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 rapidly-
evolving *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 hiatus 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_ (Colignoniceras) _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. lamarki_ 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 silty- and sandy-upward successions, metres to tens of metres thick, although intervals characterized by random interbeds are
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 concre-
tions, 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.

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**CENOMANIAN-TURONIAN BOUNDARY IN WESTERN ALBERTA, CANADA**

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.
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).

*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
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;
*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), al-
though 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 ar-
eas *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 re-
gion. The *Mytiloides* and ammonites date it precisely to
the middle part of the *M. kossmati* Zone and the *Vasco-
ceras birchbyi* Zone of the Pueblo section, and the sam-
ple is thus stratigraphically higher than any of the previ-
ous reports of *Inoceramus* (invariably referred to *I. pictus*)
from the basal Turonian (e.g., Elder 1989; Tröger 1989;
Gale et al. 2005; Iirim 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; *In-
oceramus* 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 flavius
pictoides* 1965 (see Kauffman 1977, pl. 5, fig. 2; Kauff-
man and Powell 1977, pl. 1, fig. 4, pl. 2, fig. 4) or to *I. pre-
fragilis* Stephenson, 1953. It also resembles *I. pictus
rabenauensis* Tröger, 2015 (p. 383, pl. 2, fig. 1). The mor-
photype 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 indis-
tinct growth lines. Our specimens closely resemble the il-
lustrated type material of Pergament (1966, pl. 28. par-
ticularly 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 cov-
ered with regular, moderately-spaced rugae, and super-
imposed 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 *In-
oceramus flavius flavius* Sornay 1965 (see e.g., Kauffman
1977, pl. 6, fig. 2). This morphotype also resembles *In-
oceramus 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 *In-
oceramus* 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 bio-
geographic behaviour of the genus in the Early Turon-
ian 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. gin-
terensis*, both being dominant Late Cenomanian line-
ages known from the Western Interior Basin. Conse-
quently, 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 (Eu-
ramerican) 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 Ceno-
manian (Kauffman 1977; Kauffman and Powell 1977;
Kauffman et al. 1978, 1993). Such representation indi-
cates that, at least until the mid Early Turonian, no im-
migration events, at a biogeographic scale, can be sug-
gested 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 spec-
imens) indicates a taxonomically highly variable Early
Turonian assemblage of *Inoceramus* in the Western In-
terior Basin. It may be inferred that potentially a still
higher number (?most) of the Late Cenomanian *In-
oceramus* lineages survived the suggested extinction
events at the Cenomanian – Turonian boundary.

4. The evolutionary transitions among *Inoceramus* line-
ages, which led to the appearance of the Middle Tur-
onian *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 sin-
gle sample may be interpreted in various ways:

(i). The simplest interpretation is that the sample stud-
ied 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
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