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Arnaud Brayard, James F. Jenks, Kevin G. Bylund, Gilles Escarguel, Emmanuel Fara, et al.. Ammonoids and nautiloids from the earliest Spathian Paris Biota and other early Spathian localities in southeastern Idaho, USA.. *Geobios*, 2019, 54, pp.13-36. 10.1016/j.geobios.2019.04.007 . hal-02168391

HAL Id: hal-02168391

<https://hal.science/hal-02168391>

Submitted on 25 Oct 2021

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Ammonoids and nautiloids from the earliest Spathian Paris Biota and other early Spathian localities in southeastern Idaho, USA *

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Abstract

Intensive sampling of three earliest Spathian sites represented by the Lower Shale unit and coeval beds within the Bear Lake vicinity and neighboring areas, southeastern Idaho, yielded several new ammonoid and nautiloid assemblages. These new occurrences overall indicate that the lower boundary of the *Tirolites* beds, classically used as a regional marker for the base of the early Spathian, and therefore the regional Smithian/Spathian boundary, must be shifted downward into the Lower Shale unit and coeval beds. Regarding ammonoids, one new genus (*Caribouceras*) and two new species (*Caribouceras slugense* and *Albanites americanus*) are described. In addition, the regional temporal distribution of *Bajarunia*, *Tirolites*, *Columbites*, and *Coscaites* is refined, based on a fourth sampled site containing a newly reported occurrence of the early Spathian *Columbites* fauna in coeval beds of the Middle Shale unit. As a complement to ammonoids, changes observed in nautiloid dominance are also shown to facilitate correlation with high-latitude basins such as Siberia during this short time interval, and they also highlight the major successive environmental fluctuations that took place during the late Smithian–early Spathian transition.

Keywords:

Ammonoidea

Nautiloidea

Early Triassic

Panthalassa

Sonoma Foreland Basin

Biostratigraphy

1. Introduction

Pioneering contributions regarding our knowledge of Early Triassic ammonoids from the northern part of the western USA basin were accomplished by White (1879), Hyatt and Smith (1905) and Smith (1932). They were the first to report and illustrate various taxa from the Smithian-Spathian interval in the Bear Lake area of southeastern Idaho (Guex et al., 2010; Jenks et al., 2015; Fig. 1). Smith (1932) also proposed the first regional Early Triassic biozonation based on these organisms by using their successive occurrences observed in several localities within this area. In particular, he recognized the iconic middle and late Smithian *Meekoceras* and *Anasibirites* beds, and the early Spathian *Tirolites* and *Columbites* beds. Kummel (1943, 1954, 1969) continued the exploration of this area and completed the

biozonation for the middle Spathian. Kummel (1954, 1957) also documented the major Lower Triassic lithologic units found in the Bear Lake area, provided ammonoid zonal-based ages for each unit and suggested correlation of these units between studied sections (Fig. 2). Additionally, Kummel (1953) reviewed the rare Early Triassic coiled nautiloid occurrences known for this area and noted that a large majority came from the early Spathian *Columbites* beds. Recently, Guex et al. (2005a, 2005b, 2010) and Jenks et al. (2013) significantly refined these previous works and provided an ammonoid zonation for the Spathian, with particular emphasis on the early Spathian, achieving a much higher resolution than elsewhere in the world (see Jenks et al., 2015 for a review of global Early Triassic correlations).

Here we focus on ammonoids and nautiloids recently found in the earliest Spathian of the Bear Lake area, which yields specimens of both clades (Brayard et al., 2017). Based on data from the Paris Biota and coeval beds in neighboring sites in the Bear Lake area (Fig. 1), we document the first reported occurrence of the ammonoids *Tirolites harti*, *Tirolites* aff. *cassianus* and *Bajarunia* cf. *pilata*, as well as a new genus *Caribouceras* nov. gen. and two new species *Caribouceras slugense* nov. gen., nov. sp. and *Albanites americanus* nov. sp. from the earliest Spathian platy shale and siltstone interval underlying the Middle Limestone unit and coeval beds. The Middle Limestone unit and coeval beds, which contains *Tirolites harti*, has been commonly considered as marking the beginning of the early Spathian in southeastern Idaho. This unit is overlain by the classic early Spathian assemblage of *Columbites parisianus* and *Tirolites smithi*, both species being common in the Bear Lake area. These new ammonoid occurrences in the Lower Shale unit or coeval beds, therefore, necessitate a downward revision of the Smithian/Spathian boundary (SSB) in the region and also modify the assumed correlation among sections in this area.

2. Previous local-to-regional early Spathian biostratigraphy

2.1. Ammonoids

After the severe late Smithian extinction (Tozer, 1982; Brayard et al, 2006; Jattiot et al. 2016), the appearance of the ammonoid genus *Tirolites* is consensually acknowledged as characterizing the early Spathian worldwide (Balini et al., 2010; Jenks et al., 2015; Shigeta and Nakajima, 2017). This certainly was the case for the western USA basin (e.g., Silberling and Tozer, 1969), based on data from ammonoids collected in the Bear Lake area by Hyatt and Smith (1905) and Smith (1932), and then revised by Kummel (1954). However, Guex et al. (2005a, 2005b, 2010) have recently suggested that in westernmost Utah, the first occurrence of *Tirolites* is probably preceded by the earliest Spathian *Bajarunia confusionensis*

and *Cowboyiceras farwestense* horizons. This implies that the oldest *Tirolites* occurrences do not represent the very base of the Spathian, not only regionally but also globally. A similar observation was made in South Primorye (Zakharov et al., 2004; Shigeta and Zakharov, 2009; Shigeta and Kumagae, 2016) where, for instance, *Bajarunia* and a few other taxa occur below the lowest occurrence of *Tirolites*. A putative earliest Spathian ammonoid assemblage underlying the first *Tirolites* beds was also reported by Brayard and Bucher (2008) from South China. *Bajarunia* was also sampled at the base of the Spathian in high latitude basins such as Spitsbergen and Siberia. However, *Tirolites* has not been recorded from these basins, thus preventing the acquisition of superpositional information for both genera for these areas (Dagys and Ermakova, 1988, 1995; Dagys and Weitschat, 1993; Dagys et al., 1996; Mørk et al., 1999; Zakharov and Moussavi Abnavi, 2013; but see Kummel, 1969 for a possible exception in Siberia).

In southeastern Idaho, despite considerable sampling efforts, the *Bajarunia confusionensis* horizon of Guex et al. (2010) has not yet been found, revealing a significant gap in the ammonoid record between the late Smithian *Anasibirites* and *Xenoceltites-Glyptohiceras* beds and the next overlying Spathian *Tirolites* fauna (Jenks et al., 2013). Thus, for the entire Bear Lake area, the record of earliest Spathian ammonoids has classically consisted of only the *Tirolites harti* beds from the Middle Limestone unit (Fig. 2). *Tirolites harti* was first documented from Paris Canyon (Fig. 1) by Smith (1932; “*Tirolites* beds”). However, correlation between Paris Canyon and neighboring sections is not straightforward and uncertainty remains when suggesting superpositional relationships between the *T. harti* beds of Paris Canyon and, for instance, the “*Tirolites* beds” reported from Hot Springs (e.g., Caravaca et al., 2017; Fig. 1). Indeed, although the “*Tirolites* Limestone” visible on the north side of Paris Canyon is expected to be coeval with the “*Tirolites* beds” at Hot Springs, and the lithology of at least parts of both levels appears rather similar (i.e., the Middle Limestone unit), *Tirolites harti* has not yet been found at Hot Springs. At this section, *Tirolites* represented by *T. smithi* only occurs within the younger *Columbites* beds from the base of the Middle Shale unit (Kummel, 1954; Guex et al., 2010; Jenks et al., 2013). Therefore, the position of the base of the Spathian at a locality such as Hot Springs is impossible to determine based only on the occurrence of *Tirolites*. This problem is exacerbated by the complete lack of exposures of the Lower Shale unit at Hot Springs, due to the near vertical attitude of the beds and relative incompetence of this shale interval.

The use of *Bajarunia confusionensis* as a marker for the base of the Spathian in the western USA basin is also problematic. Indeed, this species described by Guex et al. (2005b)

has only been documented from the Confusion Range (western Utah), and the type series is very poorly preserved, which probably prevents a firm assignment to *Bajarunia* as initially erected by Dagys (1983). Dagys also initially included several younger Spathian genera within *Bajarunia*, potentially generating confusion regarding the temporal distribution of this genus within and among distant basins (Zakharov and Smyshlyayeva, 2016). Similarly, Guex et al. (2010) assigned specimens of *Meekoceras pilatum* Hyatt et Smith from the *Columbites* beds in Bear Lake area to *Bajarunia*. Overall, this genus may have a potential temporal distribution within the western USA and other basins spanning the early Spathian, and not just the earliest Spathian.

2.2. Nautiloids

Kummel (1953, 1954, 1964) reported the occurrence of various orthoconic and coiled nautiloid genera from different strata in the Bear Lake area. However, due to the paucity of sampled specimens, no regional biostratigraphic zonation based on nautiloids was proposed. Nevertheless, Schastlivtseva (1988) and Sobolev (1989, 1994) recognized co-occurrences of some of these taxa among geographically-distant basins during restricted time intervals. For instance, the coiled genus *Phaedrysmocheilus*, which is abundant in the *Columbites* beds at the Hot Springs section (Figs. 1, 2), shows a cosmopolitan distribution from low to high latitudes during the early Spathian. Sobolev (1989, 1994) therefore suggested the first long-distance correlation between basins based on this taxon. He also defined the first Early Triassic zonation based on nautiloids, by integrating Kummel's (1953) preliminary data from the Bear Lake area. In this nautiloid framework, the Smithian substage is mainly characterized by abundant various orthoconic nautiloids, whereas the Spathian is distinguished by the occurrence of coiled nautiloids such as *Phaedrysmocheilus*, immediately after the SSB (Sobolev, 1994). Our field observations and sampling in the western USA basin refine this scheme by showing that orthoconic nautiloids continued to be common immediately after the SSB (e.g., in the Paris Biota; Brayard et al., 2017) and during the early Spathian (e.g., in the *Columbites* beds of the Bear Lake area and the Confusion Range, western Utah; unpubl. obs. and Brayard et al., 2011, respectively). This is also in agreement with similar observations in, e.g., Albania (Arthaber, 1911), Vietnam (Shigeta et al., 2014), and South Primorye (Shigeta et al., 2009). Focusing on the Smithian-Spathian transition, coiled nautiloids occur sparsely in the western USA *Tirolites* beds (*sensu* Smith, 1932), but become common in the *Columbites* beds, thus allowing for a tentative worldwide correlation. In this basin, the earliest Spathian immediately following the SSB is therefore probably characterized by orthoconic nautiloids.

This regional renewal of nautiloid abundance at the SSB and continuing up to the *Columbites* beds may complement classical ammonoid and conodont zonations. As observed for these nekto-pelagic clades, the change in nautiloid assemblages may be linked to the important geochemical and temperature fluctuations known during the Smithian and through the SSB (Galfetti et al., 2007a, 2007b; Romano et al., 2013; Clarkson et al., 2016; Thomazo et al., 2016, in press).

At Hot Springs, coiled nautiloids occur only in the lower two intervals of the *Columbites* beds (*Yvesgalleticeras montpelierense* nodular limestone bed and overlying *C. parisianus* concretions; authors pers. obs.; see Jenks et al., 2013 for detailed subdivisions of the *Columbites* beds at this locality). They completely disappear in the overlying two horizons (*Arctomeekoceras popovi* and *C. isabellae*), although orthoconic nautiloids are common in the *C. isabellae* horizon. This may indicate a potential new change in environmental conditions during the early Spathian, at least locally.

3. Exposures and sampled material

Early Triassic marine exposures of the western USA basin mainly consist of shale-limestone alternations of the Thaynes Group (*sensu* Lucas et al., 2007). These sediments were deposited over a large area covering western Wyoming, southern Montana, Idaho, Utah, and Nevada. They represent epicontinental marine environments of the Sonoma Foreland Basin, which was located within the northern intertropical zone on the western margin of Pangea during the Permian-Triassic transition (Dickinson, 2013). Based on a detailed account of lithologies, thickness and subsidence rates within the basin, Caravaca et al. (2018) showed a North-South differentiation and interpreted it as the potential result of the combined control of rheological properties of the basement terranes and spatial heterogeneity of the Golconda Allochthon. Jattiot et al. (2018) also emphasized this N-S distinction based on the non-random distribution of ammonoids within the basin. The Thaynes Group is generally characterized by sediments indicating relatively shallow environments. In this setting, the maximum extent of the regional transgression of the Early Triassic epicontinental sea occurred during the Smithian-Spathian transition (Lucas et al., 2007; Brayard et al., 2013; Vennin et al. 2015; Olivier et al., 2018). Earliest Spathian sediments in northern Utah and southeastern Idaho generally correspond to mid-outer ramp environments (Brayard et al., 2017; Grosjean et al. 2018).

Specimens of ammonoids and nautiloids were collected from four localities where the Lower Shale and Middle Shale units (or equivalents) of the Lower Triassic Thaynes Group

are exposed. Obviously, these facies do not favor optimal ammonoid and nautiloid preservation and the amount of compaction varies significantly between localities, thus rendering taxonomic identification difficult for many specimens. Fortunately, some ammonoids retain traces of ornamentation and most specimens preserve adequate 2D geometry, allowing for reasonably accurate measurement of diameter, whorl height and umbilical width.

The first locality consists of four studied exposures on both the north and south side of Paris Canyon, west of the city of Paris in Bear Lake County, Idaho (Fig. 1). These exposures crop out intermittently, dip gently northward and have a combined thickness of ~20 m. *Tirolites harti* occurs throughout the exposures, which underlie the Spathian Middle Limestone unit (“*Tirolites* beds” of Smith, 1932) and overlie the Smithian Lower Limestone unit. However, the contact with the Lower Limestone unit is not visible in this area. The studied outcrops mainly consist of grey-blue to orange, thin-bedded silty limestones containing an exceptionally well preserved and remarkably complex fauna: the Paris Biota (Brayard et al., 2017; Doguzhaeva et al., 2018; Botting et al., 2019; Brayard et al., 2019; Charbonnier et al., 2019; Iniesto et al., 2019; Romano et al., 2019; Saucède et al., 2019; Thuy et al., 2019). Younger sedimentary layers in nearby Sleight Canyon also yielded well preserved specimens of rarely reported horseshoe crabs (Lerner et al., 2017; Lockley et al., 2018). Ammonoids are mostly compressed, but some specimens preserve sufficient 3D features such as ribs and tubercles, thus providing robust evidence for taxonomic assignment. After careful observation of numerous *Tirolites harti* specimens from the overlying *Tirolites* beds (*sensu* Smith, 1932) at the same locality and contrary to the first statement of Brayard et al. (2017), the shape and density of the ventrolateral nodes and ribs of *Tirolites* specimens from the studied exposures fit within the intraspecific variation documented for *Tirolites harti* (Fig. 2). In addition, recently sampled, rare ammonoid specimens that exhibit apparently smooth flanks and venters as well as an intermediate involution may correspond to the overall shape and ornamentation of *Bajarunia* cf. *pilata*. However, due to the extreme compaction of the latter specimens, this occurrence remains questionable at Paris Canyon. Additionally, some sampled specimens show thickened ventrolateral nodes that become more and more closely spaced during ontogeny. This ornamentation pattern roughly resembles the dense nodes observed, e.g., on some *Albanites* species from Tethyan and Mangyshlak localities (M. Balini, pers. comm. 2018), as well as crenulated ventrolateral margins observed on *A. sheldoni* from the younger *Columbites* beds at the neighboring Hot Springs section (Guex et al., 2010; Fig. 1) and in Japan (Ehiro et al., 2016). However, the Paris Canyon specimens

differ by their apparently more compressed whorl section as well as their more pronounced nodes, thus justifying the erection of the new species *Albanites americanus*. Orthoconic nautiloids also occur in the Paris Biota, sometimes reaching large size (up to ~20 cm). Coiled nautiloids have not yet been found in the Paris Biota, but do occur very rarely in the overlying Middle Limestone unit and are abundant in the younger *Columbites* beds at the neighboring Hot Springs section (Fig. 2).

The second sampled site is located on the west flank of Schmid Ridge, northeast of Georgetown and east of Soda Springs, in Caribou County (Fig. 1). Kummel's (1954) stratigraphic subdivisions for the Bear Lake Valley (e.g., Lower Shale unit) are not strictly applicable in this area. Instead, a rarely exposed, platy shale interval more or less equivalent in age to the studied horizon in Paris Canyon, occurs in the upper part of the 200 to 260 m-thick Lower Black Shale Member of Cressman and Gulbrandsen (1955). This member includes by definition the middle Smithian *Meekoceras* limestone at its base. Exposures of this early Spathian platy shale interval contain *Tirolites harti*, *Tirolites* aff. *cassianus*, *Bajarunia* cf. *pilata* and *Caribouceras slugense* nov. gen., nov. sp., and are here more nodular and darker than at Paris Canyon, suggesting potentially more disoxic to anoxic local conditions (Fig. 2). At this site, specimens are not as compressed as in the Paris Biota. Consequently, 3D preservation is much better. Nautiloids are apparently absent from this locality.

The third site, also in Caribou County, is located in Stewart Canyon on the east side of Dry Ridge, east of Schmid Ridge (Fig. 1). Here, early Spathian shales exhibit a very dark and silty facies indicative of a potential anoxic environment. These strata are included in the ~200 m-thick A Member of the Thaynes Group (Montgomery and Cheney, 1967), which is roughly equivalent to the Lower Black Shale Member at Schmid Ridge. The *Meekoceras* limestone is also included at its base, and rare latest Smithian nodules with *Pseudosageceras augustum* have been found a short distance above the *Meekoceras* beds (Fig. 2). Ammonoid specimens are extremely flattened and rarely show diagnostic ornamentation. *Tirolites* is seemingly absent, but *Bajarunia* cf. *pilata* occurs sparsely only a few meters above the latest Smithian nodules. Orthoconic nautiloids (up to ~25 cm) are common. The rest of the Spathian rocks here are covered.

The last sampled site, also occurring within the A Member, is located in Timothy Canyon, on the northwestern side of the Webster Range (Fig. 1). Smithian rocks here are still mainly massive limestones containing a poorly preserved *Meekoceras* fauna, but the early Spathian is represented by sporadically outcropping, organic matter-rich, dark blue to dark

brownish, very finely laminated shales. The base of these shales is mostly covered, but shales cropping out higher in the section include abundant co-occurring *Columbites parisianus*, *Bajarunia cf. pilata*, *Tirolites smithi*, *Coscaites crassus* and Hedenstroemiidae gen. indet., sp. indet. (note that this type of assemblage was not initially documented by Guex et al., 2010), as well as numerous orthoconic nautiloids (Fig. 2).

4. Systematic paleontology

Ammonoid systematic descriptions follow the classification of Tozer (1981), and that further refined by Guex et al. (2005a, 2005b, 2010) and Jenks et al. (2013). Nautiloid systematic descriptions mainly follow the classifications of Sobolev (1989) and Shigeta et al. (2014). Exact quantitative morphological ranges for all ammonoid taxa are not permitted because of the compressed preservation of many specimens. We thus mainly report estimates for the diameter (D), whorl height (H) and umbilical diameter (U) of the best preserved specimens. Whorl width (W) is also given when possible. Scatter diagrams of H, W and U, as well as H/D, W/D and U/D are provided only when the number of measured specimens is higher than five. Measurements are given in Table 1. Repository of figured specimens collected from private land is abbreviated UBGD (Université de Bourgogne, Géologie Dijon). Specimens collected from US public land are repositied in the Idaho Museum of Natural History (IMNH; John A. White Paleontological Repository) in Pocatello. A list of classified specimens and their assigned inventory numbers is given in Table 2. The number of sampled specimens (very fragmentary to complete) for each taxon and locality is indicated as “n =”.

Order Ammonoidea Zittel, 1884

Suborder Ceratitina Hyatt, 1884

Superfamily Dinaritoidea Mojsisovics, 1882

Family Tirolitidae Mojsisovics, 1879

Genus *Tirolites* Mojsisovics, 1879

Type species: *Ceratites idrianus* Hauer, 1865.

Remarks: Compressed, evolute to rather evolute shell with tubercles or prominent spines on or near the ventrolateral margin. Suture line typical of Dinaritoidea with a relatively simple architecture often showing only two large lateral saddles. This taxon is a typical genus marking the early Spathian from low paleolatitude basins. *Tirolites* has been reported from South China (e.g., Chao and Wang, 1974; Galfetti et al., 2007a), South Primorye (Buriy and Zharnikova, 1981; Zakharov et al., 2004; Shigeta and Kumagae, 2016; Zakharov and

Smyshlyaeva, 2016), Japan (Shigeta and Nakajima, 2017), northeastern Vietnam (e.g., Shigeta et al., 2014), Pakistan (Guex et al., 1978), Afghanistan (Collignon, 1973), Iran (Tozer, 1972; Balini et al., 2009), Mangyshlak (Shevyrev, 1968; Gavrilova 1989, 2007; Balini et al., 2000; Zakharov and Popov, 2007; Gavrilova and Snigirevskaya, 2018), Romania (Cavin and Gradinaru, 2014), Hungary (Posenato, 1992; Hips and Pelikan, 2002), Balkans (e.g., Krystyn, 1974; Golubić, 1996, 2000), southwestern Alps (e.g., Neri and Posenato, 1985; Broglio Loriga et al., 1990; Posenato, 1992), northern Mexico (Lucas et al., 1997), and western USA (Hyatt and Smith, 1905; Smith, 1932; Kummel, 1969; Guex et al., 2010; Jenks et al., 2013; Hofmann et al., 2013). This genus includes numerous species, which display a large intra-specific variation, especially in terms of ornamentation (tubercles and ribs). A revision of these regional species based on new material may help to clarify the taxonomy of this genus and establish the respective temporal distribution of the remaining valid species.

Tirolites harti Smith, 1932

Fig. 3(A-C)

1932. *Tirolites harti* Smith - p. 83, pl. 57, figs. 9-10.

1932. *Tirolites knighti* Smith - p. 84, pl. 57, figs. 1-4.

1932. *Tirolites peali* Smith - p. 84, pl. 57, figs. 5-8.

1969. *Tirolites harti* Kummel - p. 501, pl. 71, figs. 1-7.

2010. *Tirolites harti* Guex et al. - p. 29, pl. 50, figs. 1-3.

Occurrence: Rather common in the early Spathian Lower Shale and Middle Limestone units at Paris Canyon (n = 6), and in equivalent aged beds at Schmid Ridge (n > 10). Apparently absent from Dry Ridge and Webster Range.

Measurements: See Table 1.

Description: Evolute shell with a rectangular whorl section. Venter is slightly arched. Typical ribbed ornamentation with numerous tubercles on the ventrolateral shoulder. Tubercles are generally rather coarse and rounded at their base but may be relatively spiny on a few small specimens and more elongated on a few rare specimens. Tubercles are developed at the end of delicate ribs. Space between tubercles can be variable within and among specimens, but often relatively regularly spaced in inner whorls. Ribs are generally perpendicular to the coiling. Umbilical margin rounded. Suture line not preserved on our specimens.

Remarks: *Tirolites knighti* and *T. peali* fall within the large intraspecific variation of *T. harti* by exhibiting distinctive tubercles at the ventrolateral margin and a variable intensity of ornamentation, justifying their synonymy. *Tirolites smithi* found in the younger *Columbites*

beds can be easily distinguished from *T. harti* by its more involute coiling and its tubercles, which are located just below the ventral shoulder and more widely and regularly spaced. *Tirolites harti* resembles the European species *T. cassianus* and *T. haueri*, but both often exhibit more numerous and coarser ribs and bullate-like tubercles, which are also often more projected forward (Kummel, 1969; Detre et al., 1986; Posenato, 1992; Golubić, 2000). The type species, *T. idrianus*, shows more forward projected and distant bullate-like tubercles and fewer ribs, although this pattern may vary from one specimen to another (Kummel, 1969; Posenato, 1992). The specimen attributed to *Tirolites mangyshlakensis* by Krystyn (1974) is closer to *T. smithi*. Tubercles on *T. cf. ussuriensis* are located just below the ventral shoulder (Shigeta and Nakajima, 2017). *Tirolites cf. cassianus* from northeastern Vietnam is distinguished by its backward projected tubercles (Shigeta et al., 2014). *Tirolites longilobatus* from South Primorye (Shigeta and Kumagae, 2016) and *Tirolites* nov. sp. from northeastern Vietnam (Shigeta et al., 2014) exhibit much more elongated and spiny tubercles.

Tirolites aff. *cassianus* (Quenstedt, 1849)

Fig. 3(D-H)

Occurrence: Common in the early Spathian Lower Shale Member at Schmid Ridge (n = 15). Apparently absent from other sampled localities.

Measurements: See Table 1.

Description: Shell coiling similar to *T. harti*. Ornamentation highly variable, consisting of ribs and pronounced bullate-like tubercles extending on flanks, which are often strongly projected forward and irregularly spaced in some specimens. Ribs and tubercles tend to become denser or fade at large size. Umbilical shoulders appear to be rounded. Suture line not preserved on our specimens.

Remarks: As stated by, e.g., Posenato (1992), specimens included in *T. cassianus* exhibit a highly variable ornamentation, and a reappraisal of the numerous synonymized species is urgently needed. However, a revision of the genus *Tirolites*, which requires comparison among distant populations, has rarely been attempted because of several other equally challenging problems. These include the relative scarcity of the original specimens that served as the basis for the erection of the oldest named species, e.g., *T. cassianus*, a lack of good illustrations for many of the well-preserved specimens, and information regarding their exact stratigraphic occurrences. In this way, Posenato (1992) tried to circumvent these problems by including in his work figures, measurements and re-descriptions of the type specimens from the classical European sites of Dalmatia, Bakony and Dolomites. This work did not

completely clarify the classification of the various *Tirolites* species found in these localities. However, it did show that a relative distinction among species could be made from the number of tubercles/nodes on the last whorl, as well as the degree of involution of the shell; *T. cassianus* especially exhibits a very high number of tubercles/nodes on the last whorl and a relatively more evolute coiling when compared to other studied species.

The low number of sampled specimens from southern Idaho, as well as their poor preservation prevent a similar comparison. However, the intraspecific variation of our specimens fits rather well with many illustrated specimens worldwide (e.g., Iran; Tozer, 1972), especially from western Tethyan localities such as Muć in Dalmatia (Kittl, 1903; Kummel, 1969; Krystyn 1974; Golubić, 2000). Thus, our sampled specimens are possibly conspecific with *T. cassianus*, but their poor preservation and the lack of a suture line prevent a firm taxonomic attribution. *Tirolites* aff. *cassianus* can be distinguished from co-occurring *T. harti* by its coarser ribs and bullate-like tubercles, which are also more forward projected and often more irregularly spaced. *Tirolites* aff. *cassianus* differs from *T. smithi* by the ventrolateral position of its tubercles, which are also denser. *Tirolites* cf. *cassianus* illustrated from Vietnam by Shigeta et al. (2014) displays more conspicuous tubercles that are not always projected forward. Ornamentation on the Vietnamese specimens also apparently fades at a larger size. *Tirolites cassianus* illustrated from South Primorye (Buriy and Zharnikova, 1981) may fit with the intraspecific variation of Tethyan specimens, but ornamentation appears less forward projected.

Tirolites smithi Kummel, 1969

Fig. 4(L)

1932. *Tirolites illyricus* Smith - p. 84, pl. 49, figs. 12-16.

1932. *Tirolites smithi* Kummel - p. 501, pl. 54, figs. 1-5.

2010. *Tirolites smithi* Guex et al. - p. 27, pl. 4, figs. 1-2 ; pl. 53, figs. 1-2.

v.2013. *Tirolites smithi* Jenks et al. - p. 274, fig. 10A-D.

Occurrence: Only one specimen from the early Spathian Member A exposures in the Webster Range. Classical species with a large regional distribution, but not common in the Bear Lake area (Smith, 1932; Kummel, 1969; Guex et al., 2010). Not found at Schmid Ridge and Dry Ridge.

Measurements: Not available from this unique specimen.

Description: Shell coiling more involute than *T. harti* and *T. aff. cassianus*. Ornamentation consisting of rather regular and slightly projected ribs fading toward the venter. The latter is

arched to sub-tabulate and becomes apparently more rounded at very large size. Conspicuous tubercles are present on flanks near the ventrolateral margin, and are regularly and widely spaced on inner whorls, becoming slightly denser at large size. Ribs tends to fade at larger sizes where they more resemble weak folds. Umbilicus rather deep and exhibits rounded shoulders. Suture line not preserved.

Remarks: *Tirolites smithi* can be easily distinguished from *T. harti* and *T. aff. cassianus* by its more involute coiling and its regularly, widely spaced tubercles located high on the flank rather than on the ventrolateral margin. Large-sized specimens of *Tirolites* assigned to *T. carniolicus?* by Guex et al. (2010) may fit within the intraspecific variation of *T. smithi*, but their poor preservation prevents a firm assignment.

Family Columbitidae Spath, 1934

Genus *Columbites* Hyatt et Smith, 1905

Type species: *Columbites parisianus* Hyatt et Smith, 1905.

Remarks: Serpenticonic shell showing dense, often strong ribs and occasional constrictions, which cross the venter. On robust specimens, ribs often tend to form delicate tubercles at the ventrolateral margin. Flanks tend to become smooth at large size. Suture line ceratitic exhibiting a simple structure with two large lateral saddles. *Columbites* is a typical early Spathian genus, commonly found in the western USA basin (e.g., Kummel, 1969; Jenks et al., 2013; Hautmann et al., 2013). This taxon has been reported from other early Spathian exposures worldwide, most often from the tropical realm (Arthaber, 1908, 1911; Astakhova, 1960; Shevyrev, 1968; Tozer, 1972; Zharnikova, 1985; Germani, 1997; Mertmann and Jacobshagen, 2003; Galfetti et al., 2007a; Balini et al., 2009; Shigeta et al., 2014; Ehiro et al., 2015), but poor preservation often precludes a firm genus assignment in many localities (Kummel, 1969). Additionally, *Columbites* includes several species (e.g., Guex et al., 2010; Shigeta et al., 2014) and is morphologically close to some other columbitid genera, with which it often partly shares large overlapping intraspecific variation. This sometimes makes it difficult to identify poorly preserved specimens.

Columbites parisianus Hyatt et Smith, 1905

Figs. 5(A-I), 6

1905. *Columbites parisianus* Hyatt and Smith - p. 51, pl. 1, figs. 9-14; pl. 61, figs. 1-21; pl. 72, figs. 1-24.

1932. *Columbites spencei* Smith - p. 108, pl. 77, figs. 1-21; pl. 78, figs. 1-16.

1932. *Columbites consanquineus* Smith - p. 106, pl. 46, figs. 1-13.
1932. *Columbites ligatus* Smith - p. 106, pl. 47, figs. 1-8.
1932. *Columbites ornatus* Smith - p. 107, pl. 46, figs. 14-21.
- ?1968. *Columbites* cf. *parisianus* Zakharov - p. 106, pl. 20, fig. 5a, b.
1969. *Columbites parisianus* Kummel - p. 424, pl. 39, figs. 1-10; pl. 40, figs. 1-11; pl. 41, figs. 1-7; pl. 42, figs. 1-9; pl. 43, figs. 4-5.
- ?1974. *Columbites parisianus* Bando and Shimoyama - p. 301, pl. 40, figs. 2, 4, 6, 8; pl. 41, figs. 1, 10; pl. 42, figs. 1, 3.
2007. *Tirolites* sp. Lucas and Orchard - fig. 6b, c.
2010. *Columbites parisianus* Guex et al. - p. 30, pl. 6, figs. 1-7; pl. 7, figs. 1-4, pl. 53, fig. 5.
2013. *Columbites* cf. *parisianus* Hautmann et al. - p. 264, fig. 1.
- v.2013. *Columbites parisianus* Jenks et al. - p. 275, fig. 9A-D.
- ?2014. *Columbites* sp indet. Shigeta et al. - p. 155, fig 114.

Occurrence: Abundant in the early Spathian Member A exposures in the Webster Range (n > 30). Classical species also abundant in the Bear Lake area (Smith, 1932; Kummel, 1969; Guex et al., 2010; Jenks et al., 2013). Not found in Schmid Ridge and Dry Ridge.

Measurements: See Fig. 7 and Table 1. Maximum size is estimated to be close to 20 cm, but specimens reaching this size are extremely rare.

Description: Serpenticonic shell with a more or less quadratic whorl section and an arched to rounded venter, when preserved in 3D (e.g., Fig. 6(C)). Ornamentation typically consists of often dense strong ribs, which are usually prorsiradiate and sometimes cross the venter where they can be strongly projected forward. Some rare weak constrictions may be present. On the ventral margin, ribs can also tend to form small spiny tubercles on some specimens (Figs. 5(C), 6(J)). Ornamentation is weaker on compressed specimens and rapidly tends to totally fade when specimen reaches large size (Fig. 6(A, B)). Umbilicus relatively shallow with a rounded margin. Suture line not preserved on the available specimens.

Remarks: Our specimens fit within the typical large intraspecific variation observed for this classical American taxon (Guex et al., 2010). Specimens of *C. parisianus* illustrated from Japan by Bando and Shimoyama (1974) and Ehiro et al. (2015, 2016) exhibit many similarities with the present ones, but the ornamentation on some specimens appears weaker and more sickle-shaped, rather than prorsiradiate. The specimen of *Columbites* cf. *parisianus* from South Primorye illustrated by Zakharov (1968) also fits well within the intraspecific variation of *C. parisianus*, but more material is needed for a firm attribution. *Columbites parisianus* described by Zharnikova (1985) from South Primorye probably should be

reassigned to *Neocolumbites* Zakharov, 1968, based on its rounded venter and fading ornamentation at small size. Specimen UBGD 30663 illustrated in Fig. 6(A, B) is by far the largest example of this taxon (and any other Spathian ammonoid taxa in the western US basin) ever found, and the lack of intermediate sizes makes its attribution to *C. parisianus* somewhat suspicious. However, the specimen does exhibit all the characteristics of a rather less ornamented variant of *C. parisianus*.

Superfamily Meekoceratoidea Waagen, 1895

Family Albanitidae Tozer, 1994

Genus *Albanites* Arthaber, 1909

Type species: *Pronorites triadicus* Arthaber, 1908.

Remarks: Compressed shell with a moderately evolute coiling, typically showing a subtabulate to tabulate venter with a crenulated ornamentation. This taxon has been reported from various localities worldwide: Albania (Arthaber, 1908, 1911; Germani, 1997), Chios (Renz and Renz, 1948; Mertmann and Jacobshagen, 2003), Iran (Tozer, 1972; Balini et al., 2009), Mangyshlak (Shevyrev, 1968; Balini et al., 2000; Gavrilova and Snigirevskaya, 2018), South Primorye (Zakharov and Smyshlyaeva, 2016), Japan (Ehiro et al., 2016) and it also probably occurs in Arctic Canada (“*Neomeekoceras scalariforme*” Tozer, 1994; Guex et al., 2010). One species, *A. sheldoni*, occurs within the *Columbites* beds of southeastern Idaho (Kummel, 1969; Guex et al., 2013).

Albanites americanus nov. sp.

Fig. 4(A-E)

v.2017. *Tirolites* sp. Brayard et al. - Supplementary Material, fig. S15a, c, e, f.

Derivation of the name: The specific name is derived from the American continent.

Holotype: UBGD 30535 (Fig. 4(B) and fig. S15e in Brayard et al., 2017).

Paratypes: seven specimens UBGD 30671, UBGD 30673 to UBGD 30675, UBGD 30531, UBGD 30533, and UBGD 30536 (Fig. 4(A, C-E) and fig. S15a, c, f in Brayard et al., 2017).

Type locality and horizon: Paris Canyon, Bear Lake County, Idaho, USA; Early Triassic, early Spathian, Lower Shale Member, *Tirolites harti* beds.

Occurrence: Only from the type locality and horizon, but very abundant (n > 50).

Measurements: See Table 1.

Diagnosis: Compressed *Albanites* species showing a pronounced ornamentation on its flanks, even at a small size, and exhibiting the same crenulated pattern on the venter with initial widely spaced nodes evolving toward denser and thickened nodes during ontogeny.

Description: Compressed, moderately evolute shell with flanks slightly converging to a subtabulate or weakly arched venter. Ornamentation consists of a marked crenulation on the ventral margin resulting from existence of dense thickened nodes at the site, and weak, thin folds crossing the venter. Nodes are widely spaced on inner whorls and become more and more closely spaced during ontogeny. Folds crossing the venter are usually barely perceptible. Ornamentation also includes regular but weak and slightly projected folds and striae on flanks. Umbilical wall apparently low with a large rounded margin. Suture line unknown.

Remarks: This new species differs from younger *A. sheldoni* mainly by the more pronounced ornamentation on its flanks (striae, folds and thickened nodes), even at a small size, repeating the same crenulated pattern of initial widely spaced nodes evolving toward more dense nodes. In contrast, the crenulation pattern of *A. sheldoni* is more regular and appears later during ontogeny. Additionally, some *A. sheldoni* specimens show only very weak signs of crenulation (Guex et al., 2010). *Albanites americanus* nov. sp. can be distinguished from *A. vulgaris* (South Primorye; Zakharov and Smyshlyaeva, 2016) by its more marked ornamentation; from Chios and Albania species by its more compressed whorl section, and the ontogenetic evolution of its crenulated venter and weaker ribs crossing the venter (e.g., Arthaber, 1911; Renz and Renz, 1948; Mertmann and Jacobshagen, 2003). It also differs from Mangyshlak specimens by an apparently more compressed whorl section and by a different evolution of the crenulated ventral pattern, the latter being apparently reversed on specimens from Mangyshlak (M. Balini, pers. comm. 2018). Specimens of various *Albanites* species described from Iran by Tozer (1972) and Balini et al. (2009) appear thicker and apparently do not show marked node-thickenings at the ventral margin.

When poorly preserved, the early ontogenetic stages of this new species can be rather easily confused with *Tirolites* specimens, but the latter often shows true ribs that are absent in *A. americanus* nov. sp. This new earliest Spathian species enlarges the temporal distribution of *Albanites* in the western USA basin, demonstrating that it is not confined to the *Columbites* beds (Guex et al., 2010), but occurs soon after the SSB. It also probably represents one of the oldest occurrence of *Albanites* reported thus far (see usual co-occurring taxa in, e.g., Renz and Renz, 1948; Balini et al., 2009, 2010; Ehiro et al., 2016).

Family Hedenstroemiidae Waagen, 1895

Hedenstroemiidae gen indet., sp. indet.

Fig. 5(I, J)

Occurrence: Only one specimen from the Webster Range.

Measurements: See Table 1.

Description: Occluded and highly compressed shell, with smooth flanks. Venter apparently narrow. Suture line shows several adventitious elements and indentations on lateral lobe.

Remarks: The shell shape and suture line of the sampled specimen fits with representatives of the Hedenstroemiidae such as *Pseudosageceras* or *Cordillerites*, which are both found in southeastern Idaho (Guex et al., 2010; Jattiot et al., 2018; Jenks and Brayard, 2018).

Nevertheless, its preservation and the fact that its venter is not visible, prevent a firm attribution, based only on morphology. Additionally, the visible portions of the suture line do not reveal if the typical trifid lateral lobe of *Pseudosageceras* is present, and the number of adventitious elements cannot be counted, which would help to discriminate between *Pseudosageceras* and *Cordillerites*.

Suborder Phylloceratina Zittel, 1884

Family Ussuritidae Hyatt, 1900

Genus *Coscaites* Guex et al., 2005

Type species: *Coscaites crassus* Guex et al., 2005.

Remarks: Robust ussuritid showing typical strong and large, bulbous ribs, especially at large size. Suture line typical of ussuritids with a large first lateral lobe and a narrow second lateral saddle bent toward the umbilicus; a short auxiliary series is also present.

Coscaites crassus Guex et al., 2005b

Fig. 4(J, K)

2005b. *Coscaites crassus* Guex et al. - p. 11, pl. 2, fig. 1; pl. 6, fig. 4.

2010. *Coscaites crassus* Guex et al. - p. 66, pl. 34, fig. 4; pl. 35, fig. 1, pl. 57, fig. 4.

v.2013. *Coscaites crassus* Jenks et al. - p. 280, fig. 11T-W.

Occurrence: Only one specimen from the Webster Range. Also rare in the Bear Lake area (Guex et al., 2005a, 2005b, 2010). Not found in other studied exposures.

Measurements: See Table 1.

Description: Moderately involute coiling with a high whorl section. When preserved in 3D, whorl section becomes progressively wider on outer whorls (Guex et al., 2010); venter is

rounded and does not exhibit distinct shoulders. Ornamentation typically consists of large, strong bulbous type ribs at large size, whereas flanks are smooth on inner whorls. Umbilicus is rather deep with a vertical to slightly overhanging wall and a rounded margin. Suture line partly preserved on our unique specimen, showing the typical large first lateral lobe and narrow second lateral saddle bent toward the umbilicus (Fig. 4(K)).

Remarks: This taxon is relatively easy to recognize at large size based on its typical marked ribbing, especially when compared to other co-occurring taxa. However, its determination at smaller sizes is much more difficult, its flanks being smooth on inner whorls.

Superfamily and Family *incertae sedis*

Genus *Bajarunia* Dagys, 1983

Type species: *Ceratites euomphalus* Keyserling 1945.

Remarks: Compressed shell showing a more or less intermediate whorl involution and a relative high whorl. Venter generally varies from somewhat ogival on first juvenile stages to rounded in later ontogenetic stages. Ornamentation mainly consists of sigmoidal growth lines that sometimes form undulations on flanks. When visible, the suture line differs slightly among existing described species. For instance, it resembles that of *Meekoceras gracilitatis* with three broad saddles and weakly indented, lobes in North American *B. pilata* and *B. confusionensis* (Guex et al., 2010), whereas it exhibits more phylloid saddles and deeper lobes in *B. euomphala* and *B. eiekitensis* from Siberia (Dagys and Ermakova, 1988; Dagys et al., 1996).

Compared with the initial description of *Bajarunia* by Dagys (1983), this genus now includes several taxa with more or less similar shell morphologies, but with some slightly differing characters such as the suture line, which may call for an in-depth reappraisal of assigned species. If valid, the differences observed in the suture lines of North American species may justify the attribution of these specimens to a new genus. However, as the number of sampled North American specimens remains low and their preservation is rather poor (e.g., for *B. confusionensis*), a conservative approach is to continue to attribute these specimens to *Bajarunia* keeping in mind that the genus is potentially polyphyletic and possibly groups taxa of different origin.

Another possible point of confusion is that Dagys (1983) included his new genus in the family Meekoceratidae Waagen, 1895, and this attribution is still in use by some authors (e.g., Smyshlyayeva and Zakharov, 2015). However, this family includes highly disparate taxa with markedly divergent characters. As these taxa are likely of different phylogenetic origin,

it is not logical from an evolutionary point of view to keep them grouped in the same family. Additionally, because its type genus *Meekoceras* is now assigned to the Prionitidae (Brühwiler et al., 2012), the existence of the family Meekoceratidae is now obsolete. Thus, based on the taxonomic, systematic and phylogenetic uncertainties surrounding the genus *Bajarunia*, we follow the opinion of Guex et al. (2010) and leave this genus in family *incertae sedis*.

Bajarunia cf. *pilata*

Figs. 6(I), 8(A-J)

Occurrence: Rare in Paris Canyon (n = 3) and Dry ridge (n = 4), common at Schmid Ridge (n > 15) and Webster Range (n > 10).

Measurements: See Fig. 9 and Table 1.

Description: When preserved in 3D, the shell of *B. pilata* is compressed with a moderate involute coiling and an ogival section at first ontogenetic stages (Guex et al., 2010; Jenks et al., 2013). Flanks likely parallel but abruptly converging towards the venter at ~2/3 of whorl height. When preserved in 2D, like most of our specimens, flanks are often apparently rather smooth with only sinuous, fine growth lines. However, some specimens display marked, rather sinuous undulations, especially near the umbilical margin of inner whorls. Rare specimens show undulations at all ontogenetic stages. Suture line known only from a single specimen. Although poorly preserved, it clearly shows the presence of large saddles that agree rather well with those illustrated for *B. pilata* by Guex et al. (2010).

Remarks: Our specimens resemble *B. pilata* by having a weak, projected ribbing at large size, and a similar structure of suture line, but a firm attribution is prevented due to the compressed preservation state of most specimens. The shell morphology of the type species *B. euomphala* is nearly identical to *B. pilata* from the *Columbites* beds of Hot Springs (Guex et al., 2010; Jenks et al., 2013). Both taxa apparently differ mainly by their suture line. For *B. pilata*, the suture line needs to be better described from additional material to definitively determine if differences are valid. *Bajarunia eiekitensis* Popov, 1962 differs from the type species by its more evolute coiling and more marked undulations on its inner whorls.

?*Bajarunia* sp. indet.

Figs. 8(J-right)

Occurrence: Only one specimen from the Webster Range.

Measurements: See Fig. 9 and Table 1.

Description: Specimen showing an overall shape resembling *Bajarunia* cf. *pilata* with a moderate involute coiling and a high whorl section. Flanks apparently smooth but with very delicate, radial lirae and growth lines. Suture line unknown.

Remarks: The overall shell morphology of this specimen is close to *Bajarunia* cf. *pilata* (see Fig. 9 for comparison of H/D and U/D ratios). However, the flanks show very delicate, radial lirae, which (i) are not visible in co-occurring specimens of *B.* cf. *pilata*, and (ii) have not been documented in other *Bajarunia* species. As its suture line is unknown, we tentatively assign this specimen to *Bajarunia* based on its overall morphology. Inner whorls exhibit a polygonal shape resulting from extreme compaction, thus making it difficult to relate this specimen to *Nordophiceratoides* (Guex et al., 2010). Additional material is needed to firmly determine its taxonomical identity.

Genus *Caribouceras* nov. gen.

Derivation of the name: Derived from the name of Caribou County, Idaho, USA, where the type locality, Schmid Ridge is located. Gender *neuter*.

Type species: *Caribouceras slugense* nov. gen., nov. sp.

Occurrence: Only two specimens found at Schmid Ridge, bed S2, Caribou County.

Diagnosis: Compressed shell with a moderate involute coiling and a lanceolate section at first ontogenetic stages. Small specimens exhibit a delicate keel. Flanks showing only a weak folding. Suture line unknown.

Remarks: Such form with a lanceolate section and a keel are extremely rare in the early Spathian; the morphologically closest taxon being *Dorikranites* Hyatt, 1900. This new taxon differs from all other somewhat similar species. *Caribouceras slugense* nov. gen., nov. sp. exhibits a keel only during the first ontogenetic stages and rather smooth flanks, whereas *Dorikranites* shows a keeled lanceolate section throughout ontogeny as well as a marked ornamentation on flanks, including ribs and nodes. As our specimens do not preserve any suture line, no family attribution can be made.

Caribouceras slugense nov. gen., nov. sp.

Fig. 4(F-I)

Derivation of the name: The specific name refers to Slug creek, close to the type locality.

Holotype: IMNH IP-287/958 (Fig. 4(F-H)).

Paratype: IMNH IP-287/959 (Fig. 4(I)).

Type locality and horizon: Schmid Ridge, Caribou County, Idaho, USA; Early Triassic, early Spathian, Lower Shale Member, *Tirolites harti* beds.

Occurrence: only from the type locality and horizon.

Measurements: See Table 1.

Diagnosis: As for the genus, by monotypy.

Order Orthoceratida Kuhn, 1940

Family Orthoceratidae M'Coy, 1844

Genus *Trematoceras* Eichwald, 1851

Type species: *Orthoceras elegans* Münster, 1841.

Remarks: Moderately expanding orthoconic shell with a circular whorl cross-section. Ornamentation mainly consists of fine lirae. Siphuncle located centrally with cylindrical connecting ring. Suture line straight. *Trematoceras* has been reported from various Early Triassic localities (e.g., Schastlivtseva, 1988; Sobolev 1989, Shigeta and Zakharov, 2009; Shigeta et al., 2014). Distinction between species is mainly based on the angle of shell expansion and type of lirae.

Trematoceras sp. indet.

Fig. 10

Occurrence: Rather common in all studied sites, except Schmid Ridge.

Measurements: Sampled specimens reach very large sizes, more than 20 cm in length.

Description: Orthoconic shell showing a very low angle of shell expansion and very fine, dense transverse lirae. Very weak folds are apparently present on largest specimens. Suture line not clearly visible on our specimens, but apparently straight. Siphuncle likely central.

Remarks: Our specimens are assigned to *Trematoceras* based on the very low angle of shell expansion and the presence of very fine lirae. A firm species assignment is not possible due to their preservation. They resemble the nearly coeval *Trematoceras* sp. indet. from Vietnam (Shigeta et al., 2014). They differ from *T. subcampanile* by their transverse lirae instead of reticulate lirae, and from *T. mangishlakense* and *T. insperatum* by the lower angle of shell expansion (Shigeta and Zakharov, 2009; Shigeta et al., 2014).

Order Nautilida Agassiz, 1847

Family Tainoceratidae Hyatt, 1883

Genus *Phaedrysmocheilus* Shimansky et Erlanger, 1955

Type species: *Nautilus subaratus* Keyserling, 1847

Remarks: Loosely coiled shell at youngest stages becoming more involutely coiled during ontogeny, leaving a small perforated umbilicus. It exhibits a slightly depressed whorl section at small size becoming rectangular to quadratic at large size. Flanks are slightly rounded at small size and become flatter at large size. Ornamentation highly variable and consists of tubercles on the ventral and umbilical margins at least during first volutions, as well as weak ribs on some species. Suture line simple, only slightly undulating. *Phaedrysmocheilus* is also reported from the Spathian beds of Siberia (e.g., Sobolev, 1989), possibly indicating long-distance dispersal between this basin and the western USA basin at that time.

Phaedrysmocheilus idahoensis (Kummel, 1953)

Figs. 11-13

?1953. *Metacoceras (Mojsvaroceras) frenchi* Kummel - p. 23, pl. 2, figs. 1-10, pl. 4, figs. 8-10.

?1953. *Germanonautilus montpelierensis* Kummel - p. 30, pl. 3, fig. 11.

1953. *Pleuronautilus idahoensis* Kummel - p. 37, pl. 4, figs. 2-4.

?1953. *Pleuronautilus newelli* Kummel - p. 41, pl. 4, fig. 1.

Occurrence: Rather common (n = 20) in the *Columbites* beds (*Yvesgalleticeras montpelierense* and *Columbites parisianus* horizons; Guex et al., 2010; Jenks et al., 2013), Middle Shale Member at Hot Springs, Bear Lake County, Idaho.

Measurements: See Fig. 14 and Table 1.

Description: Typical *Phaedrysmocheilus*, resembling the Siberian species *P. ornatus*, but with ventrolateral tubercles still present at very large size. Tubercles are rather spiny at small size (well visible when the shell is preserved) and become more blunt at large size. At small size, they generally display a “pair pattern”, one located at the umbilical margin, the other on the ventrolateral margin with both linked by a weak rib. In very rare cases, the tubercles are positioned in staggered rows on the first few whorls (Fig. 12(E)). Ribbing tends to disappear during ontogeny being rapidly replaced by large folds. Tubercles also tend to fade more rapidly on the ventrolateral margin than on the umbilical margin. During ontogeny, tubercles and ribs fade progressively but reappear rapidly when reaching large size (Fig. 12(A, B)). Ornamentation also includes strong growth striae projected backward when crossing the ventrolateral margin and forming a sinus on the venter. A faint strigation is also visible on the venter and flanks (at least near the ventrolateral margin) on many specimens. During ontogeny, the venter is successively rounded, arched and more and more depressed at the

level of the sinus. The umbilicus is very deep with an almost vertical wall throughout nearly all growth stages. The umbilical margins are rounded. Siphuncle is central, but with a slightly more dorsal position at small size. Suture line very simple, only slightly undulating, resembling that of *P. ornatus*.

Remarks: This taxon mainly differs from Siberian species by its ventrolateral tubercles still present at large size and more marked ornamentation at large size. Specimens illustrated from the *Columbites* beds of Hot Springs and from a neighboring coeval exposure in Montpelier Canyon, described as *Metacoceras frenchi* n. sp., *Germanonautilus montpelierensis* n. sp., *Pleuronautilus idahoensis* n. sp., and *Pleuronautilus newelli* n. sp. by Kummel (1953) are likely conspecific with our sampled specimens. However, the few published W/D and U/D ratio measurements of the holotypes of these species (Kummel, 1953; Fig. 14) are not completely congruent with ours. Because of the many similarities documented among these species, the large intraspecific and ontogenetic variations observed on our specimens, and the fact that they are all found in the very same beds, we elect to assign our specimens to *Phaedrysmocheilus idahoensis*. More work is needed to definitively solve the question of a unique *Phaedrysmocheilus* species occurrence in the *Columbites* beds of the Middle Shale Member of the Bear Lake area, but based on currently available evidence, this seems very likely.

5. Discussion

Extensive sampling of the studied outcrops clearly indicates that the lower Spathian deposits of the Lower Shale unit in Bear Lake County and coeval rocks in Caribou County (i.e., below the *Tirolites* [*sensu* Smith, 1932] and *Columbites* beds; Fig. 2) contain *Tirolites harti*, *Bajarunia* cf. *pilata*, and *Albanites americanus* nov. sp. The co-occurrence of *T. harti* and *B. cf. pilata* is common. At Dry Ridge, only *B. cf. pilata* has been found in the very base of the Spathian. At Schmid Ridge, two other taxa, *Caribouceras slugense* nov. gen., nov. sp. and *Tirolites* aff. *cassianus* co-occur with *T. harti* and *B. cf. pilata*.

Overall, these new occurrences indicate that the lower boundary of the *Tirolites* beds, and therefore the regional SSB must be shifted downward into the Lower Shale unit and coeval beds (Fig. 2). Accurately locating this boundary in the field is extremely difficult as the SSB is also located above late Smithian nodules (e.g., containing *Anasibirites* and/or *Pseudosageceras augustum*, authors pers. obs.). These nodules crop out only very sporadically at the base of the Lower Shale unit, and almost certainly are not present everywhere in the Bear Lake area. Additionally, at this point in our investigation, we cannot

eliminate the possibility that some nodules occurring even higher in the nodule horizon in the Lower Shale unit, e.g., the Georgetown section (Romano et al., 2012; Fig. 1), are not earliest Spathian in age. In summary, the occurrence of *T. harti*, *T. aff. cassianus*, *B. cf. pilata*, *Albanites americanus* nov. sp. and *Caribouceras slugense* nov. gen., nov. sp. in the earliest Spathian beds of the Bear Lake area indicates that *Tirolites* is not an ideal marker genus to characterize this short time interval in the western USA basin, as earlier suggested by Guex et al. (2010) in Utah. Nevertheless, it reaffirms that *Tirolites* is a diagnostic time marker for the early Spathian.

Bajarunia specimens of earliest Spathian age were collected for the first time from southeastern Idaho. However, the preservation of the sampled specimens prevents firm identification at the species level as well as comparisons with *Bajarunia confusionensis* found in Utah or elsewhere in the world (see above, Section 4). One significant result is that the temporal distribution of this genus in southeastern Idaho likely extends downward from the early Spathian *Columbites* beds to the older earliest Spathian beds in the Lower Shale unit and coeval beds (Guex et al., 2010; Jenks et al., 2013; this work).

Regarding nautiloids, the most striking apparent change is the appearance of coiled forms in the *Tirolites harti* (*sensu* Smith, 1932) and *Columbites* beds, which contrasts with the unique dominance of orthoconic nautiloids in the underlying Lower Shale unit. This may result from the successive environmental changes documented around the SSB, but the main nautiloid assemblage shift apparently occurs in slightly younger levels. During deposition of the basal *Columbites* beds, the occurrence of a taxon such as *Phaedrysmocheilus*, which is also found in high-latitude settings (e.g., Sobolev, 1994), may indicate rather homogeneous environmental conditions during this short time interval.

Acknowledgements

This work is a contribution to the ANR project AFTER (ANR-13-JS06-0001-01) and was also supported by the French “Investissements d’Avenir” program, project ISITE-BFC (ANR-15-IDEX-03). We acknowledge the Bear Lake County road department and private land owners D. M. Clow (Ogden, Utah), L. Rasmussen (Grace, Idaho) and his gate-keeper L. Hildreth (Soda Springs, Idaho) for allowing access to studied exposures. We are grateful to M. Balini and Y. Zakharov for helpful discussions. S. Lucas and M. Balini provided detailed reviews, which helped to improve this article. We thank A.S. Grosjean, P. Guenser and T. Hurd for their help on the field. All studied exposures in Caribou County lie on US Public Land; we thank the Bureau of Land Management (BLM, Paleontological Resource Use

Permit IDI-38297) and US Forest Service, Caribou National Forest (USFS, Special Use Permit CT5.01) for allowing access and collection.

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Table and Figure captions

Table 1. Measurements of some early Spathian ammonoids and nautiloids from the Paris Biota and Bear Lake area. D: Diameter; H: whorl height; W: whorl width; U: umbilical diameter; *: estimated.

Table 2. Number of repositied specimens for each identified taxon.

Fig. 1. Map of southeastern Idaho showing the location of sampled localities.

Fig. 2. Simplified composite stratigraphic logs showing main Early Triassic units in the Bear Lake area (modified after Romano et al., 2012 and Brayard et al., 2017). Stratigraphy follows the main units defined by Kummel (1943, 1954), Cressman and Gulbrandsen (1955), and Montgomery and Cheney (1967). Not all biostratigraphical horizons shown in logs are actual continuous occurrences. Biostratigraphical ammonoid zonation is therefore a generalization based on Brayard et al. (2009, 2013), Guex et al. (2010), Jenks et al. (2013), Jattiot et al. (2016, 2017), and this work (see described sections in the text for actual occurrences). Abbreviations: LL: Lower Limestone; LS: Lower Shale; ML: Middle Limestone; MS: Middle Shale; UCS: Upper Calcareous Siltstone; *Meek*: *Meekoceras* beds; *Anasib*: *Anasibirites* beds; *Tirol*: *Tirolites* beds; *Colum*: *Columbites* beds. Open circle indicates the questionable occurrence of *Bajarunia cf. pilata* in Paris Canyon.

Fig. 3. A-C. *Tirolites harti*, IMNH IP-287/950 to IMNH IP-287/952. **D-H.** *Tirolites* aff. *cassianus*, IMNH IP-287/953 to IMNH IP-287/957. All specimens from bed 2S, *Tirolites* beds, Lower Shale Member, Schmid Ridge, early Spathian. Identification of IMNH IP-287/955 (F) is questionable due to its extreme compaction, but its overall shape and ornamentation (especially nodes on inner and outer whorls) fits within the intraspecific variation of *T. aff. cassianus*. Scale bars: 10 mm.

Fig. 4. A-E. *Albanites americanus* nov. sp. UBGD 30671, UBGD 30535, UBGD 30670, UBGD 30673, and UBGD 30675 (B; holotype). All specimens from the Paris Biota beds, base of the Lower Shale Member, Paris Canyon, early Spathian. **F-I.** *Caribouceras slugense* nov. gen., nov. sp., IMNH IP-287/958 (F-H; holotype) and IMNH IP-287/959 (I; paratype);

both specimens from bed 2S, *Tirolites* beds, Lower Shale Member, Schmid Ridge, early Spathian. G: oblique view of the venter to highlight the presence of a keel; H: interpretative drawing of the restored whorl section based on F and G. **J.** *Coscaites crassus*, UBGD 30660, specimen from bed Tim1, shaly Member A, Webster Range, early Spathian. **K.** Suture line of UBGD 30660 at H = 26.7 mm. **L.** *Tirolites smithi*, UBGD 30661, specimen from bed Tim1+5, shaly Member A, Webster Range, early Spathian. Scale bars: 10 mm.

Fig. 5. A-H. *Columbites parisianus*. IMNH IP-289/970 to IMNH IP-289/977. **I.** *Columbites parisianus* (left) and Hedenstroemiidae gen. indet., sp. indet. (right), UBGD 30678. **J.** Suture line of Hedenstroemiidae gen. indet., sp. indet. on slab UBGD 30678 at H = 26.7 mm. All specimens from bed Tim1, shaly Member A, Webster Range, early Spathian. Scale bars: 10 mm.

Fig. 6. *Columbites parisianus*. **A, B.** UBGD 30663 (positive and negative imprints). **C.** UBGD 30664. **D.** UBGD 30665. **E.** UBGD 30666. **F.** UBGD 30667. **G.** UBGD 30668. **H.** UBGD 30669. **I.** UBGD 30670. **J.** UBGD 30672. All specimens from bed Tim1 (except for F and J from Tim1-2), shaly Member A, Webster Range, early Spathian. Specimen UBGD 30670 (I) is associated with *Bajarunia cf. pilata*. Scale bars: 10 mm.

Fig. 7. Scatter diagrams of H, U, H/D and U/D for *Columbites parisianus*. All specimens (n = 15) from beds Tim1 and Tim1-2, shaly Member A, Webster Range, early Spathian.

Fig. 8. A-I. *Bajarunia cf. pilata*. A-G: IMNH IP-287/960 to IMNH IP-287/965; all specimens from bed 2S, *Tirolites* beds, Lower Shale Member, Schmid Ridge, early Spathian; D, suture line of IMNH IP-287/961 at H = 14.8 mm; H, I: IMNH IP-288/967 and IMNH IP-288/968; specimens from bed Stw-MISS, base of the shaly Member A, Dry Ridge, early Spathian. **J.** *Bajarunia cf. pilata* (left; UBGD 30677) and ?*Bajarunia* sp. indet. (right; UBGD 30677). Specimens from bed Tim1, shaly Member A, Webster Range, early Spathian. Scale bars: 10 mm.

Fig. 9. Scatter diagrams of H, U, H/D and U/D for *Bajarunia cf. pilata* and one specimen of ?*Bajarunia* sp. indet. (*). Six specimens from the bed 2S, *Tirolites* beds, Lower Shale Member, Schmid Ridge; 2 from bed Stw-MISS, base of the shaly Member A, Dry Ridge; 2 from bed Tim1, shaly Member A, Webster Range; all specimens are early Spathian in age.

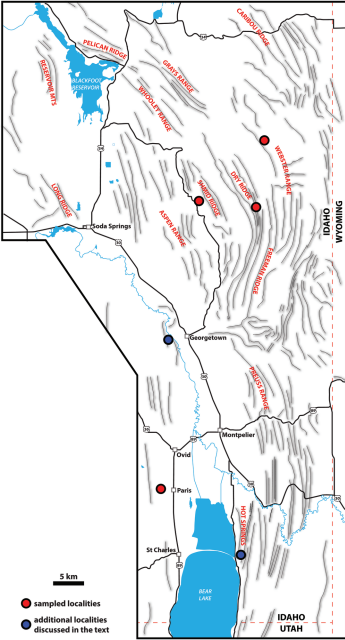
Fig. 10. *Trematoceras* sp. indet. **A, B.** IMNH IP-289/982 and IMNH IP-289/983. Both specimens from bed Tim1, shaly Member A, Webster Range, early Spathian. **C.** UBGD 30662, Lower Shale Member, Paris Canyon, early Spathian. **D.** UBGD 30676, *Columbites* beds, Hot Springs, early Spathian. Scale bars: 10 mm.

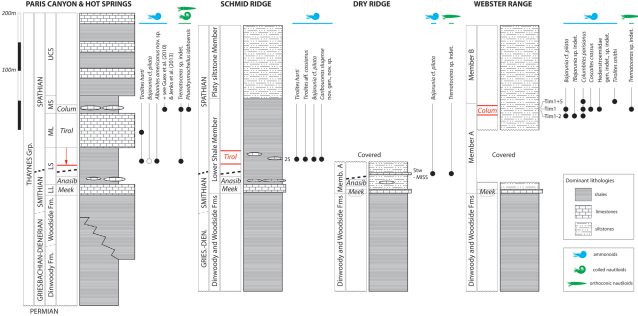
Fig. 11. *Phaedrysmocheilus idahoensis*. **A-C.** UBGD 30653. **D, E.** UBGD 30644. **F, G.** UBGD 30659. **H.** UBGD 30645. **I-K.** UBGD 30649. All specimens from the *Columbites* beds, Middle Shale Member, Hot Springs, early Spathian. Scale bars: 10 mm.

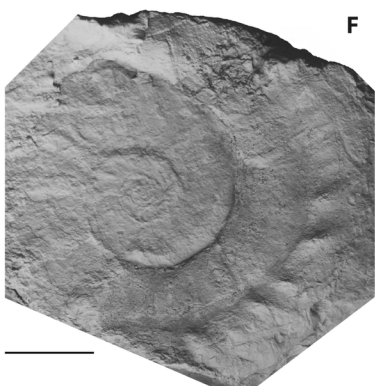
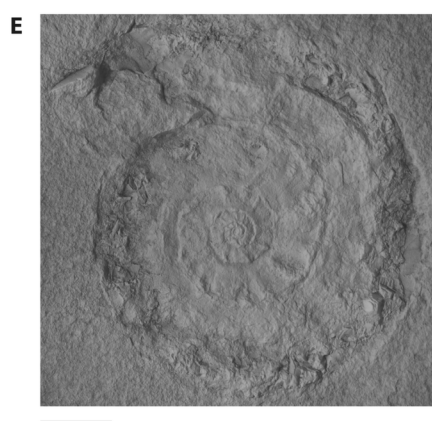
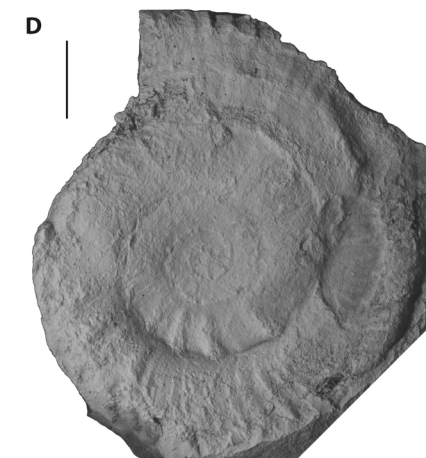
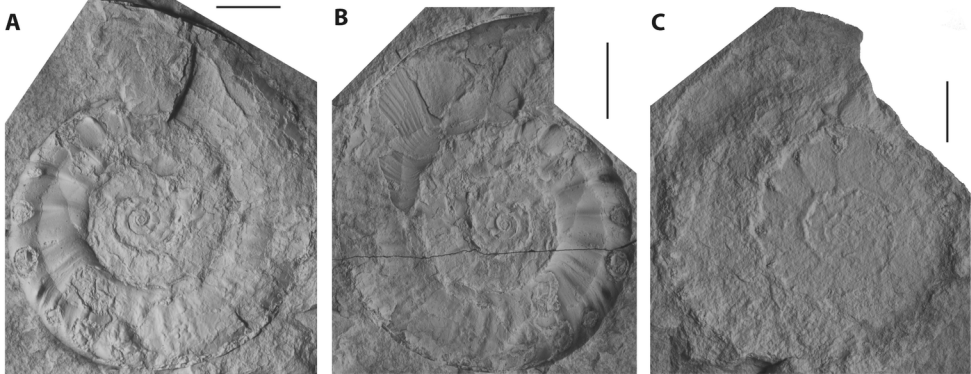
Fig. 12. *Phaedrysmocheilus idahoensis*. **A, B.** UBGD 30656. **C.** UBGD 30648. **D.** UBGD 30651. **E.** UBGD 30655. **F.** UBGD 30657. **G.** UBGD 30647. **H.** UBGD 30646. **I, J.** UBGD 30650. **K, L.** UBGD 30658. All specimens from the *Columbites* beds, Middle Shale Member, Hot Springs, early Spathian. Scale bars: 10 mm.

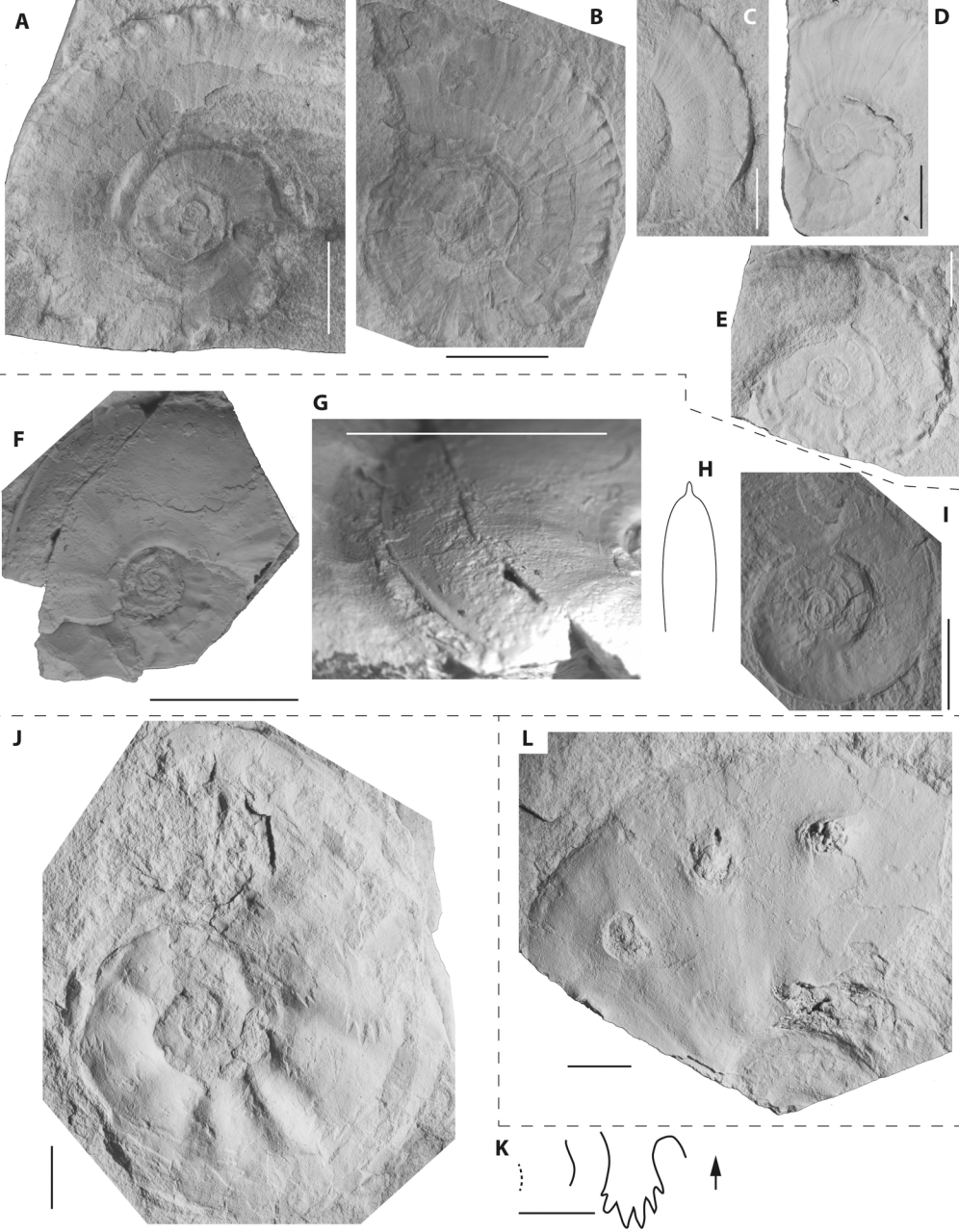
Fig. 13. *Phaedrysmocheilus idahoensis*. **A-C.** UBGD 30652. **D, E.** UBGD 30654. **F.** Suture line of UBGD 30647 at H = 21 mm. **G.** Suture line of UBGD 30655 at H = 14.2 mm. All specimens from the *Columbites* beds, Middle Shale Member, Hot Springs, early Spathian. Scale bars: 10 mm.

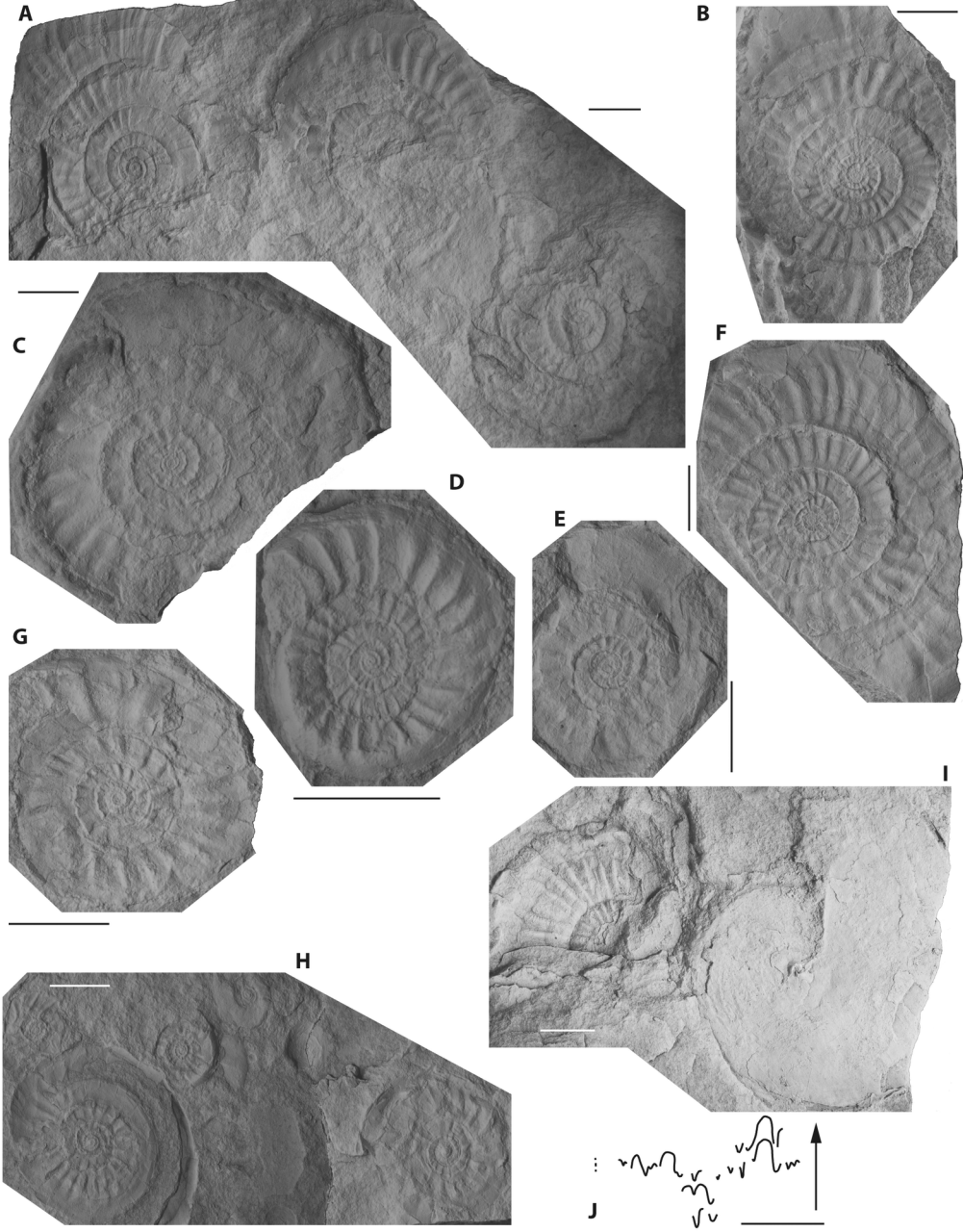
Fig. 14. Scatter diagrams of H, W and U, and H/D, W/D and U/D for *Phaedrysmocheilus idahoensis*. All specimens (n = 15) from the *Columbites* beds, Middle Shale Member, Hot Springs, early Spathian. For comparisons, measurements of holotypes of *Metacoceras frenchi* and *Pleuromutilus idahoensis* described by Kummel (1953) are highlighted in blue and red, respectively.

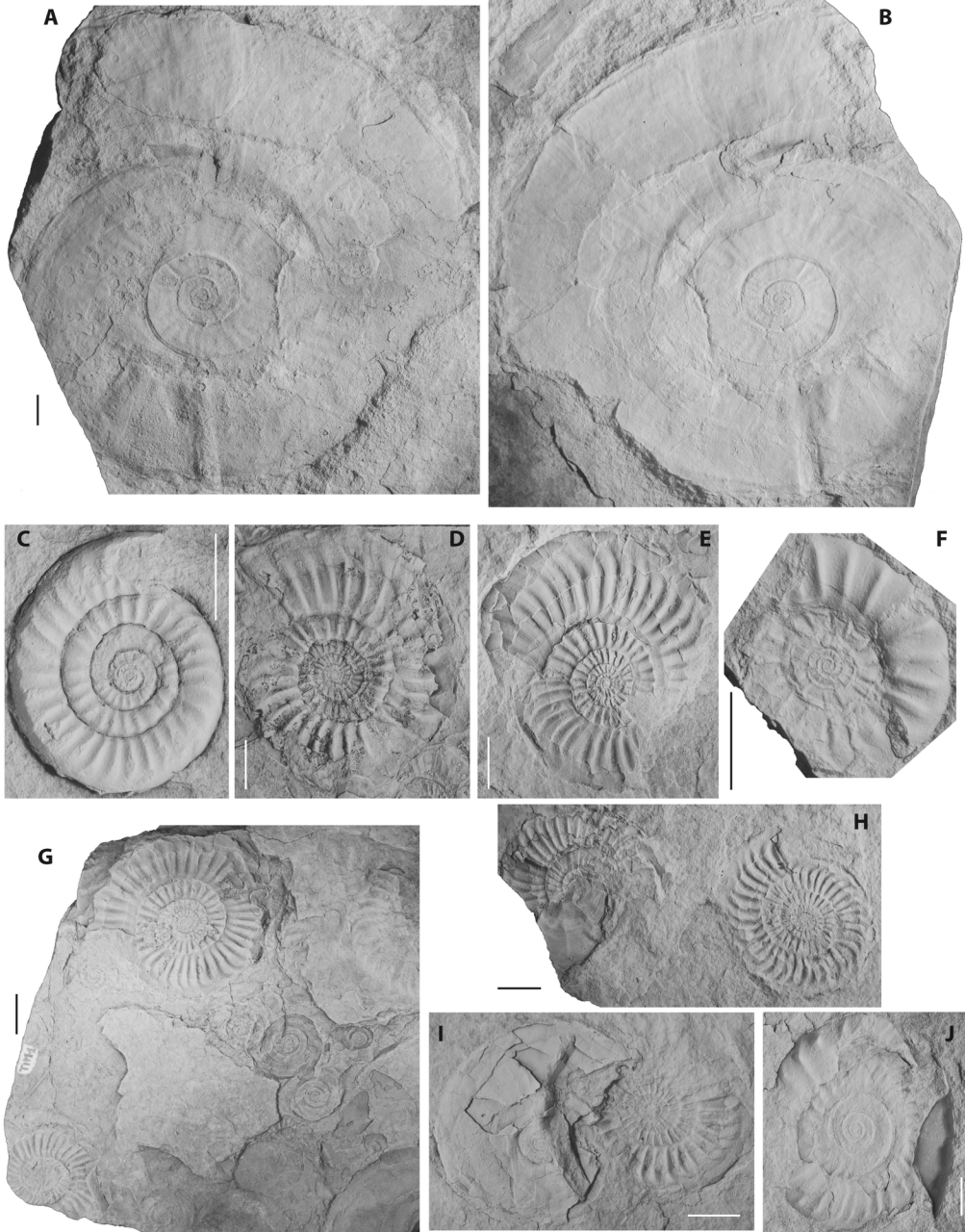


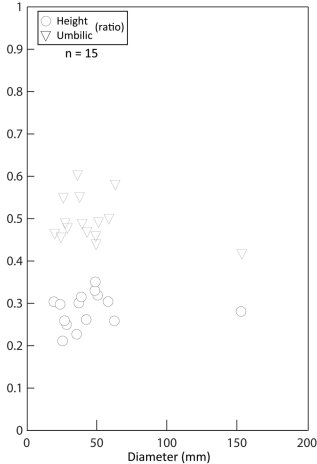
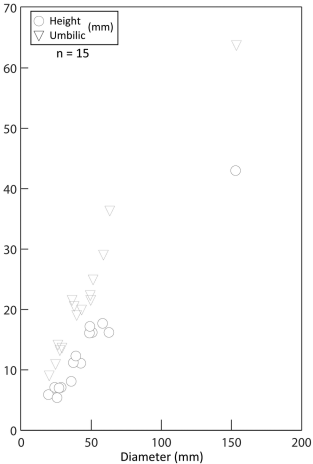


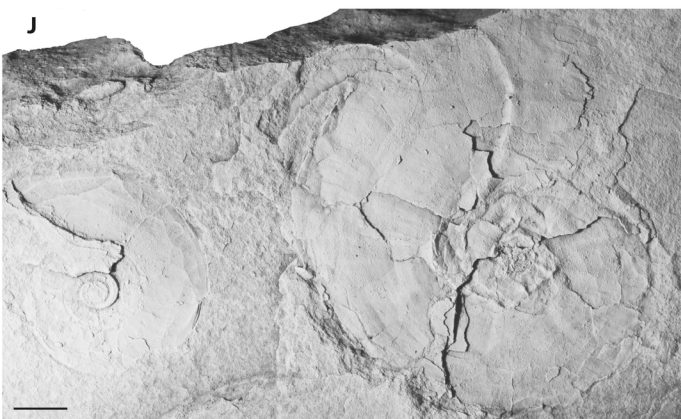
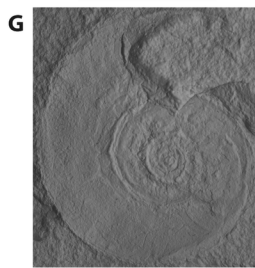
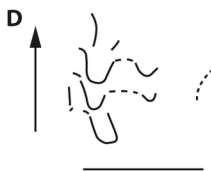
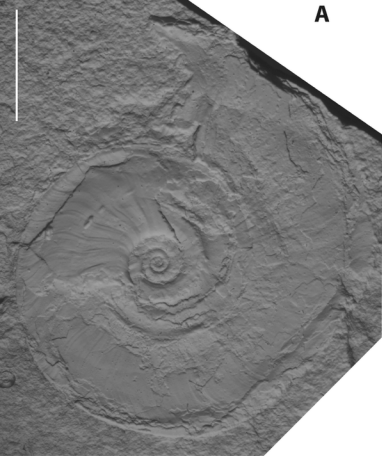


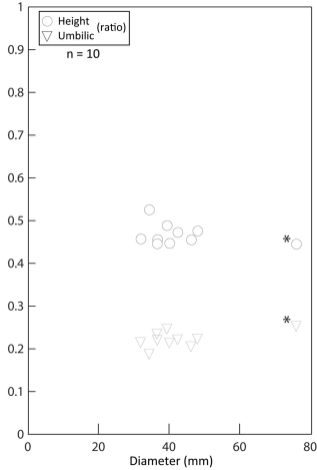
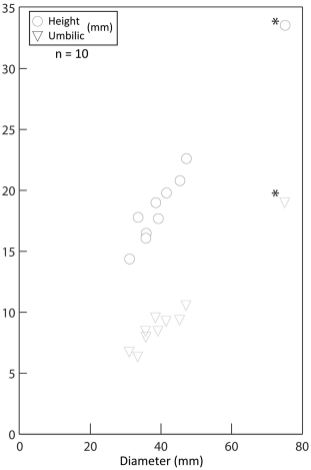


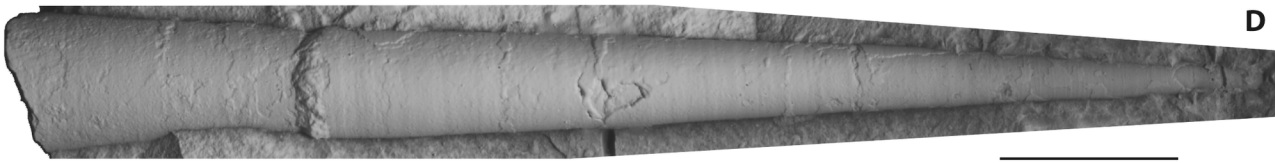


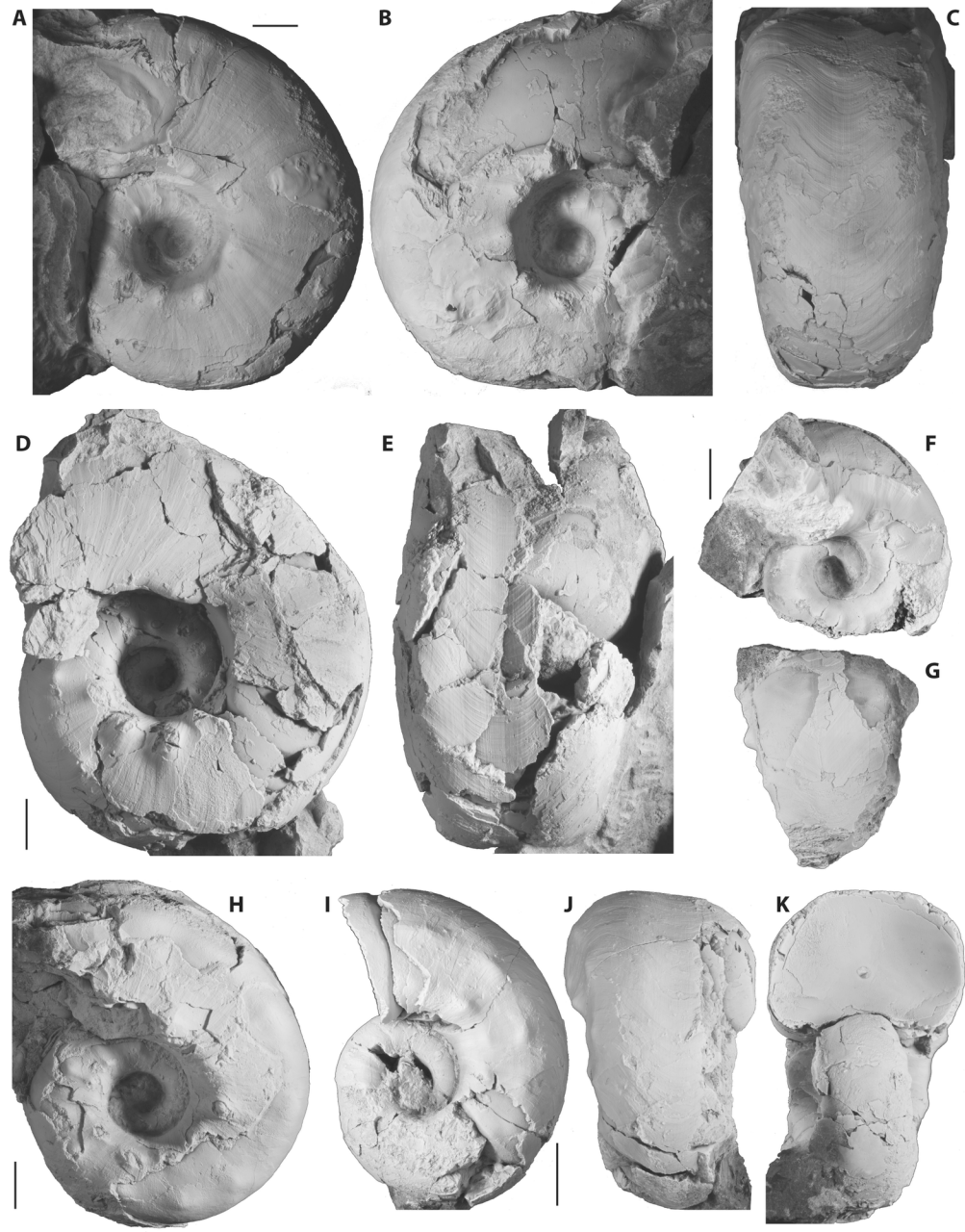


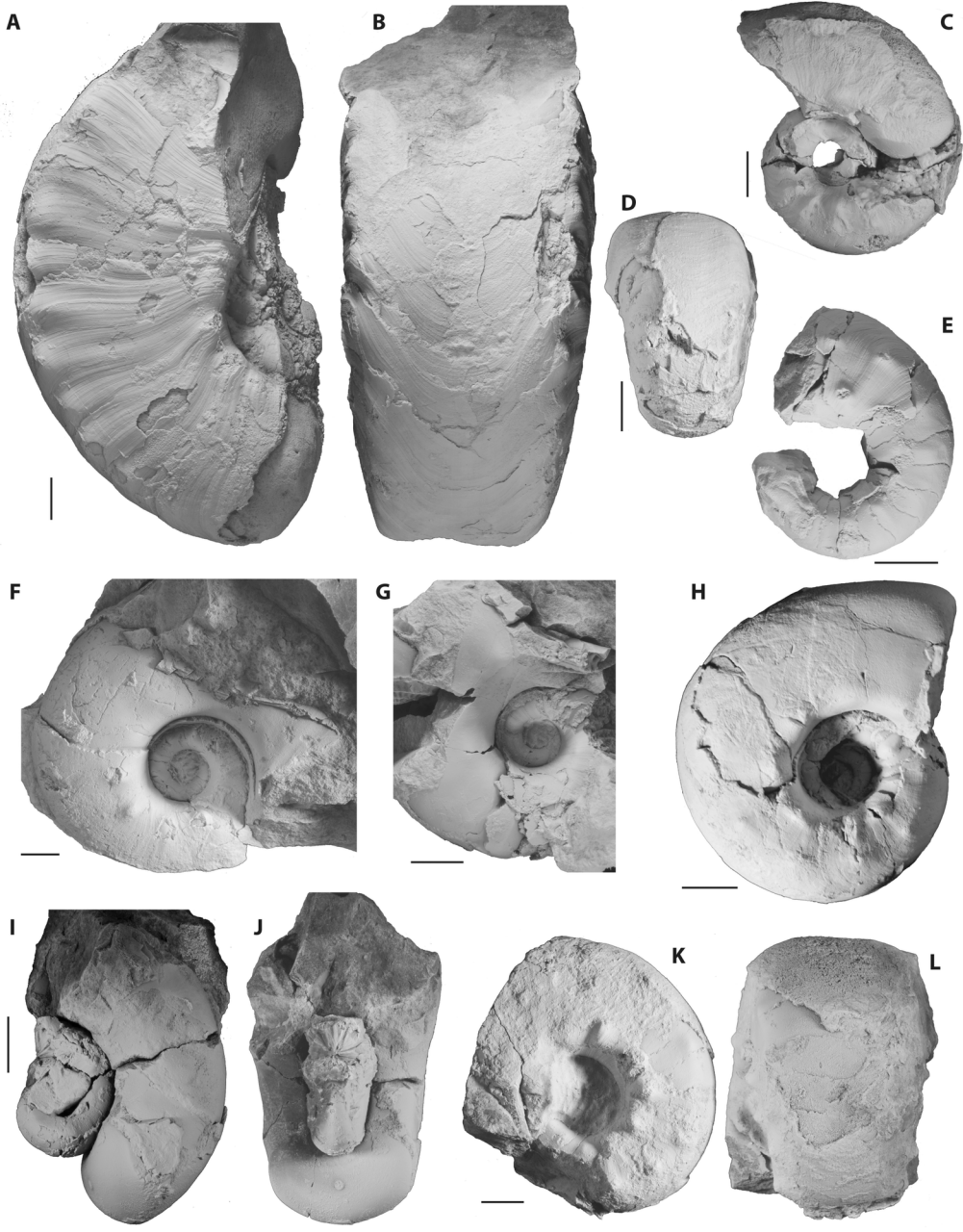


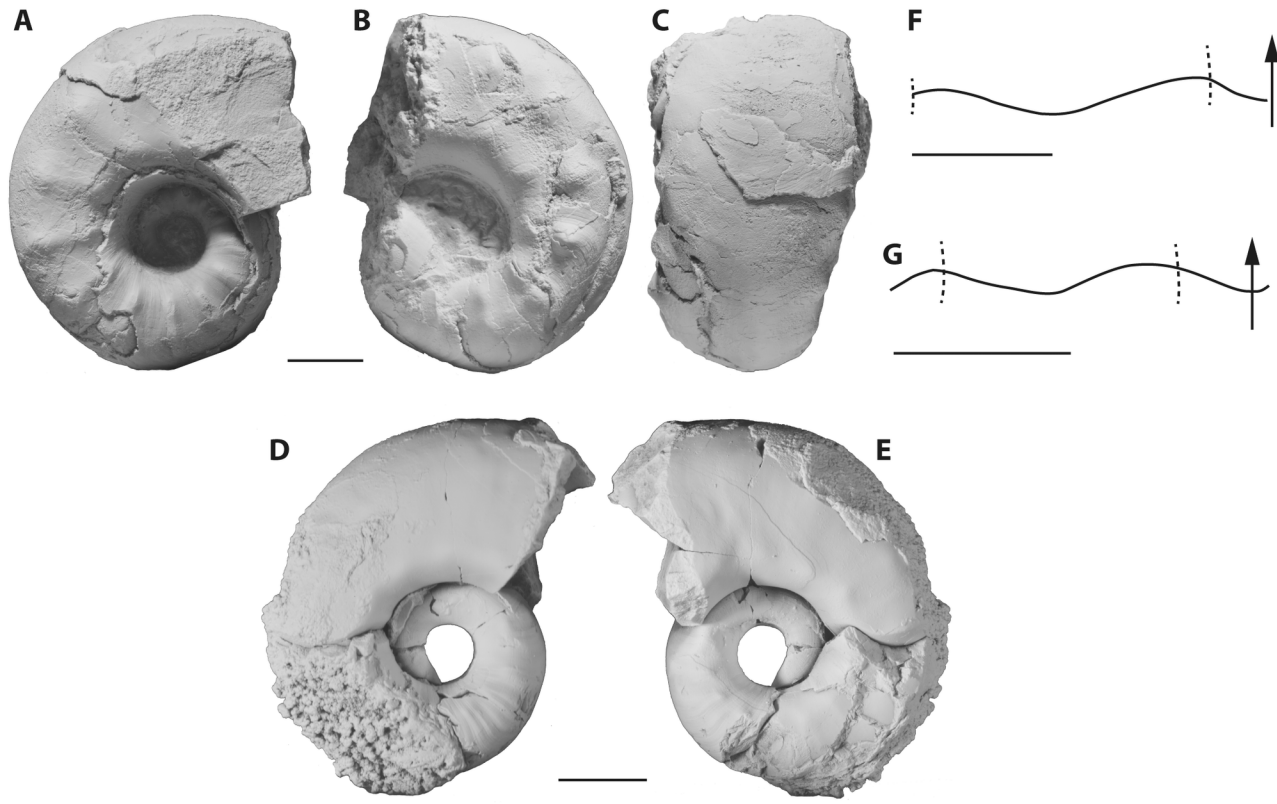


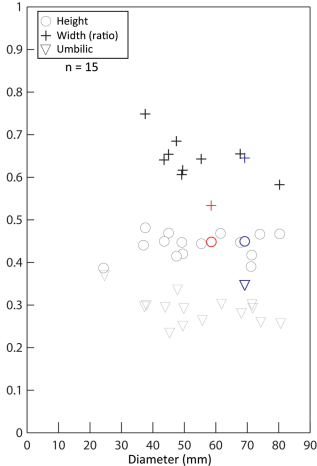
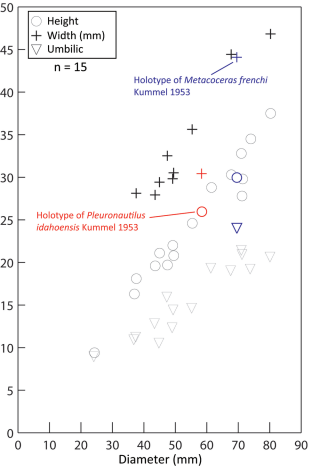












Brayard et al. Figure 14

Table 1.

Genus	Species	Specimen number	D	H	W	U	Remarks
<i>Tirolites</i>	<i>harti</i>	IMNH IP-287/951	48	14.4	-	23.3	
<i>Tirolites</i>	<i>harti</i>	IMNH IP-287/952	57.5	19.4*	-	24.8	
<i>Tirolites</i>	aff. <i>cassianus</i>	IMNH IP-287/954	51.5*	15.3	-	25.9	crushed near the ventral margin
<i>Tirolites</i>	aff. <i>cassianus</i>	IMNH IP-287/955	44	15.8	-	17	crushed on flank
<i>Tirolites</i>	aff. <i>cassianus</i>	IMNH IP-287/956	41.2	12.2*	-	21	
<i>Tirolites</i>	aff. <i>cassianus</i>	IMNH IP-287/957	25.4	8.8	-	9.3	
<i>Caribouceras</i> nov. gen.	<i>slugense</i> nov. sp.	IMNH IP-287/959	23.3	5.7*	-	9*	paratype
<i>Columbites</i>	<i>parisianus</i>	IMNH IP-289/970	42.5	11.13	-	19.89	
<i>Columbites</i>	<i>parisianus</i>	IMNH IP-289/971	62.6	16.2	-	36.3	
<i>Columbites</i>	<i>parisianus</i>	IMNH IP-289/972	58.1	17.7	-	29	
<i>Columbites</i>	<i>parisianus</i>	IMNH IP-289/973	50.7	16.2	-	24.9	
<i>Columbites</i>	<i>parisianus</i>	IMNH IP-289/974	19.4	5.9	-	9	
<i>Columbites</i>	<i>parisianus</i>	IMNH IP-289/975	25.6	5.41	-	14.05	
<i>Columbites</i>	<i>parisianus</i>	IMNH IP-289/976	35.7	8.11	-	21.51	
<i>Columbites</i>	<i>parisianus</i>	IMNH IP-289/977	28.5	7.13	-	13.6	
<i>Columbites</i>	<i>parisianus</i>	UBGD 30669	37.2	11.2	-	20.48	
<i>Columbites</i>	<i>parisianus</i>	UBGD 30667	23.9	7.12	-	10.88	
<i>Columbites</i>	<i>parisianus</i>	UBGD 30663	153	43	-	63.7	
<i>Columbites</i>	<i>parisianus</i>	UBGD 30664	27	7	-	13.2	
<i>Columbites</i>	<i>parisianus</i>	UBGD 30665	48.7	16.1	-	22.3	
<i>Columbites</i>	<i>parisianus</i>	UBGD 30666	39	12.3	-	19	
<i>Columbites</i>	<i>parisianus</i>	UBGD 30668	49	17.2	-	21.5	
<i>Albanites</i>	<i>americanus</i> nov. sp.	UBGD 30535	29.3	12.4	-	9.5	holotype
<i>Albanites</i>	<i>americanus</i> nov. sp.	UBGD 30671	43.9*	16.2	-	15.6	paratype
<i>Albanites</i>	<i>americanus</i> nov. sp.	UBGD 30675	45.4*	15.9*	-	15.4*	paratype

Hedenstroemiidae gen. indet.	sp. indet.	UBGD 30678	56.5*	19.3	-	-	
<i>Coscaites</i>	<i>crassus</i>	UBGD 30660	58	27.7*	-	16.5	crushed near the ventral margin
<i>Bajarunia</i>	cf. <i>pilata</i>	IMNH IP-287/960	33.8	17.8	-	6.3*	
<i>Bajarunia</i>	cf. <i>pilata</i>	IMNH IP-287/961	45.6	20.8	-	9.3	
<i>Bajarunia</i>	cf. <i>pilata</i>	IMNH IP-287/963	39.5	17.7	-	8.4*	
<i>Bajarunia</i>	cf. <i>pilata</i>	IMNH IP-287/964	36.1	16.5	-	7.9	
<i>Bajarunia</i>	cf. <i>pilata</i>	IMNH IP-287/965	30.8	11.3*	-	6*	
<i>Bajarunia</i>	cf. <i>pilata</i>	IMNH IP-287/966	31.4	14.4	-	6.7	not illustrated
<i>Bajarunia</i>	cf. <i>pilata</i>	IMNH IP-288/967	36	16.1	-	8.4*	
<i>Bajarunia</i>	cf. <i>pilata</i>	IMNH IP-288/968	47.4	22.6	-	10.5	
<i>Bajarunia</i>	cf. <i>pilata</i>	UBGD 30670	41.8	19.8	-	9.2	
<i>Bajarunia</i>	cf. <i>pilata</i>	UBGD 30677 (left)	38.8	19	-	9.5	
? <i>Bajarunia</i>	sp. indet.	UBGD 30677 (right)	75.2*	33.5*	-	18.9*	
<i>Phaedrysmocheilus</i>	<i>idahoensis</i>	UBGD 30644	71.2	27.8	-	21.5	
<i>Phaedrysmocheilus</i>	<i>idahoensis</i>	UBGD 30645	71.4	29.8	-	21	
<i>Phaedrysmocheilus</i>	<i>idahoensis</i>	UBGD 30646	61.5	28.8	-	194	
<i>Phaedrysmocheilus</i>	<i>idahoensis</i>	UBGD 30647	49.5	20.8	30.6*	14.5	
<i>Phaedrysmocheilus</i>	<i>idahoensis</i>	UBGD 30648	45	21.1	29.5	10.6	
<i>Phaedrysmocheilus</i>	<i>idahoensis</i>	UBGD 30649	55.4	24.6	35.7	14.7	
<i>Phaedrysmocheilus</i>	<i>idahoensis</i>	UBGD 30650	24.3	9.4	-	9	
<i>Phaedrysmocheilus</i>	<i>idahoensis</i>	UBGD 30651	47.5	19.7*	32.6	16	
<i>Phaedrysmocheilus</i>	<i>idahoensis</i>	UBGD 30652	49.2	22	29.9	12.4	
<i>Phaedrysmocheilus</i>	<i>idahoensis</i>	UBGD 30653	80.3	37.5	46.9	20.7	
<i>Phaedrysmocheilus</i>	<i>idahoensis</i>	UBGD 30654	43.6	19.6	28	12.9	
<i>Phaedrysmocheilus</i>	<i>idahoensis</i>	UBGD 30655	37	16.3	-	11	
<i>Phaedrysmocheilus</i>	<i>idahoensis</i>	UBGD 30657	74*	34.5*	-	19.3	
<i>Phaedrysmocheilus</i>	<i>idahoensis</i>	UBGD 30658	67.8	30.3	44.5	19.1	
<i>Phaedrysmocheilus</i>	<i>idahoensis</i>	UBGD 30659	37.6	18.1	28.2	11.3	

Table 2.

Genus	Species	Locality	Bed	Number of repositied specimens	Inventory numbers
<i>Tirolites</i>	<i>harti</i>	Schmid Ridge	2S	3	IMNH IP-287/950 to 952
<i>Tirolites</i>	aff. <i>cassianus</i>	Schmid Ridge	2S	5	IMNH IP-287/953 to 957
<i>Tirolites</i>	<i>smithi</i>	Webster Range	Tim1+5	1	UBGD 30661
<i>Caribouceras</i> nov. gen.	<i>slugense</i> nov. sp.	Schmid Ridge	2S	2	IMNH IP-287/958 and 959
<i>Albanites</i>	<i>americanus</i> nov. sp.	Paris Canyon	Lower Shale Mb.	9	UBGD 30531, 30533, 30535, 30536, 30671, 30670, and 30673-30675
<i>Coscaites</i>	<i>crassus</i>	Webster Range	Tim1	1	UBGD 30660
<i>Columbites</i>	<i>parisianus</i>	Webster Range	Tim1	16	IMNH IP-289/970 to 977, UBGD 30663-30670
<i>Columbites</i>	<i>parisianus</i>	Webster Range	Tim1-2	1	UBGD 30672
Hedenstroemiidae gen. indet.	sp. indet.	Webster Range	Tim1	1	UBGD 30678
<i>Bajarunia</i>	cf. <i>pilata</i>	Schmid Ridge	2S	7	IMNH IP-287/960 to 966
<i>Bajarunia</i>	cf. <i>pilata</i>	Dry Ridge	Stw-MISS	2	IMNH IP-288/967 and 968
<i>Bajarunia</i>	cf. <i>pilata</i>	Webster Range	Tim1	2	UBGD 30677(left)
? <i>Bajarunia</i>	sp. indet.	Webster Range	Tim1	1	UBGD 30677(right)
<i>Trematoceras</i>	sp. indet.	Webster Range	Tim1	2	IMNH IP-289/982 and 983
<i>Trematoceras</i>	sp. indet.	Paris Canyon	Lower Shale Mb.	1	UBGD 30662
<i>Trematoceras</i>	sp. indet.	Hot Springs	<i>Columbites</i> beds	1	UBGD 30676
<i>Phaedrysmocheilus</i>	<i>idahoensis</i>	Hot Springs	<i>Columbites</i> beds	16	UBGD 30644-30659