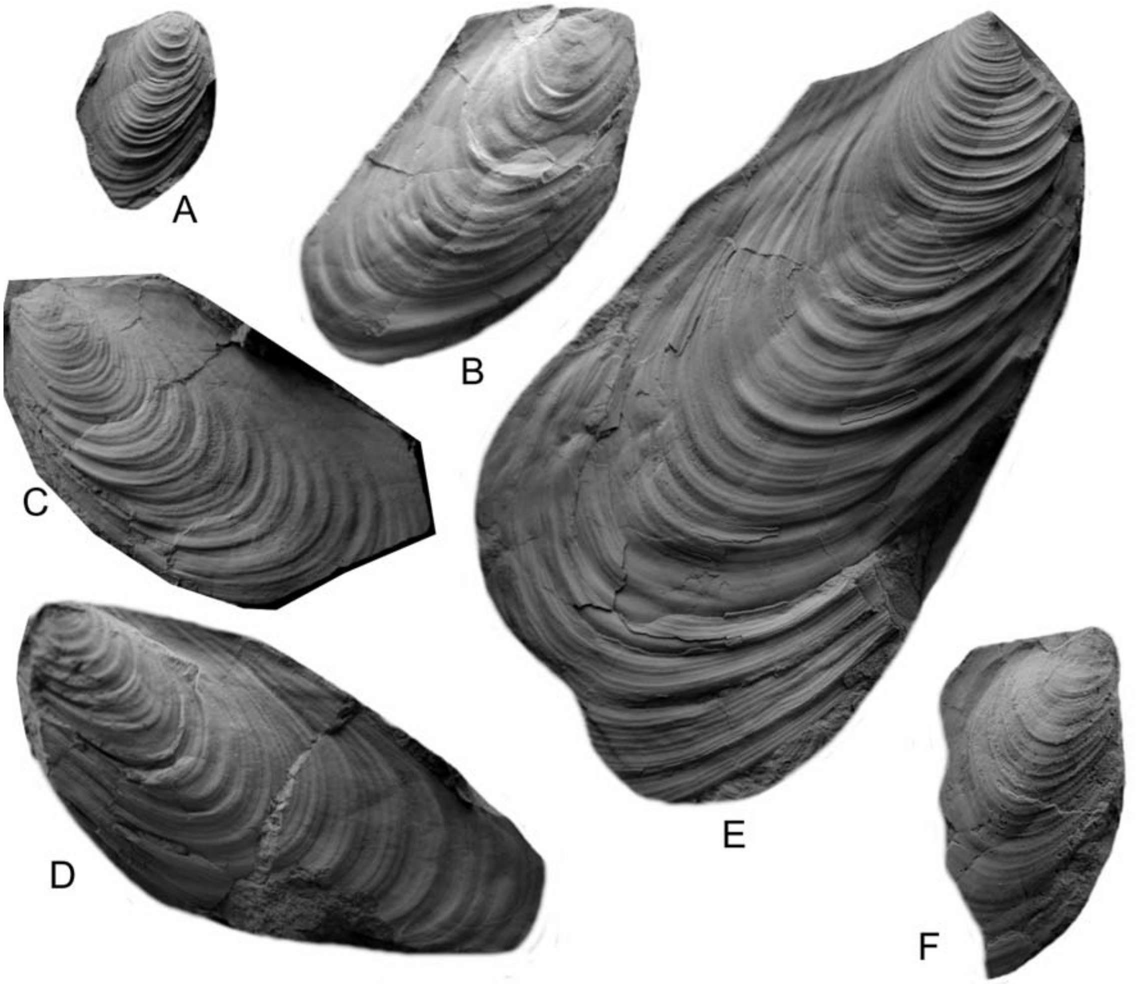
Of particular importance is the material from sample 60. Besides *Mytiloides* species, referable mostly to *M. kossmati*, the sample yielded a multi-species assemblage of the genus *Inoceramus sensu stricto* (Text-fig. 7), discussed at length below. Five distinct morphotypes are recognized in this assemblage.

A slightly younger acme level of inoceramids is noted in sample 102, which is about 51 m above the Bighorn River bentonite. All forms represent *M. kossmati* and transitional form to *Mytiloides mytiloides* (Mantell, 1822). Unequivocal *M. mytiloides* starts however in a higher horizon represented by samples 139-141, at 70-71 m above the Bighorn River Bentonite, with numerous, moderate to large size specimens (Text-fig. 5).

Sample 139-141 is the highest sample documented from the Lower Turonian interval of the Ram River section. The next inoceramid sample is from a horizon at 175 m above the Bighorn Bentonite (sample 350), containing advanced *Inoceramus*, evidently of a Middle Turonian age.



Text-fig. 4. A – *Mytiloides kossmati* (Heinz, 1930), TMP 2016.041.0448; B, C, F, G – *Mytiloides goppelnensis* (Badillet and Sornay, 1980); B, TMP 2016.041.0449a, C, TMP 2016.041.0450, F, TMP 2016.041.0451, G, TMP 2016.041.0452; D – *Mytiloides* sp.; TMP 2016.041.0453; E – *Mytiloides hattini* Elder, 1991, TMP 2016.041.0454. All specimens are housed in Royal Tyrell Museum, Drumheller, Alberta, Canada. Figures are × 1



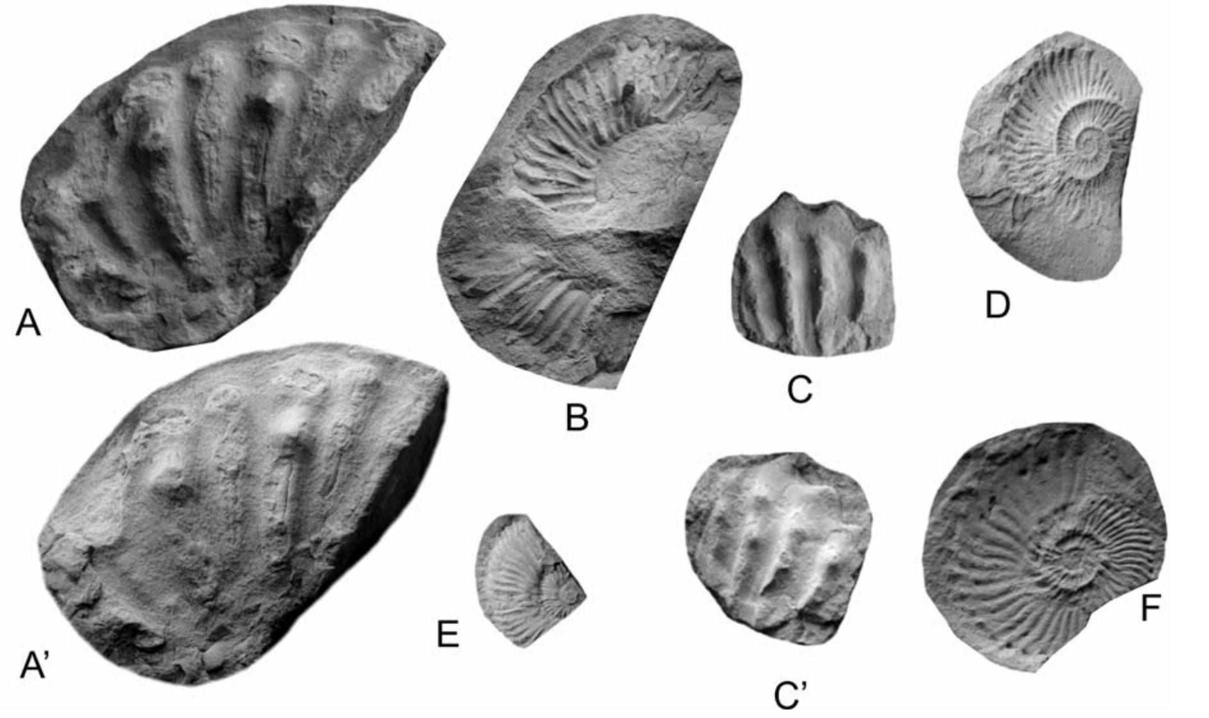
Text-fig. 5. A – *Mytiloides goppelnensis* (Badillet and Sornay, 1980), TMP 2016.041.0449b; B, C, E, F – *Mytiloides mytiloides* (Mantell, 1822); B, TMP 2016.041.0455, C, TMP 2016.041.0456, E, TMP 2016.041.0457, F, TMP 2016.041.0458; D – *Mytiloides* cf. *arcuatus* (Seitz, 1934), TMP 2016.041.0459. All specimens are housed in Royal Tyrell Museum, Drumheller, Alberta, Canada. Figures are × 1

Ammonites

Ammonites are not as common as inoceramids, although fragments occur regularly through the lower part of the Turonian succession. The stratigraphically oldest specimens are from the interval of samples 10-11 and their record ranges up to sample 102 (see Text-fig. 3 between 5.5 and 51 m). All specimens are *Watinoceras* (Text-fig. 6). The stratigraphically lowest record is *Watinoceras devonense flexuosum* Cobban, 1988, from the horizon of samples 10-11, 5.5 m level). The species ranges higher, up to sample 43 (22 m), where it is accompanied by *Watinoceras* cf. *reesidei* Warren, 1930. The latter species is also noted in sample 60 (30 m), where it is accompanied by *Watinoceras coloradoense* (Henderson, 1908). *Watinoceras* cf. *coloradoense* is noted still higher, in sample 102 (51 m).

BIOSTRATIGRAPHY

The 8-m thick topmost part of the Upper Cenomanian is referred to the *I. pictus* Zone (Text-fig. 3). Although no definitely identifiable *I. pictus* Soweby, 1829 *sensu stricto* were found, the presence of the zone is proved by the presence of rare *I.* ex gr. *pictus*, and numerous *Inoceramus corpulentus* McLearn, 1926. The latter species, described originally from Alberta (McLearn 1926), was reported from the Upper Cenomanian of the US Western Interior (see e.g., Kauffman *et al.* 1993) and apparently from equivalent strata in Far



Text-fig. 6. *Watinoceras* from the Ram River section. A, A' – *Watinoceramus coloradoense* Henderson, 1908, TMP 2016.041.0460; B – *Watinoceras reesidei* Warren, 1930; TMP 2016.041.0461; C, C' – *Watinoceramus* cf. *coloradoense* Henderson, 1908, TMP 2016.041.0462; D – *Watinoceramus* cf. *reesidei* Warren, 1930; TMP 2016.041.0463; E, F – *Watinoceramus devonense flexuosum* Cobban, 1988, E, TMP 2016.041.0464a, F, TMP 2016.041.0464b. All specimens are housed in Royal Tyrell Museum, Drumheller, Alberta, Canada. Figures are × 1

East Russia (Pergament 1966). Although the species was then variably interpreted, and thought to range much higher, even up into the Early Coniacian (e.g., Collom 2001), these younger morphotypes are taxonomically distinct.

The 1 m thick interval above the Bighorn River bentonite up to the FO of *M. kossmati*, is referred to the *M. puebloensis* Zone. No complete specimen of *M. puebloensis* was found in the section studied, however, good specimens of the species are known from the Mount Robert section in British Columbia, 525 km NW of the Ram River section (van Helmond *et al*. 2016). Above the 1 m level begins a uniform assemblage of the *M. kossmati* Zone, consisting of the eponymous species and of *M. goppelnensis*, which continues up to the horizon of sample 102 (Text-fig. 4). The lower part of the zone also contains *M. hattini* Elder, 1991.

The succession above the Bighorn River Bentonite suggests that a hiatus, if any, associated with this horizon cannot be demonstrated on biostratigraphic evidence.

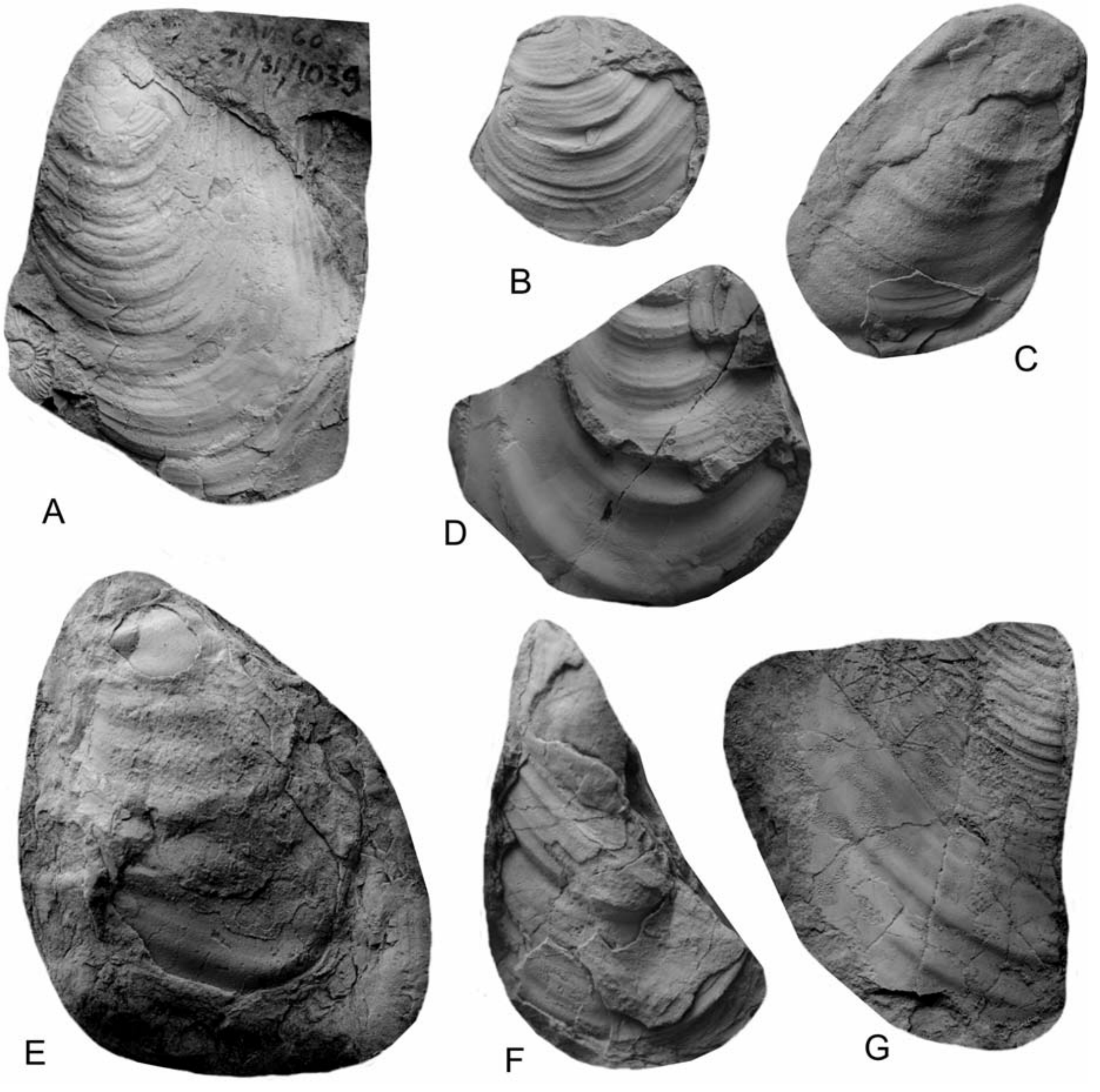
The *M. kossmati* Zone ranges upwards to sample 102, about 51 m above the Bighorn River Bentonite. In the Pueblo section, it corresponds to an interval spanning beds 90 through to 97 (see Kennedy *et al*. 2000, 2005). This correlation is confirmed by the co-occurring ammonites of the genus *Watinoceras* (Text-fig. 3). The ammonite species represented in our section are noted up to bed 97 of the Pueblo section (see Kennedy and Cobban 1991; Kennedy *et al*. 2000).

The base of the *M. mytiloides* Zone is placed at sample 102 (51 m), although the first appearance of the eponymous species might be slightly lower. The inoceramid assemblage of the zone corresponds to beds 105-118 of the Pueblo section. No ammonites were found in this zone.

In ammonite terms, the succession studied is equivalent to the *devonense, flexuosum, birchbyi* and a lower part of the *nodosoides* ammonite zones as recognised in the Pueblo section (Kennedy and Cobban 1991; Kennedy *et al*. 2000, 2005).

THE EARLY TURONIAN *INOCERAMUS* RECORD

The inoceramid succession across the Cenomanian-Turonian boundary interval, as observed in the Ram River section, reflects the general Western Interior pattern;



Text-fig. 7. A - *Inoceramus* ex gr. *pictus* Sowerby, 1829, TMP 2016.041.0465; B - *Inoceramus* ex gr. *pictus* Soweby, 1829 or *Inoceramus* cf. *yabei* Nagao and Matsumoto, 1939, TMP 2016.041.0466; C, F – *Inoceramus* sp. A, C, TMP 2016.041.0467, F, TMP 2016.041.0468; D, G - *Inoceramus* cf. *ginterensis* Pergament, 1966, D, TMP 2016.041.0469, G, TMP 2016.041.0470; E - *Inoceramus* sp. B, TMP 2016.041.0471. All specimens are housed in the Royal Tyrell Museum, Drumheller, Alberta, Canada. Figures are × 1

Inoceramus of the Late Cenomanian is replaced by *Mytiloides* in the Early Turonian, which in turn is replaced by *Inoceramus* in the Middle Turonian. The same pattern is observed over the entire Euramerican biogeographic region, although some differences are noted. The main differences between the Western Interior and Europe are (see e.g., Seitz 1934, Tröger 1967, 1981, 1989; Elder 1988, 1989; Harries and Kauffman 1991; Walaszczyk 1992; Kauffman *et al*. 1993; Harries *et al*. 1996; Kennedy *et al*. 2000): (1) a higher taxonomic variability of the latest Cenomanian inoceramid faunas in the Western Interior when compared to Europe, and (2) a delayed re-entry of *Inoceramus* in Europe compared to the Western Interior; whereas the re-entry is dated to the latest Early Turonian in the Western Interior, it is early (but not the earliest) Middle Turonian in Europe.

The pattern observed in the Euramerican biogeographic region is also noted in the South Atlantic Subprovince and in the East African Province (Sornay 1965; Hessel 1988; Andrade 2005; Walaszczyk *et al*. 2014), although the details of the Middle Turonian *Inoceramus* re-entry are not known in detail. In the Pacific area, however, all along the Asian coasts (Matsumoto and Noda 1975; Kawabe *et al*. 1996; Hirano et al. 1997; Yazykova *et al*. 2002; Takahashi 2009), and along the western margin of North America i.e. the North Pacific Province (Riccardi 1981; Haggart 1987; Elder and Box 1992), *Mytiloides* is regularly accompanied by *Inoceramus* (e.g., Pergament 1966; Takahashi 2009). Finally, in some biogeographic areas *Mytiloides* is not represented at all (as in New Zealand; Crampton 1996).

The *Inoceramus* assemblage in sample 60 (30 m in Text-fig 3) from the Ram River section, discussed herein, is thus a unique representation of the Early Turonian lag interval of the genus in the Euramerican biogeographic region. The *Mytiloides* and ammonites date it precisely to the middle part of the *M. kossmati* Zone and the *Vascoceras birchbyi* Zone of the Pueblo section, and the sample is thus stratigraphically higher than any of the previous reports of *Inoceramus* (invariably referred to *I. pictus*) from the basal Turonian (e.g., Elder 1989; Tröger 1989; Gale *et al*. 2005; Ifrim and Stinnesbeck 2008).

Although the sample is small (only 7 specimens), it comprises 5 morphotypes: *Inoceramus* ex gr. *pictus* Sowerby; *Inoceramus* cf. *ginterensis* Pergament, 1966; *Inoceramus* ex gr. *pictus* or *Inoceramus* cf. *yabei* Nagao and Matsumoto, 1939, *Inoceramus* sp. A, and *Inoceramus* sp. B. The first of the morphotypes, *Inoceramus* ex gr. *pictus* (Text-fig. 7A), represents a morphotype known from the latest Cenomanian, referred either to *Inoceramus flavus pictoides* 1965 (see Kauffman 1977, pl. 5, fig. 2; Kauffman and Powell 1977, pl. 1, fig. 4, pl. 2, fig. 4) or to *I. prefragilis* Stephenson, 1953. It also resembles *I. pictus rabenauensis* Tröger, 2015 (p. 383, pl. 2, fig. 1). The morphotype referred herein to *I.* cf. *ginterensis* (Text-fig. 7D, G) is characterised by *pictus* juvenile ornament, followed by a widely rugate adult stage, with superimposed indistinct growth lines. Our specimens closely resemble the illustrated type material of Pergament (1966, pl. 28. particularly his fig. 1; or pl. 29, fig. 1; as well as the type material (Pergament 1966, pl. 27, fig. 1). *Inoceramus* sp. B (Text-fig. 7E) is a moderately inflated form, with a vertical anterior wall and a well separated disc. It is covered with regular, moderately-spaced rugae, and superimposed sharp, flat growth lines. Such forms are known from the Upper Cenomanian of the U.S. Western Interior, and at least the illustrated specimens were referred to *Inoceramus flavus flavus* Sornay 1965 (see e.g., Kauffman 1977, pl. 6, fig. 2). This morphotype also resembles *Inoceramus subconvexus* Logan, 1898, the species known so far from a single type specimen, which comes from a level close to the Lower/Middle Turonian boundary. Two specimens herein referred to as *Inoceramus* sp. A (Text-fig. 7C, F), are poorly preserved and their final affiliation is very uncertain.

Although the Ram River mid-Early Turonian *Inoceramus* sample is small, and most of the specimens poorly preserved, it does make it possible to draw a number of inferences about the evolutionary and biogeographic behaviour of the genus in the Early Turonian of the Euramerican biogeographic region. The main points are:

1. The assemblage shows a distinct affinity with the Late Cenomanian faunas, with some specimens clearly referable to the *Inoceramus pictus* group or to *I. ginterensis*, both being dominant Late Cenomanian lineages known from the Western Interior Basin. Consequently, the sample proves that various *Inoceramus* lineages, known from the Upper Cenomanian of the Western Interior, and regarded as extinct, survived at least until the mid-Early Turonian.
2. Besides one morphotype, questionably compared to one North Pacific taxon (*I.* cf. *yabei* – Text-fig. 7B), the rest of the morphotypes represent Western Interior (Euramerican) indigenous species. Although *I. ginterensis* was also originally described from the North Pacific Province (Pergament 1966), it is well documented in the US Western Interior through much of the Upper Cenomanian (Kauffman 1977; Kauffman and Powell 1977; Kauffman *et al*. 1978, 1993). Such representation indicates that, at least until the mid Early Turonian, no immigration events, at a biogeographic scale, can be suggested as a source of the re-entry of *Inoceramus* at the onset of the Middle Turonian; this certainly, does not preclude migration events, into and from geographic refugia, within the Western Interior Basin.
3. The relatively high number of morphotypes present in the sample studied (5 in a sample consisting of 7 specimens) indicates a taxonomically highly variable Early Turonian assemblage of *Inoceramus* in the Western Interior Basin. It may be inferred that potentially a still higher number (?most) of the Late Cenomanian *Inoceramus* lineages survived the suggested extinction events at the Cenomanian – Turonian boundary.
4. The evolutionary transitions among *Inoceramus* lineages, which led to the appearance of the Middle Turonian *Inoceramus* species, had to have taken place late in the Early Turonian.
5. The *Inoceramus* sample from Ram River does not give a clear picture of the distribution of *Inoceramus* in the Early Turonian Western Interior Basin. This single sample may be interpreted in various ways:

(i). The simplest interpretation is that the sample studied marks a regular (although rare) occurrence of the genus in the Early Turonian of the Western Interior Basin, and its general absence in the Early Turonian record results from the rarity of its original populations in the Early Turonian sea. The very expanded nature of the Ram River succession (15 times thicker than the corresponding interval at Pueblo), implying a much higher subsidence rate, may have allowed preservation of a much more complete paleontological record.

(ii). An alternative interpretation is suggested by the fact that the Ram River *Inoceramus* sample comes from a single stratigraphic interval. This may suggest a short-lived dispersal event of the genus, from a refugium in an otherwise *Inoceramus*-free environment. A partial confirmation of this possibility stems from the fact that equivalent horizons in other sections in the Euramerican biogeographic area (Pueblo, Eastbourne), have yielded forms of suspected *Inoceramus* affinity (see Kennedy et al. 2000; Gale *et al*. 2005). Further studies are needed, however.

(iii). The third possibility is that the Ram River area formed part of the Early Turonian *Inoceramus* refugium.

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