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Arnaud Brayard, James F. Jenks, Kevin G. Bylund, Nicolas Olivier, Emmanuelle Vennin, et al.. Latest Smithian (Early Triassic) ammonoid assemblages in Utah (western USA basin) and their implications for regional biostratigraphy, biogeography and placement of the Smithian/Spathian boundary.. *Geobios*, 2021, 69, pp.1-23. 10.1016/j.geobios.2021.05.003 . hal-03498753

**HAL Id: hal-03498753**

**<https://hal.science/hal-03498753>**

Submitted on 13 Oct 2022

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**Latest Smithian (Early Triassic) ammonoid assemblages in Utah (western  
USA basin) and their implications for regional biostratigraphy,  
biogeography and placement of the Smithian/Spathian boundary**

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## Abstract

The late Smithian extinction represents a major event within the Early Triassic. This event generally corresponds to a succession of two and possibly three successively less diverse, cosmopolitan ammonoid assemblages, which when present, provide a robust biostratigraphic framework and precise correlations at different spatial scales. In the western USA basin, known occurrences of latest Smithian taxa are rare and until now, have only been documented from northeastern Nevada. Based on these restricted basinal occurrences, a regional zone representing the latest Smithian was postulated but not corroborated, as representative taxa had not yet been reported from outside Nevada. Here we document two new ammonoid assemblages from distant localities in northern Utah, overlying the late Smithian *Anasibirites* beds and characterized by the unambiguous co-occurrence of *Xenoceltites subevolutus* and *Pseudosageceras augustum*. The existence of a latest Smithian zone in the western USA basin is therefore validated, facilitating the identification of the Smithian/Spathian boundary and intra-basin correlation. This zone also correlates with the latest Smithian zone recognized from southern Tethyan basins. Additionally, these new data support other observed occurrences of *Xenoceltites subevolutus* throughout most of the late Smithian.

## Keywords:

Late Smithian, Early Triassic, Ammonoids, Utah, Biostratigraphy

## 1. Introduction

The Early Triassic represents a time of marked successive biological and environmental changes following the Permian/Triassic mass extinction (PTME; ~252 Ma; Baresel et al., 2017). This ~5 myr-long period is for instance associated with major fluctuations in oceanic temperatures, global carbon cycle and anoxic conditions presumably triggered by the Siberian Traps (Payne et al., 2004; Galfetti et al., 2007; Sun et al., 2012; Grasby et al., 2013; Romano et al., 2013; Zhang F. et al., 2018; Thomazo et al., 2019; Zhao et al., 2020), although evidence for such a link has not yet been firmly established for all known environmental fluctuations (Widmann et al., 2020). Several secondary extinction events occurred during the Early Triassic, including a severe one at the onset of the late Smithian and continuing through the interval containing the Smithian/Spathian boundary (SSB; ~249.2 Ma; Tozer, 1982; Dagys, 1988; Brayard et al., 2006; Orchard, 2007; Hermann et al., 2012; Zhang L. et al., 2019). With regard to its effect on ammonoids, this event, which may be almost equal in magnitude to the PTME (Jattiot et al., 2016), is associated with a change in spatial distribution of taxa, becoming highly cosmopolitan (e.g., Brayard et al., 2006, 2007), and experiencing a drastic reduction in disparity (e.g., Brosse et al., 2013). The late Smithian event is coeval to a marked cooling following a temperature maximum reached near the middle/late Smithian boundary (e.g., Goudemand et al., 2019). In some localities, associated deposits also show probable dysoxic to anoxic environments (e.g., Galfetti et al., 2008; Grasby et al., 2013; Brayard et al., 2019), although the exact location of this anoxia between the water column and the sediment remain to be elucidated. Mechanisms underlying the late Smithian extinction are still unexplained (Widmann et al., 2020) but our knowledge of this event has improved recently. It shows that successive cosmopolitan ammonoid assemblages thrived during the late Smithian cooling (Jenks et al., 2015; Jattiot et al., 2016), although it is expected that they would become more endemic when influenced by such climatic trend



(Brayard et al., 2006). Nevertheless, an overall understanding of the numerous consecutive biotic and abiotic phenomena taking place at that time still requires their placement in a robust biostratigraphic framework in order to provide precise correlations at different spatial scales.

Early Triassic biostratigraphical scales based on ammonoids (e.g., Smith, 1932; Spath, 1934) and produced prior to the beginning of the 2010s (e.g., Tozer, 1994; Ermakova, 2002; Brayard and Bucher, 2008) have often treated the late Smithian as a unique biostratigraphic entity with numerous genera of the family Prionitidae, such as *Anasibirites* and *Wasatchites*, considered as typical of this time interval. However, in the last decade, many works have shown that the late Smithian can be subdivided into at least two parts (Brühwiler et al., 2010a, 2011, 2012a, b; Brayard et al., 2013; Jattiot et al., 2017; Jenks and Brayard 2018; see Jenks et al., 2015 for a summary of late Smithian global correlations). The lower part corresponds to a marked worldwide dominance of prionitids, a species-rich family (Jattiot et al., 2016), associated with a few xenoceltitid species (e.g., *Xenoceltites subevolutus*) and rare occurrences of surviving arctoceratids, inyoitids, galfettitids and palaeophyllitids in some places (Brühwiler et al., 2012a, b; Shigeta and Kumagae, 2015; Smyshlyaeva et al., 2018; Jattiot et al., 2020; questionably in Tozer, 1994, and Piazza et al., 2017). In most regions (see Zakharov et al., 2013, in press, for a putative exception regarding late Smithian ammonoid assemblages from deep-water facies of South Primorye, which enigmatically appear relatively dissimilar and more diverse than elsewhere), the Prionitidae abruptly disappeared prior to the onset of the upper part that is characterized by the occurrence of assemblages, in which latest Smithian representatives of xenoceltitids (*Glyptophiceras*, *Xenoceltites*, *Condensoceras*) and hedenstroemiids (e.g., *Pseudosageceras augustum*, *P. plicatum*, ?*P. bullatum*) coexist (e.g., Brühwiler et al., 2012a; Jattiot et al., 2017; Jenks and Brayard, 2018). Very few of these taxa survived the SSB, but at least two other families (the proptychitids and palaeophyllitids)

virtually persisted into the Spathian (Brayard and Bucher, 2015; see also Zakharov et al., in press, for another surviving scheme based on a different phylogenetic conception).

In the western USA basin, where known occurrences of latest Smithian taxa are rare, the SSB is most often placed within the interval of separation between the late Smithian *Anasibirites* beds and the early Spathian *Bajarunia-Tirolites* beds (see Brayard et al., 2019 for a review of index taxa and correlations within this basin). Thus, the recognition of the SSB in this basin is often proposed with some temporal uncertainties. Until now, ammonoid species characterizing the second part of the late Smithian (e.g., *Pseudosageceras augustum*, *Condensoceras youngi*, *Glyptophiceras sinuatum*) were indeed firmly documented from Palomino Ridge (Jattiot et al., 2017) and Crittenden Springs (Jenks et al., 2010; Jenks and Brayard, 2018), northeastern Nevada, even though they are of prime importance for location of the SSB. Finally, a third zone potentially representing the very end of the late Smithian, and thus corresponding to a putative third part, has been newly reported from northeastern Nevada (Widmann et al., 2020). Taxa found in this unique worldwide assemblage are still undescribed but apparently correspond to intermediate forms between late Smithian *Xenoceltites* and early Spathian *Bajarunia*, *Tirolites* and *Columbites* (Widmann et al., 2020). Pending a detailed description of this new assemblage and its stratigraphic position, we consider the assemblages including *P. augustum*, *C. youngi* and *G. sinuatum* as “latest Smithian” in age.

Based on these restricted basinal occurrences, and especially on the presence of *P. augustum*, Jattiot et al. (2017) postulated the existence of a regional Unitary Association Zone (their UAZ6) representing the second part of the late Smithian. To corroborate the existence of this zone throughout the western USA basin, representatives of *P. augustum*, *Condensoceras* or *Glyptophiceras* must therefore be reported from outside Nevada. A few specimens described as *Hedenstroemiidae* gen. indet. A, and resembling *P. augustum*, were

described from the *Xenoceltitidae* gen. indet. A beds of central Utah (Brayard et al., 2013). However, their poor state of preservation prevented a firm determination and the confirmation of the presence of latest Smithian ammonoid assemblages outside Nevada. Mathews (1929) also reported the existence of specimens closely resembling *Glyptophiceras* (“*Xenodiscus hannaï*” in Mathews, 1929: pl. 1:1-4) and *P. augustum* (“*Cordillerites compressus*” in Mathews, 1929: pl. 1:15-17; “*P. intermontanum*” in Mathews, 1929: pl. 1:18-22) in the Fort Douglas area, north-central Utah. However, he never published a detailed stratigraphy showing the relative placement of each sampled taxon, but instead most often referred to coexistences within a stratigraphic unit corresponding to several beds with prionitid assemblages. We therefore strongly suspect that assemblages corresponding to the second part of the late Smithian can also be found in this area, but a complete bed-by-bed re-sampling work remains necessary to validate this hypothesis.

Here we report two new ammonoid assemblages from distant localities in northern Utah, overlying the late Smithian *Anasibirites* beds and characterized by the unambiguous co-occurrence of *Xenoceltites subevolutus* and *Pseudosageceras augustum*. These assemblages support the existence of a regional zone (UAZ6 of Jattiot et al., 2017) representing the second part of the late Smithian in the western USA basin. When present, this zone facilitates the identification of the SSB and intra-basin correlation. It also correlates with the latest Smithian zone recognized from southern Tethyan basins.

## **2. Exposures and sampled material**

The western USA basin was located within the northern intertropical zone on the western margin of the Panthalassa during the Early Triassic (Fig. 1(A)). Its sedimentary deposits presently outcrop across a wide area including Utah, northern Arizona, eastern Nevada, southeastern Idaho, western Wyoming, and southwestern Montana (Fig. 1(B)). The

two studied exposures are located in northern Utah (Fig. 1(C)). They exhibit classical shale-limestone alternations of the Early Triassic Thaynes Group (*sensu* Lucas et al., 2007), which represent relatively shallow sedimentary deposits in an epicontinental sea. The maximum extent of this epicontinental sea within the western USA basin occurred during the Smithian–Spathian transition (Lucas et al., 2007; Brayard et al., 2013, 2020; Vennin et al., 2015; Olivier et al., 2018) and was probably controlled by a North-South differentiation in regional tectonics (Caravaca et al., 2018) and by concurrent global climatic changes (e.g., Brayard et al., 2020).

Smithian ammonoid assemblages were sampled in Tooele and Morgan Counties, northern Utah (Fig. 1(C)). At both sites, ammonoid preservation is highly variable but is generally good, with test parts remaining on some specimens. Similar to many other ammonoid localities in Utah (Brayard et al., 2020), internal recrystallization is common, making the preparation of these fragile specimens often difficult. However, the extent of recrystallization at these sites is sometimes rather fine, allowing the observation of suture lines on a few specimens.

The Lower Weber Canyon locality (LWC; Figs. 1(C), 2; 41°3'50.86"N, 111°34'0.02"W – WGS84 coordinates) is located in Morgan County along Interstate Highway 84 and the Weber River. It was first mapped by Schick (1955) and Mullens and Laraway (1964), and then described by Smith (1969) who reported the occurrences of middle Smithian *Meekoceras* assemblages and late Smithian prionitids. Donovan (1986) and Yurchyk (2011) further studied some ammonoids and conodonts collected from this site for addressing specific taphonomic and geochemical issues, respectively. More recently, the LWC section was described in detail by Grosjean et al. (2018) for its lithological and sedimentological record. These authors show that unlike many other exposures of the Thaynes Group in the western USA basin, Microbially Induced Sedimentary Structures are present in middle

Smithian strata (Fig. 2: “Unit B”). They also highlighted that (i) late Smithian strata (Fig. 2: base of “Unit C”) correspond to a mid-ramp setting with frequent storm deposits and thus include bioclastic accumulations with densely packed ammonoids, and (ii) the SSB is concomitant to the maximum transgression in this area (Lucas et al., 2007; Brayard et al., 2013, 2020). Ammonoid specimens are abundant in the base of “Unit C” but sometimes fragmentary and slightly deformed. Sampled late Smithian ammonoid assemblages are typical from this time interval. A large ammonoid size spectrum is represented, ranging from less than 0.5 cm up to ~11 cm.

The second studied site is located on the southwestern end of Thumb Ridge (TR; Figs. 1(C), 3; 40°50'49.89"N, 113°11'17.35"W – WGS84 coordinates), located in Tooele County. Doelling et al. (1994) mapped this area and reported the occurrences of different Spathian assemblages, especially in ledge-forming limestones that are well exposed in the landscape. Underlying rocks were described by these authors as (i) containing sparse and poorly-preserved fossils, and (ii) corresponding to the “Dinwoody Fm.”, which is of ?Griesbachian-Dienerian age (e.g., Kummel, 1954, 1957). A recent mapping by Clark and Oviatt (2019) highlighted the presence of the middle Smithian *Owenites* beds and late Smithian *Anasibirites* beds, two informal biozones, thus indicating that these strata did not pertain to the Dinwoody Fm. Our concomitant investigations of the same strata led to the discovery of several relatively well-preserved ammonoid assemblages including characteristic late Smithian prionitids and xenoceltitids as well as the latest Smithian taxon *Pseudosageceras augustum*. Additionally, these rocks show typical alternating shale and limestone that are similar to several Thaynes Group exposures in Utah, thus supporting the fossil evidence that they do not belong to the Dinwoody Fm. Due to the high proportion of shales forming the area’s incompetent hills, fossiliferous limestones only sporadically crop out. Late Smithian ammonoids are densely clustered in storm bioclastic accumulations that resemble late

Smithian strata in LWC, thus suggesting a relatively similar depositional environments.

Fragmentary ammonoids are often found, but some specimens are almost complete.

### 3. Systematic palaeontology

Systematic descriptions mainly follow the classification of Tozer (1981), and that further refined by Brayard et al. (2013, 2020), Jattiot et al. (2016, 2017) and Jenks and Brayard (2018). Quantitative morphological ranges for identified species are illustrated by scatter diagrams based on classical measurements of the diameter (D), and corresponding whorl height (H), whorl width (W) and umbilical diameter (U). Scatter diagrams of H, W and U, and H/D, W/D and U/D are provided only when the number of measured specimens is higher than four. Detailed measurements are given in Table S1 (Appendix A). The number of sampled specimens (fragmentary to complete) for each taxon and locality is indicated as “n =”. Repository of figured specimens is abbreviated UBGD (Université de Bourgogne, Géologie Dijon, France). Abbreviations: TR: Thumb Ridge; LWC: Lower Weber Canyon.

Phylum Mollusca Linnaeus, 1758

Class Cephalopoda Cuvier, 1797

Subclass Ammonoidia Fischer, 1882

Order Ceratitida Hyatt, 1884

Superfamily Xenodiscoidea Frech, 1902

Family Xenoceltitidae Spath, 1930

Genus *Xenoceltites* Spath, 1930

**Type species:** *Xenoceltites subevolatus* = *Xenodiscus* cf. *comptoni* (non Diener) Frebold, 1930

216 **Remarks:** A thorough discussion of the different species attributed to *Xenoceltites*, as well as  
 217 a comparison with some other late Smithian xenoceltitid genera was provided by Jattiot et al.  
 218 (2017) and Jenks and Brayard (2018). Only a simplified description of *X. subevolutus* is  
 219 therefore given below.

220

221 *Xenoceltites subevolutus* Spath, 1930

222 Fig. 4

223 ?1929. *Ophiceras matheri* Mathews, p. 4, pl. 1, figs. 38-40.

224 ?1929. *Xenodiscus douglasensis* Mathews, p. 5, pl. 1, figs. 5-7.

225 1930. *Xenoceltites subevolutus* Spath, p. 12.

226 1930. *Lecanites* cf. *L. ophioneus* – Frebold, p. 12, pl. 3, figs. 4, 4a, 5.

227 1930. *Xenodiscus* cf. *X. comptoni* – Frebold, p. 14, pl. 3, figs. 1-3.

228 ?1932. *Xenodiscus rotula* – Smith, p. 45, pl. 79, figs. 5, 6 (copy of Mathew's 1929 figure and  
 229 description of *X. matheri*).

230 1934. *Xenoceltites spitsbergensis* Spath, p. 128, pl. 9, figs. 1, 2; pl. 11, figs. 5, 7, 8.

231 1934. *Xenoceltites gregoryi* Spath, p.129, pl. 5, fig. 3; pl. 6, figs. 4, 5; pl. 11, figs. 3, 4, 6.

232 1934. *Xenoceltites subevolutus* Spath, p. 130, pl. 2, fig. 2; pl. 8, fig. 2; pl. 9, fig. 4, pl. 11, fig.  
 233 2.

234 1961. *Xenoceltites subevolutus* – Tozer, p. 53, pl. 16, fig. 1.

235 1978. *Xenoceltites subevolutus* – Zakharov, pl. 11, fig. 17.

236 1978. *Xenoceltites spitsbergensis* – Weitschat and Lehmann, p. 94, pl. 11, figs. 3b, 4, 5.

237 1978. *Xenoceltites subevolutus* – Weitschat and Lehmann, p. 95, pl. 11, figs. 1, 2, 3a.

238 1990. *Xenoceltites subevolutus* – Dagys and Ermakova, p. 23, pl. 5, fig. 4.

239 1994. *Xenoceltites subevolutus* – Tozer, p. 52, pl. 36, figs. 3-8.

240 v2013. *Xenoceltites* sp. indet. A – Brayard et al., p. 160, fig. 19a-c.

241 2015. *Xenoceltites subevolutus* – Piazza, p. 48, pl. 1, figs. a-c.

242 v2017. *Xenoceltites subevolutus* – Jattiot, p. 10, pl. 1, figs. P-AD.

243 2017. *Xenoceltites subevolutus* – Piazza, p. 110, fig. 4a, b.

244 v2018. *Xenoceltites subevolutus* – Jenks and Brayard, p. 21, fig. 21.

245 **Occurrence:** Rare in LWC46 (LWC; n = 5) and more common in LWC48 and LWC49

246 (LWC; n = 7). Rare in THU A1 (TR; n = 2, but two other specimens seen in the field) and

247 common in THU A2 (TR; n = 10).

248 **Measurements:** See Fig. 5 and Table S1 (Appendix A). Estimated maximal size: ~8 cm

249 (Jenks and Brayard, 2018).

250 **Description:** Near-serpenticonic, compressed xenoceltitid exhibiting a narrowly rounded to

251 arched venter. Flanks slightly convex. Ornamentation highly variable among specimens and

252 through ontogeny, generally consisting of (i) ventral constrictions for smooth variants,

253 extending on flanks for robust specimens, and (ii) distant, low, blunt, radial to slightly

254 prosiradiate ribs arising from the umbilical shoulder and well visible on internal whorls.

255 Umbilicus relatively shallow with an oblique wall and rounded margin. Suture line ceratitic

256 typical of xenoceltitids with three broad rounded saddles decreasing in size from the venter to

257 the umbilicus. The main lateral lobe is well indented.

258 **Remarks:** *Xenoceltites subevolutus* exhibits a wide geographic distribution including USA,

259 British Columbia (Tozer, 1994), Spitsbergen (e.g., Piazza et al., 2017), and Siberia (e.g.,

260 Dagys and Ermakova, 1990); another species attributed to the genus, *X. variocostatus*, is

261 found in South China (Brayard and Bucher, 2008), Vietnam (Shigeta et al., 2014) and the

262 Northern Indian Margin (Brühwiler et al., 2012a, b). Similar to other American localities such

263 as Palomino Ridge (Jattiot et al., 2017) and Crittenden Springs (Jenks and Brayard, 2018),

264 *Xenoceltites subevolutus* is rather rare in beds where prionitids such as *Anasibirites* occur, but

265 become more common in overlying beds where *Pseudosageceras augustum* is present. This



species extends through much of the late Smithian. Among co-occurring American xenoceltitids, *X. subevolutus* mainly differs from *Glyptopheros sinuatum* by somewhat weaker forward projections, and from *Condensoceras youngi* by a more evolute, serpenticonic-like coiling and by stronger ornamentation. The wide intraspecific variation of *X. subevolutus* overlaps with that of some other late Smithian xenoceltitid species, such as *G. sinuatum*, sometimes preventing firm identification. In addition, suture lines of both species are similar (compare suture lines illustrated in Fig. 4(C), the first for American specimens of *X. subevolutus*, with *G. sinuatum* material of Jattiot et al., 2017). These observations raise the still unanswered question of a possible morphological and/or evolutionary continuum among all these species.

Two specimens described as *Ophiceras matheri* and *Xenodiscus douglasensis* by Mathews (1929) from the Fort Douglas area, north-central Utah, resemble *X. subevolutus*. However, the information provided by Mathews indicates that the stratigraphic origin of these specimens is from the early Spathian “*Columbites zone*”, thus preventing a firm assignment to *X. subevolutus*. A solution to resolve this conundrum is a future bed-by-bed sampling from the upper Smithian portion of the section in this area. If it yields specimens attributable to *Ophiceras matheri* and *Xenodiscus douglasensis*, then *X. subevolutus* potentially would have to be synonymized with these Mathew’s (1929) taxa, given that they have priority.

Superfamily Sageceratoidea Hyatt, 1884

Family Hedenstroemiidae Waagen, 1895

Genus *Pseudosageceras* Diener, 1895

**Type species:** *Pseudosageceras* sp. indet. Diener, 1895

*Pseudosageceras augustum* (Brayard and Bucher, 2008)

291 Figs. 4(M-O), 6

292 ?1929. *Cordillerites compressus* Mathews, p. 3, pl. 1, figs. 15-17.

293 ?1929. *Pseudosageceras intermontanum* Hyatt and Smith, 1905 – Mathews, p. 3, pl. 1, figs.

294 18-21.

295 v2008. *Hedenstroemia augusta* Brayard and Bucher, p. 72, pl. 39, figs. 1-11, text-fig. 63.

296 v2010. *Pseudosageceras augustum* – Jenks et al., p.35, fig. 24.

297 2010b. *Pseudosageceras augustum* – Brühwiler et al., p. 429, fig. 16: 10-11.

298 2012b. *Pseudosageceras augustum* – Brühwiler et al., p. 171, fig. 41Z-AI.

299 v2017. *Pseudosageceras augustum* – Jattiot et al., p. 43, pl. 19, figs. J-N.

300 v2018. *Pseudosageceras augustum* – Jenks and Brayard, p. 114, fig. 104.

301 **Occurrence:** Rare in LWC48, LWC49 and LWC52 (LWC; n = 8). More common in

302 THU A2 (TR; n = 10).

303 **Measurements:** See Fig. 7 and Table S2 (Appendix A). Estimated maximal size: ~9 cm.

304 (Jenks and Brayard, 2018).

305 **Description:** Involute, compressed oxyconic shell. Flanks weakly convex with maximum

306 curvature and a slight change of slope at mid-flank, producing an aspenitid-like flank contour.

307 Some specimens appear to exhibit a longitudinal line at mid-flank. The depressed umbilical

308 area appears nearly flat, the outer half of the flank being somewhat steeper. Venter narrowly

309 bicarinate and tabulate on inner mold. Surface smooth excepting for sinuous, slightly

310 biconcave and fine growth lines. Suture line ceratitic and complex, typical of the family, with

311 numerous elongated saddles, several adventitious elements and an auxiliary series.

312 **Remarks:** This species shows an intertropical, trans-Panthalassic distribution as do many

313 other Smithian species (Brayard et al., 2009a; Jenks et al., 2010). *Pseudosageceras augustum*

314 is very rare in localities from the Northern Indian Margin (Brühwiler et al., 2010b, 2012a) and

315 northeastern Nevada (Jattiot et al., 2017; Jenks and Brayard, 2018). The morphology of the

American specimens is identical to the coeval type material from South China, which is relatively a little bit more abundant (Brayard and Bucher, 2008). Illustrated suture lines are often weathered and only partially preserved (Brühwiler et al., 2010b), preventing direct comparisons among specimens from distant areas. Some of the specimens described here exhibit almost the entire suture line architecture, confirming its complexity. It also shows that the main lateral lobe is trifold, justifying the assignment of this species to the genus *Pseudosageceras* as postulated by Brühwiler et al. (2010b). Lobes of the adventitious series are bifid and saddles of the auxiliary series are squarer than in some other representatives of hedenstroemiids such as *Pseudosageceras multilobatum* or *Cordillerites*. *?Pseudosageras bullatum* from Palomino Ridge, Nevada (Jattiot et al., 2017) closely resembles *P. augustum* but differs by its regularly spaced bullae located at mid-flank. A single specimen described as *Cordillerites compressus* by Mathews (1929) and two specimens he attributed to *P. intermontanum* Hyatt and Smith (1905) from the Fort Douglas area, north-central Utah, resemble *P. augustum* by their highly compressed section and narrow venter. However, he only illustrated these three specimens with limited stratigraphic information, thus preventing a firm assignment to *P. augustum*. If future bed-by-bed sampling from the upper Smithian portion of the section in this area yields specimens attributable to *C. compressus* that exhibit a characteristic widely depressed umbilical region and trifold main lateral lobe, then *P. augustum* likely would have to be synonymized with Mathew's (1929) taxon, given that it has priority.

Based on ammonoid occurrences in the Tulong section (South Tibet), *P. augustum* may have survived the SSB up to the early Spathian *Procolumbites* beds (Brühwiler et al., 2010b), but no illustrations and firm occurrence reports of these Spathian specimens have been provided so far. Until new discoveries are made, it is therefore preferable to consider this species as characteristic only of the latest Smithian.

341 Superfamily Meekoceratoidea Waagen, 1895

342 Family Prionitidae Waagen, 1895

343 Genus *Gurleyites* Mathews, 1929

344 **Type species:** *Gurleyites smithi* Mathews, 1929

345 **Remarks:** Brayard et al. (2020) provided a comprehensive revision and review of the

346 taxonomy of *Gurleyites smithi*, previously assigned to the doubtful genus *Arctoprionites*. We

347 follow the conclusions of this work and thus do not include the complete description for this

348 species.

349

350 *Gurleyites smithi* Mathews, 1929

351 Figs. 8, 9(A-I)

352 v2020. *Gurleyites smithi* – Brayard et al., figs. 7-8, 9A-J, 10 [cum syn.].

353 **Occurrence:** Abundant in LWC45, LWC46 (LWC; n = 45) and rare in THU A1 (TR; n = 2).

354 **Measurements:** See Fig. 10 and Table S3 (Appendix A). Estimated maximal size: ~15 cm

355 (Jenks and Brayard, 2018).

356 **Description:** Compressed and moderately involute prionitid showing a slightly egressive

357 coiling, and a marked intraspecific variation among specimens and throughout ontogeny.

358 Ornamentation typically consists of forward projected, bullate, elongated and sinuous ribs that

359 stem near the umbilical shoulder and fade rapidly toward the venter. Ribs may cross the

360 venter forming a slightly crenulated venter. Strigation may also be visible on the venter and

361 on the ventrolateral margins of well-preserved specimens, as already discussed in Brayard et

362 al. (2020). In some cases, elevated bullate ribs almost form tubercles. Umbilical margin is

363 broadly arched with an inclined wall. The suture line exhibits three large, arched saddles,

364 decreasing in size from the ventrolateral to the umbilical margin. Lobes are well indented.

**Remarks:** This species shows a marked intraspecific variation that overlaps with other highly variable species belonging to several prionitid genera, such as *Wasatchites* and *Anasibirites*, but more specifically with *Hemiprionites typus*, thus making some specimen assignments difficult (see Brayard et al., 2020 for a discussion on this point). Six specimens sampled at LWC also show a specificity that had rarely been noticed before. These specimens are indeed clearly more evolute at identical sizes than the others (Figs. 9(A-D), 10). Rare specimens with a similar coiling have already been illustrated in Jenks and Brayard (2018: e.g., fig. 87A-C). This feature generally concerns specimens having a diameter greater than 50 mm. All have the typical and variable ornamentation of *G. smithi*, as well as an identical suture line, supporting their assignment to *G. smithi*. These extreme morphologies highlight the wide intraspecific variation of this taxon.

As with many other prionitids, *Gurleyites smithi* shows a rather cosmopolitan distribution (Spitsbergen: Frebold, 1930, Piazza et al., 2017; British Columbia: Tozer, 1994) but is often relatively rare. This species has been found at several places in the western USA basin (Brayard et al., 2013; Jattiot et al., 2017, 2018; Jenks and Brayard, 2018), but it has been abundantly sampled only in southwestern-most Utah up to now (Brayard et al., 2020). LWC is a new site where *G. smithi* is relatively rather abundant.

Genus ***Wasatchites*** Mathews, 1929

**Type species:** *Wasatchites perrini* Mathews, 1929

**Remarks:** The reader is referred to Brayard et al. (2013) for a thorough discussion of the typical early late Smithian genus *Wasatchites*. Brayard et al. (2013), Jattiot et al. (2017) and Jenks and Brayard (2018) provided the most recent detailed descriptions and discussions of *W. perrini*. Based on the conclusions of these works, we thus only include below a simplified description for this species.

390

391 *Wasatchites perrini* Mathews, 1929

392 Fig. 11

393 v2020. *Wasatchites perrini* – Brayard et al., fig. 9K-L [cum syn.].

394 **Occurrence:** Common in LWC45, LWC46 (LWC; n = 22). Not found in THU A1 (TR).

395 **Measurements:** see Fig. 12 and Table S4 (Appendix A). Estimated maximal size: ~20 cm

396 (Jenks and Brayard, 2018).

397 **Description:** Coiling generally moderately involute. Trapezoidal whorl section.

398 Ornamentation typical and showing (i) very conspicuous tubercles on umbilical shoulders that

399 become more bullate or nodate on mature whorls, but then tend to rapidly lose strength near

400 the aperture, and (ii) alternating strong and weak, fasciculate ribs that stem from the tubercles

401 and cross the venter. The venter is subtabulate to slightly arched. Suture line typical of

402 prionitids with three rounded saddles, decreasing in size toward the umbilicus, and a deep first

403 lateral lobe.

404 **Remarks:** *W. perrini* can be distinguished from other co-occurring taxa by its conspicuous,

405 regularly spaced ornamentation. It also differs from *W. cf. distractus* by its more tabulate-to-

406 arched venter and the more umbilicate position of its tubercles, and fasciculate ribs.

407

408 Genus *Anasibirites* Mojsisovics, 1896

409 **Type species:** *Sibirites kingianus* Waagen, 1895

410 **Remarks:** Reader should refer to Jattiot et al. (2016) for a comprehensive review of the

411 taxonomy of the various *Anasibirites* species and associated diagnostic characters, as well as

412 Jattiot et al. (2016) and Brayard et al. (2020) for complete synonymy lists.

413

414 *Anasibirites cf. kingianus* (Waagen, 1895)

415 Fig. 9(J-N)

416 v2016. *Anasibirites kingianus* – Jattiot et al., p. 183, figs. 4, 6-9, 10A–M, 12, 15–18 [cum

417 syn.].

418 v2017. *Anasibirites kingianus* – Jattiot and Bucher in Jattiot et al., p. 29, pl. 11, figs. A–F.

419 2017. *Anasibirites kingianus* – Piazza in Piazza et al., fig. 4F-I.

420 v2018. *Anasibirites kingianus* – Jenks and Brayard, p. 73, fig. 74A–C.

421 **Occurrence:** Very rare in LWC45, LWC46 (LWC; n = 5). Not found in THU A1 (TR).

422 **Measurements:** See Fig. 13 and Table S5 (Appendix A). Estimated maximal size: ~10 cm

423 (Jattiot et al., 2016).

424 **Description:** Prionitid with a rather involute coiling. Coiling is more evolute and whorl

425 section is generally quadrate for small-sized (<20 mm) specimens, but becomes more involute

426 and compressed for larger specimens. Venter varies from tabulate to arched. Ornamentation

427 on inner whorls typically consists of megastriae, variable in strength, and becoming denser

428 and weaker during ontogeny. Ribs are also visible on some specimens. Suture line not visible

429 on our specimens.

430 **Remarks:** *A. kingianus* is one of the most abundant late Smithian taxon worldwide outside

431 the western USA basin. *A. kingianus* is rare in this area (Mathews, 1929; Jattiot et al., 2016;

432 Jenks and Brayard, 2018), where the late Smithian prionitid fauna is often dominated by *A.*

433 *multiformis* (Brayard et al., 2013, 2020). In accordance with this observation, *A. cf. kingianus*

434 is rare in LWC and was not found in TR. The reader is referred to Jattiot et al. (2016) for a

435 thorough morphological comparison between the two co-occurring species *A. kingianus* and

436 *A. multiformis*, and for a discussion on their respective cosmopolitan distribution. As it is

437 difficult to distinguish both *Anasibirites* species based on small and imperfectly preserved

438 specimens (Jattiot et al., 2016; Jenks and Brayard, 2018), the determination of specimens

439 belonging to *A. kingianus* was mainly based on the presence of irregular, marked megastriae  
440 disappearing during ontogenesis. Thus, attribution of these five specimens can be questioned.

441

442 *Anasibirites multiformis* Welter, 1922

443 Fig. 14

444 v2016. *Anasibirites multiformis* – Jattiot et al., p. 184, figs. 10N–S, 21–23 [cum syn.].

445 v2017. *Anasibirites multiformis* – Jattiot and Bucher in Jattiot et al., p. 30, pl. 11, figs. G-AA.

446 v2018. *Anasibirites multiformis* – Jenks and Brayard, p. 79, figs. 74D-F, G(4,5), 75.

447 v2020. *Anasibirites multiformis* – Brayard et al., fig. 11.

448 **Occurrence:** Abundant in LWC45, LWC46 (LWC; n = 80) and THU A1 (TR; n = 6).

449 **Measurements:** See Fig. 15 and Table S6 (Appendix A). Estimated maximal size: ~10 cm

450 (Jattiot et al., 2016).

451 **Description:** Simplified description from Brayard et al. (2020): rather involute, compressed

452 prionitid with near isometric growth. Ornamentation typically consists of weak and dense

453 megastriae throughout ontogeny. Suture line ceratitic with deep and well indented lobes.

454 Broad saddles are gently bend toward umbilicus, especially on larger specimens (Fig. 14(R)).

455 **Remarks:** see above, discussion of *A. cf. kingianus*.

456

457 Genus *Hemiprionites* Spath, 1929

458 **Type species:** *Goniodiscus typus* Waagen, 1895

459

460 *Hemiprionites typus* (Waagen, 1895)

461 Figs. 9(C), 16, 17(A-K)

462 1895. *Goniodiscus typus* Waagen, p. 128, pl. 9, figs. 7-10.

463 1929. *Goniodiscus typus* – Mathews, p. 31, pl. 5, figs. 12-21.



464 1929. *Goniodiscus americanus* – Mathews, p. 32, pl. 5, figs. 22-27.

465 1929. *Goniodiscus shumardi* – Mathews, p. 33, pl. 6, figs. 11-14.

466 1929. *Goniodiscus utahensis* – Mathews, p. 33, pl. 6, figs. 29-31.

467 1929. *Goniodiscus slocomi* – Mathews, p. 34, pl. 6, figs. 15-17.

468 1929. *Goniodiscus butleri* – Mathews, p. 35, pl. 6, figs. 18-21.

469 1932. *Anasibirites typus* – Smith, p. 76, pl. 80, figs. 6-8.

470 1932. *Anasibirites utahensis* – Smith, p. 77, pl. 80, figs. 9, 10.

471 1934. *Hemiprionites typus* – Spath, p. 331, figs. 114ac.

472 vp2008. *Hemiprionites* cf. *H. butleri* – Brayard and Bucher, p. 58, pl. 29, figs. 1, 4, 7 only,

473 text- fig. 50.

474 2012b. *Hemiprionites typus* – Brühwiler and Bucher, p. 103, figs. 89A-AH.

475 v2013. *Hemiprionites* cf. *H. typus* – Brayard et al., p. 197, fig. 66.

476 v2017. *Hemiprionites typus* – Jattiot and Bucher in Jattiot et al., p. 31, pl. 12, figs. A-M, pl.

477 13, figs. A-X.

478 vp2018. *Hemiprionites typus* – Jenks and Brayard, p. 81, figs. 77, 78A-C, 78G-R, 79A-F, 79J-

479 O.

480 v2020. *Hemiprionites typus* – Brayard et al., fig. 12J-S.

481 2020. *Hemiprionites typus* – Jattiot et al., p. 56, pl. 29, figs. U-AL.

482 **Occurrence:** Abundant in LWC45, LWC46 (LWC; n = 74) and rare in THU A1 (TR; n = 3).

483 **Measurements:** See Fig. 18 and Table S7 (Appendix A). Estimated maximal size: ~10 cm

484 (Jattiot et al., 2017).

485 **Description:** Main diagnostic characteristics of *Hemiprionites* species have recently been

486 reviewed by Jattiot et al. (2017). We only repeat here the simplified description recently given

487 by Brayard et al. (2020): “compressed shell with variable involution and a typical marked

488 egressive coiling at mature stage. A small depression on the outer edge of the flank, just

below the ventral margin, is also visible on some specimens. Spiral lines are sometimes visible on the venter and/or near the ventrolateral margin. Flexuous and slightly biconcave growth lines are visible and may bundle into small folds that may cross the venter. Suture line ceratitic with a deep and flared first lateral lobe. Saddles appear pinched”. One specimen from LWC46 (Fig. 16(J, K)) exhibits umbilical saddles that are slightly bent toward umbilicus and somewhat flattened on their ventral side. This feature may be included in the rather large intraspecific variation of the suture line known for *H. typus* (Jattiot et al., 2017, 2020; Jenks and Brayard, 2018).

**Remarks:** *H. typus* can be distinguished from the co-occurring *H. walcotti*, by its often wider venter and more evolute and egressive coiling. Some specimens of *H. typus* also exhibit a small depression near the ventral margin. As discussed by Brayard et al. (2020), the morphological variability of *H. typus* partly overlaps with that of *Gurleyites smithi*, but the latter appears more ornamented and slightly more evolute. Its saddles are also generally more broadly rounded.

*Hemiprionites walcotti* (Mathews, 1929)

Fig. 17(L-R)

p1922. *Anasibirites multiformis* Welter, p. 17, figs. 4-7, 11-14.

1929. *Goniodiscus walcotti* Mathews, p. 32, pl. 6, figs. 1-5.

1934. *Hemiprionites timorensis* Spath, p. 331.

vp2008. *Hemiprionites* cf. *H. butleri* – Brayard and Bucher, p. 58, pl. 29, figs. 2, 3, 6 only.

v2008. *Hemiprionites klugi* Brayard and Bucher, p. 59, pl. 30, figs. 1-4.

p2012a. *Hemiprionites* cf. *H. butleri* – Brühwiler and Bucher, p. 33, pl. 19, figs. 10 only.

p2012b. *Anasibirites angulosus* – Brühwiler and Bucher, p. 103, figs. 87H-J, N-P only.

2012b. *Hemiprionites klugi* – Brühwiler and Bucher, p. 103, figs. 87Q-AB.

514 v2017. *Hemiprionites walcotti* – Jattiot and Bucher in Jattiot et al., p. 34, pl. 14, figs. A-Y.

515 v2018. *Hemiprionites walcotti* – Jenks and Brayard, p. 83, figs. 79Q-V.

516 v2020. *Hemiprionites walcotti* – Brayard et al., fig. 12A-I.

517 2020. *Hemiprionites walcotti* – Jattiot et al., p. 57, pl. 29, figs. AO-BG.

518 **Occurrence:** Proportionally rare in LWC45, LWC46 (LWC; n = 8) and more common in  
519 THU A1 (TR; n = 4).

520 **Measurements:** See Fig. 19 and Table S8 (Appendix A). Estimated maximal size: ~7 cm  
521 (Jattiot et al., 2017).

522 **Description:** See the taxonomic revision of *Hemiprionites* species by Jattiot et al. (2017).

523 **Remarks:** See *H. typus* discussion.

524

## 525 4. Discussion

### 526 4.1. Late Smithian ammonoid biostratigraphy in the western USA Basin

527 At both LWC and TR, two distinct, successive late Smithian assemblages were  
528 sampled. The lowest corresponds to the *Anasibirites multiformis* beds found elsewhere in the  
529 western USA basin (UAZ5 of Jattiot et al., 2017). It contains the cosmopolitan prionitid taxa  
530 typical of the first part of the late Smithian, such as *Anasibirites*, *Wasatchites*, *Gurleyites* and  
531 *Hemiprionites*. Some rare specimens of *Xenoceltites subevolutus* also co-occur, similarly to  
532 other sites in Nevada (Jattiot et al., 2017; Jenks and Brayard, 2018). This assemblage is thus  
533 correlative of the *Anasibirites* and *Wasatchites* beds found worldwide (e.g., Jenks et al.,  
534 2015). *Xenoceltites subevolutus* and *Pseudosageceras augustum* are the only two species that  
535 co-occur in the overlying assemblage. Although species-poor compared to coeval  
536 assemblages from Nevada, where some other hedenstroemiids (e.g., ?*Pseudosageceras*  
537 *bullatum*) and xenoceltitids (e.g., *Glyptophiceras sinuatum*) taxa can also be present (Jattiot et  
538 al., 2017; Jenks and Brayard, 2018), this association is typical of the second part of the late

Smithian in Nevada and worldwide. It thus validates the existence of a regional zone representing this interval outside Nevada (postulated UAZ6 of Jattiot et al., 2017) in the western USA basin. This zone also therefore correlates with the latest Smithian UAZ S-14 recognized from southern Tethyan basins (*G. sinuatum* beds; Brühwiler et al., 2011). It consequently significantly expands possible correlation between these very distant areas and thus enhance inter-basin comparisons during this crucial time interval. Additionally, these new data corroborate other occurrences of *Xenoceltites subevolutus* throughout most of the late Smithian (Brühwiler et al., 2011; Jattiot et al., 2017; Jenks and Brayard, 2018).

#### 4.2. The biogeography of middle and late Smithian American ammonoids

As a preliminary attempt to synthesize and compare the available middle to late Smithian ammonoid records through time and space, we compiled the published generic occurrences for three major, well-documented and distant areas: the Panthalassic western USA basin (data from Brayard et al., 2009a, 2013, 2020; Jenks et al., 2010; Jattiot et al., 2016, 2017; Jenks and Brayard, 2018) and South China (data from Brayard and Bucher, 2008) and the Tethyan Northern Indian Margin (data from Brühwiler et al., 2012a, b) (Fig. 20). Among the 79 genera recorded in these three areas, 71 occur in the middle Smithian and 11 in the late Smithian, including only three genera crossing the middle/late Smithian boundary (*Hemiprionites*, *Pseudosageceras* and *Subvishnuites*).

Among the 71 middle Smithian genera, 40 of them (56%) appear endemic to one of the three areas, 13 in the western USA basin, 16 in the Northern Indian Margin, and 10 in South China. Conversely, 13 genera co-occur in the western USA basin and South China, whereas the Northern Indian Margin basin shares only 4 and 3 genera with South China and the western USA basin, respectively. The 12 remaining genera are found in the three areas. A total of 41 middle Smithian genera are found in the western USA basin, among which five of

564 them are from a single locality – Crittenden Springs (Jenks and Brayard, 2018). Excluding  
565 these endemic taxa, 75% of the western USA middle Smithian ammonoid genera are therefore  
566 found in at least one of the two other compared areas, which highlights a well-established  
567 trans-Panthalassic circulation of ammonoids at that time (Brayard et al., 2007, 2009a, 2009b;  
568 Jenks et al., 2010; Shigeta and Kumagae, 2015; Jenks and Brayard, 2018). They are also often  
569 long-ranging with temporal distributions extending throughout the middle Smithian (Jattiot et  
570 al., 2017).

571 Departing from this highly diversified and well contrasted middle Smithian  
572 biogeographical configuration, the late Smithian assemblages include 11 genera among which  
573 8 are known from western USA localities, 9 occur in the Northern Indian Margin, and 6 in  
574 South China. Out of these 11 genera, 4 are restricted to one of the three compared areas,  
575 whereas 2 are found in two areas, and 5 occur in the three areas, pointing toward a late  
576 Smithian ammonoid distribution significantly more cosmopolitan than during the middle  
577 Smithian (one-tailed Fisher's exact test:  $p = 0.038^*$ ). Based on the three compared areas, the  
578 global extinction event occurring at the middle/late Smithian boundary and further impacting  
579 late Smithian assemblages worldwide once again appears as a time of significant  
580 biogeographical homogenization. This event echoes the effect of the Permian/Triassic mass  
581 extinction on ammonoid biogeographic distribution, as already discussed in previous works  
582 (Brayard et al., 2006, 2007, 2009b, 2013, 2015; Jattiot et al., 2016, 2018; Dai and Song,  
583 2020). A possible exception to this global homogenization pattern is represented by the  
584 unusual late Smithian ammonoid assemblages reported from South Primorye (Zakharov et al.,  
585 2013, in press). However, the local ammonoid occurrences and correlations between this  
586 region and other worldwide localities must be further deciphered to determine its exact  
587 significance in understanding late Smithian events and in the survival and evolution of  
588 ammonoids through the SSB.

#### 4.3. *Extending the late Smithian ammonoid record – a conclusive remark*

With respect to the western USA ammonoid record, the new occurrences of the late Smithian UAZ6 outside Nevada as described in this work suggest that this typical ammonoid assemblage can likely be found more broadly within the western USA basin. This time interval corresponds to a marine regression at a global scale (e.g., Widmann et al., 2020), but to a transgression in the northern part of the western USA basin (Caravaca et al., 2018; Brayard et al., 2020). Potential fossiliferous localities are therefore most likely to be found in a reduced number within the basin and preferentially in places where regional subsidence is able to compensate for the global regression. Such localities are likely scarce in the southern part of the basin where the sea had already receded by that time (Lucas et al., 2007; Olivier et al., 2018; Brayard et al., 2020), but are more likely present in the western and northern parts of the basin where local subsidence was potentially able to compensate for this regression (Caravaca et al., 2018). However, deposits corresponding to UAZ6 often form incompetent hills, where outcrops are rare and hardly discernible in the landscape, and where the high proportion of shales does not facilitate a high quality of preservation in these localities. The same observations probably apply to the new, potentially latest Smithian ammonoid assemblage reported from northeastern Nevada by Widmann et al. (2020), and it is likely that its record elsewhere will be very sparse. A detailed knowledge of this potential latest Smithian ammonoid zone will likely be crucial in understanding the evolutionary history of ammonoids through the SSB and postulate refined phylogenetic links between late Smithian and early Spathian ammonoids.

#### **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). The final version of this paper benefited from constructive reviews by Marco Balini and Yuri Zakharov. We thank G. Caravaca and A.-S. Grosjean for their help in the field, and private land owners (Scott Rees – south side of Weber River and Mrs. Monte Brough – north side of Weber River) for allowing access to their lands. The Thumb Ridge section is located on US public land under the stewardship of the Bureau of Land Management (BLM) of the US Department of the Interior; access to these lands is gratefully acknowledged.

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## Figure captions

**Fig. 1.** Early Triassic (A) and present-day (B) locations of the western USA basin. C. Map of northern Utah showing the location of the two sampled localities.

**Fig. 2.** Simplified stratigraphic log showing ammonoid occurrences at Lower Weber Canyon (Morgan County, Utah). Stratigraphy follows the main units described by Grosjean et al. (2018).

**Fig. 3.** Simplified stratigraphic log showing ammonoid occurrences at Thumb Ridge (Tooele County, Utah).

**Fig. 4. A–L, P. *Xenoceltites subevolutus*. M–O. *Xenoceltites subevolutus* (Xs) and *Pseudosageceras augustum* (Pa).** Specimens A–E from bed LWC46, Lower Weber Canyon, Utah, early late Smithian; specimens F–J from bed LWC48, Lower Weber Canyon, Utah, latest Smithian; specimens K–P from bed THU A2, Thumb Ridge, Utah, latest Smithian. A, B: lateral and ventral views of UBGD 32330; C: suture line of UBGD 32330 at H = 15.7 mm; D: UBGD 32331; E: UBGD 32332; F–L: UBGD 32333–32339; M, N: lateral and ventral views of UBGD 32340; O: UBGD 32341; P: UBGD 32342. Black arrows indicate the position of the corresponding ventral view. Scale bars: 10 mm (A, B, D–P), 5 mm (C).

**Fig. 5.** Scatter diagrams of H, W and U, and H/D, W/D and U/D for *Xenoceltites subevolutus*. Open symbols indicate specimens from Lower Weber Canyon and Thumb Ridge, Utah (n = 7). Grey symbols indicate specimens from Palomino Ridge (data from Jattiot et al., 2017; n = 7) and Crittenden Springs (data from Jenks and Brayard, 2018; n = 32), northeastern Nevada.

**Fig. 6. A–R. *Pseudosageceras augustum*** from beds LWC48 and LWC49, Lower Weber Canyon, Utah, latest Smithian (A–G) and from bed THU A2, Thumb Ridge, Utah, latest Smithian (H–R). A–C: lateral, ventral and apertural views of UBGD 32343; D–G: UBGD 32344–32347; H, I: lateral and ventral views of UBGD 32348; J: suture line of UBGD 32348 at H = 16.4 mm; K: UBGD 32349; L, M: lateral and ventral views of UBGD 32350; N: UBGD 32351; O, P: lateral and ventral views of UBGD 32352; Q, R: lateral and ventral views of UBGD 32353. Black arrows indicate the position of the corresponding ventral view. The position of the drawn suture line J is indicated by the asterisk. Scale bars: 10 mm (A–I, K–R), 5 mm (J).



**Fig. 7.** Scatter diagrams of H, W and U, and H/D, W/D and U/D for *Pseudosageceras augustum*. Open symbols indicate specimens from Lower Weber Canyon and Thumb Ridge, Utah (n = 7). Grey symbols indicate specimens from Crittenden Springs, northeastern Nevada (data from Jenks and Brayard, 2018; n = 7), South Tibet (data from Brühwiler et al., 2010; n = 2), Spiti (data from Brühwiler et al., 2012a; n = 2) and South China (data from Brayard and Bucher, 2008; n = 31).

**Fig. 8. A–Q.** *Gurleyites smithi* from bed LWC46, Lower Weber Canyon, Utah, early late Smithian. A, B: Lateral and ventral views of UBGD 32354; C: UBGD 32355; D, E: Lateral and ventral views of UBGD 32356; F: UBGD 32357; G: UBGD 32358; H: Suture line of UBGD 32358 at H = 16.9 mm (note this suture line is asymmetrical with expected ventral axis [blue arrow] shifted on the left side); I–K: UBGD 32359–32361; L: Suture line of UBGD 32361 at H = 23.5 mm (slightly weathered); M: UBGD 32362; N: UBGD 32363; O, P: Lateral and ventral views of UBGD 32364; Q: UBGD 32365. Black arrows indicate the position of the corresponding ventral view. Scale bars: 10 mm (A–G, I–K, M–Q), 5 mm (H, L).

**Fig. 9. A–I.** *Gurleyites smithi*. **J–N.** *Anasibirites kingianus*. Specimens from bed LWC46, Lower Weber Canyon, Utah, early late Smithian. A–E: specimens illustrating most evolute morphs of *G. smithi* (A, block UBGD 32366 with four specimens illustrating the large intraspecific variation of the species; B, UBGD 32367; C, block UBGD 32368 with one evolute specimen of *G. smithi* and one specimen of *Hemiprionites typus* (H); D, E, lateral and ventral views of UBGD 32369); F–I: lateral views of UBGD 32370–32373; J–L: lateral views of UBGD 32374, 32375 and 32376; M, N: lateral and ventral views of UBGD 32377. Black arrows indicate the position of the corresponding ventral view. Scale bars: 10 mm.

879

880 **Fig. 10.** Scatter diagrams of H, W and U, and H/D, W/D and U/D for *Gurleyites smithi*. Open  
881 symbols indicate specimens from Lower Weber Canyon and Thumb Ridge, Utah (n = 25).  
882 Grey symbols indicate specimens from Workman Wash (data from Brayard et al., 2020; n =  
883 40), southern Utah, and Palomino Ridge (data from Jattiot et al., 2017; n = 7) and Crittenden  
884 Springs (data from Jenks and Brayard, 2018; n = 14), northeastern Nevada. Blue symbols  
885 indicate six similarly sized specimens from Lower Weber Canyon that exhibit a much more  
886 evolute coiling than other specimens.

887

888 **Fig. 11. A–Q.** *Wasatchites perrini* from bed LWC46, Lower Weber Canyon, Utah, early late  
889 Smithian. A, B: lateral and ventral views of UBGD 32378; C: UBGD 32379; D:  
890 UBGD 32380; E–G: lateral and ventral views of UBGD 32381; H: UBGD 32382; I:  
891 UBGD 32383; J, K: lateral and ventral views of UBGD 32384; L: poorly preserved suture  
892 line of UBGD 32384 at H = 15 mm; M: UBGD 32385; N, O: lateral and ventral views of  
893 UBGD 32386; P, Q: lateral views of UBGD 32387. Black arrows indicate the position of the  
894 corresponding ventral view. Scale bars: 10 mm (A–J, L–Q), 5 mm (K).

895

896 **Fig. 12.** Scatter diagrams of H, W and U, and H/D, W/D and U/D for *Wasatchites perrini*.  
897 Open symbols indicate specimens from Lower Weber Canyon, Utah (n = 10). Grey symbols  
898 indicate specimens from the Confusion Range (data from Brayard et al., 2013; n = 2), western  
899 Utah, and Palomino Ridge (data from Jattiot et al., 2017; n = 4) and Crittenden Springs (data  
900 from Jenks and Brayard, 2018; n = 2), northeastern Nevada.

901

902 **Fig. 13.** Scatter diagrams of H, W and U, and H/D, W/D and U/D for *Anasibirites kingianus*.  
903 Open symbols indicate specimens from Lower Weber Canyon, Utah (n = 4). Grey symbols

indicate specimens from Palomino Ridge (data from Jattiot et al., 2017; n = 5) and the compilation of measurements from Timor, Salt Range and Spitsbergen (data from Jattiot et al., 2016; n = 903).

**Fig. 14. A–R.** *Anasibirites multiformis* from bed LWC46, Lower Weber Canyon, Utah, early late Smithian (A–P) and from bed THU A1, Thumb Ridge, Utah, early late Smithian (Q, R). A–N, P: UBGD 32388–32401; O: suture line of UBGD 32401 at H = 15.3 mm; P: UBGD 32402; Q: UBGD 32403; R: suture line of UBGD 32403 at H = 30.1 mm. Scale bars: 10 mm (A–N, P, Q), 5 mm (O, R).

**Fig. 15.** Scatter diagrams of H, W and U, and H/D, W/D and U/D for *Anasibirites multiformis*. Open symbols indicate specimens from Lower Weber Canyon, Utah (n = 27). Grey symbols indicate specimens from Workman Wash (data from Brayard et al., 2020; n = 14), Palomino Ridge (data from Jattiot et al., 2017; n = 54) and Timor (data from Jattiot et al., 2016; n = 21).

**Fig. 16. A–M.** *Hemiprionites typus* from bed LWC46, Lower Weber Canyon, Utah, early late Smithian. A–C: blocks UBGD 32404–32406 with several *H. typus* specimens showing the characteristic ventral minute depression (A: *Anasibirites*); D: UBGD 32407; E, F: lateral and ventral views of UBGD 32408; G: UBGD 32409; H, I: lateral and ventral views of UBGD 32410; J: UBGD 32411; K: suture line of UBGD 32411 at H = 10 mm; L: UBGD 32412; M: UBGD 32413. Scale bars: 10 mm (A–J, L, M), 5 mm (K).

**Fig. 17. A–K.** *Hemiprionites typus*. **L–R.** *Hemiprionites walcotti*. Specimens from bed LWC46, Lower Weber Canyon, Utah, early late Smithian (A–J, L–R) and from bed THU A1,

929 Thumb Ridge, Utah, early late Smithian (K, with a crenulated venter). A–D: UBGD 32414–  
 930 32417; E, F: lateral and ventral views of UBGD 32418; G: UBGD 32419; H: suture line of  
 931 UBGD 32419 at H = 14.4 mm; I: UBGD 32420; J: UBGD 32421; K: UBGD 32422; L, M:  
 932 lateral and ventral views of UBGD 32423; N: UBGD 32424; O: UBGD 32425; P, Q: lateral  
 933 and ventral views of UBGD 32426; R: suture line of UBGD 32426 at H = 22 mm. Scale bars:  
 934 10 mm (A–G, I–R), 5 mm (H).

935  
 936 **Fig. 18.** Scatter diagrams of H, W and U, and H/D, W/D and U/D for *Hemiprionites typus*.  
 937 Open symbols indicate specimens from Lower Weber Canyon, Utah (n = 22). Grey symbols  
 938 indicate specimens from Workman Wash (data from Brayard et al., 2020; n = 6), southern  
 939 Utah, Palomino Ridge (data from Jattiot et al., 2017; n = 58) and Crittenden Springs (data  
 940 from Jenks and Brayard, 2018; n = 23), Nevada, Salt Range (data modified from Brühwiler et  
 941 al., 2012b; n = 20), Pakistan, and Timor (data from Jattiot et al., 2020; n = 186).

942  
 943 **Fig. 19.** Scatter diagrams of H, W and U, and H/D, W/D and U/D for *Hemiprionites walcotti*.  
 944 Open symbols indicate specimens from Lower Weber Canyon and Thumb Ridge, Utah (n =  
 945 5). Grey symbols indicate specimens from Workman Wash (data from Brayard et al., 2020;  
 946 n = 5), southern Utah, Palomino Ridge (data from Jattiot et al., 2017; n = 26) and Crittenden  
 947 Springs (data from Jenks and Brayard, 2018; n = 2), Nevada, and Timor (data from Jattiot et  
 948 al., 2020; n = 11).

949  
 950 **Fig. 20.** Biogeographical distribution of middle and late Smithian ammonoids within three  
 951 main areas: South China, the western USA basin and the Northern Indian Margin. Genera  
 952 reported in this study are highlighted in bold. Abbreviations: mSm: middle Smithian = UAZ4  
 953 in the western USA basin; late Sm: late Smithian; lS1: early late Smithian = UAZ5 in the

954 western USA basin = UAZ S-13 in the Northern Indian Margin = *Anasibirites* beds s.s. in  
955 South China; IS2: latest Smithian = UAZ6 in the western USA basin = UAZ S-14 in the  
956 Northern Indian Margin = upper *Anasibirites* beds in South China. For correlations between  
957 biostratigraphical scales, see Brühwiler et al. (2011), Jenks et al. (2015), Jattiot et al. (2017)  
958 and Jenks and Brayard (2018).

959

960

#### 961 **Appendix A. Supplementary information.**

962 Shell measurements (D: diameter, H: height W: width, and U: umbilical diameter) for some  
963 late Smithian ammonoids from Lower Weber Canyon and Thumb Ridge, Utah. Some  
964 measurements for these taxa sampled elsewhere are also given for comparison.

965 **Table S1:** *Xenoceltites subevolutus*.

966 **Table S2:** *Pseudosageceras augustum*.

967 **Table S3:** *Gurleyites smithi*.

968 **Table S4:** *Wasatchites perrini*.

969 **Table S5:** *Anasibirites kingianus*.

970 **Table S6:** *Anasibirites multiformis*.

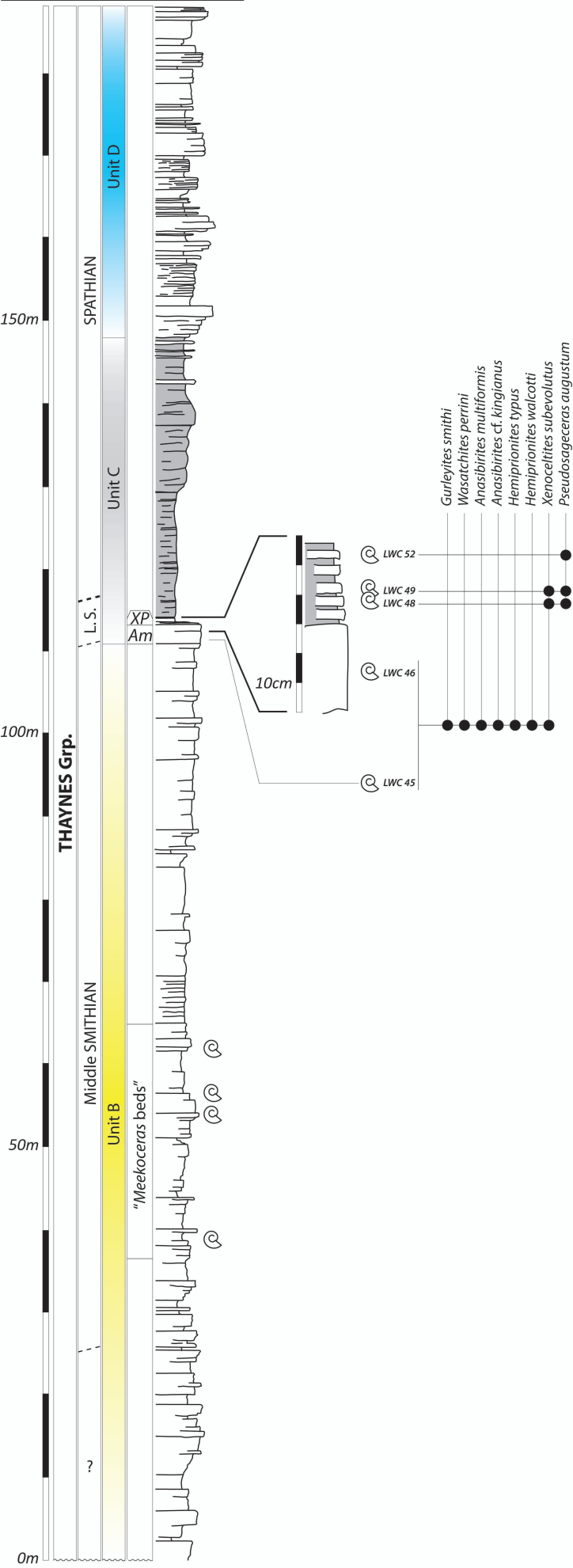
971 **Table S7:** *Hemiprionites typus*.

972 **Table S8:** *Hemiprionites walcotti*.

973



# Lower Weber Canyon



# Thumb Ridge

