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LATE GRIESBACHIAN (EARLY TRIASSIC) AMMONOIDS AND NAUTILOIDS FROM THE DINWOODY FORMATION AT CRITTENDEN SPRINGS, ELKO COUNTY, NEVADA

by
JAMES F. JENKS, TAKUMI MAEKAWA, DAVID WARE, YASUNARI SHIGETA, ARNAUD BRAYARD and KEVIN G. BYLUND
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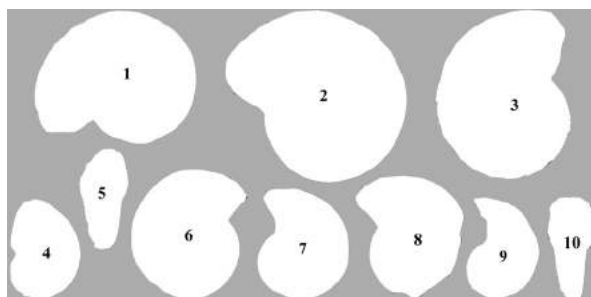
Cover illustration: Crittenden Springs Early Triassic (Late Griesbachian) ammonoids and nautiloids: 1-*Wordieoceras wordiei* (Spath), 2-*Wordieoceras wordiei* (Spath), 3-*Ophimullericeras paullae* n. gen., n. sp., 4-*Xiaohenautilus mulleni* n. sp., 5- *Xiaohenautilus mulleni* n. sp., apertural view, 6-*Kyoktites* cf. *K. hebeiseni* Ware and Bucher, 7- *Ophimullericeras paullae* n. gen., n. sp., 8-*Wordieoceras mullenae* n. sp., 9- *Xiaohenautilus mulleni* n. sp., 10- *Xiaohenautilus mulleni* n. sp., apertural view

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Abstract—We document a relatively small but very important late Griesbachian ammonoid and nautiloid assemblage from the Dinwoody Formation at Crittenden Springs, Elko County, Nevada. This discovery represents the first significant report of late Griesbachian ammonoids in the low-paleolatitudes of eastern Panthalassa, and it also signifies the first report of *Wordieoceras wordiei* and two co-occurring taxa outside of the Boreal Realm. This similarity in ammonoid faunas, irrespective of paleolatitude, provides support for the concept of weak latitudinal diversity gradients following the end-Permian extinction. The finding is even more noteworthy given the Dinwoody Formation's reputation for poor fossil preservation and a near complete absence of documented and identifiable ammonoid and nautiloid occurrences. Consisting of four taxa of which two are newly described, the ammonoid fauna includes *Wordieoceras wordiei* (Spath), *Kyoktites* cf. *K. hebeiseni* Ware and Bucher, *Wordieoceras mullenae* n. sp. and a new taxon belonging to the Mullericeratidae family, *Ophimullericeras paullae* n. gen., n. sp. The nautiloids are attributed to a newly described species, i.e., *Xiaohenautilus mulleni* n. sp., a genus heretofore unknown in eastern Panthalassa but commonly reported from the late Griesbachian of South Primorye and the late Griesbachian/early Dienerian of South China.

INTRODUCTION

The Permian-Triassic mass extinction some 252 million years ago, the most severe eradication of life in the Phanerozoic, resulted in the disappearance of nearly 90% of all marine species (Raup, 1979; Stanley, 2016). Although the ammonoids and nautiloids survived, their diversity was severely diminished from pre-extinction levels, with the ammonoids reduced to only three surviving lineages (Brayard et al., 2007; Brayard and Bucher, 2015; Dai et al., 2019). Quite remarkably, however, and contrary to the suggestions of a delayed recovery by some workers (Hallam, 1991; Tong et al., 2007; Chen and Benton, 2012), the ammonoids, together with a few other groups, i.e., conodonts and foraminifers, recovered their diversity following this event much faster than other organisms (Brayard et al., 2009; Song et al., 2011, 2013). Evidence of this recovery in the ammonoid record, at least for the earliest part, i.e., the Induan, and, in particular, the Griesbachian substage, is not all that abundant, with occurrences limited to a few localities (Fig. 1C) in the Boreal Realm (Arctic Canada [Tozer, 1967, 1971, 1994a], East Greenland [Spath, 1930, 1935; Bjerager et al., 2006] and NE Siberia [Dagys and Ermakova, 1996]), the Tethys (North Indian Margin [NIM] [Zhang et al., 2017; Ware et al., 2018], South China [Mu et al, 2007; Brühwiler et al., 2008; Dai et al., 2019]) and South Primorye (Shigeta and Zakharov, 2009). Until now, the ammonoid record for the Griesbachian in low-paleolatitude eastern Panthalassa was virtually non-existent.

Recently, a relatively small, *in situ* late Griesbachian ammonoid assemblage and several float nautiloids in close stratigraphic proximity were inadvertently discovered in the Dinwoody Formation, while sampling for conodonts on the north side of Long Canyon, a short distance east-northeast of the well-known Crittenden Springs Smithian ammonoid site, e.g., recently monographed by Jenks and Brayard (2018) (Fig. 2). While preservation is highly variable (Fig. 3), about half of the ammonoid specimens retain fairly well-preserved diagnostic features, i.e., whorl shape and suture lines, thus facilitating

reasonably accurate identification.

The newly reported ammonoid assemblage consists of four taxa, of which two are newly described. Three of the taxa have exclusive Boreal affinities, i.e., *Wordieoceras wordiei, W. mullenae* n. sp. and *Ophimullericeras paullae* n. gen., n. sp., the latter rather loosely based on a somewhat dubious taxon from East Greenland that Spath (1930, 1935) assigned to *Ophiceras (Lytophiceras) dubium*. The fourth taxon, i.e., *Kyoktites* cf. *K. hebeiseni*, is based on a poorly known taxon erected by Ware and Bucher (2018a) from the latest Griesbachian/earliest Dienerian of Spiti (India) and the Salt Range of Pakistan. Until now, confirmed occurrences of *Wordieoceras* have been documented only from the late Griesbachian of the Boreal Realm (Tozer, 1994a; Dagys and Ermakova, 1996; Bjerager et al., 2006). The nautiloids, which comprise a newly described taxon, *Xiaohenautilus mulleni* n. sp., consist of five float specimens from a narrow stratigraphic interval (Figs. 4, 5) relatively close to the ammonoid bed. *Xiaohenautilus*, erected by Xu (1988) for late Griesbachian/early Dienerian taxa from South China (Mu et al., 2007), also includes an additional taxon similar to the present specimens, i.e., *X. abrekensis* Shigeta and Zakharov 2009, from Abrek Bay, South Primorye. Interestingly, the apparent western Panthalassa affinity of the nautiloids contrasts with the Boreal affinity of the ammonoid fauna. Conodont diversity in the ammonoid-bearing section is rather low, and not unexpectedly, none of the samples from the stratigraphic proximity of the fossiliferous siltstone beds yielded conodonts. However, samples from a bivalve coquina limestone bed ~50 m stratigraphically higher (201507a, b; Fig. 5) contained a few typical Griesbachian-aged conodonts, i.e., *Clarkina* spp. and *Hindeodus* spp.

LOCALITY AND GEOLOGICAL CONTEXT

Location

The Griesbachian ammonoid site is located ~75 m stratigraphically below the top of the Dinwoody Formation,
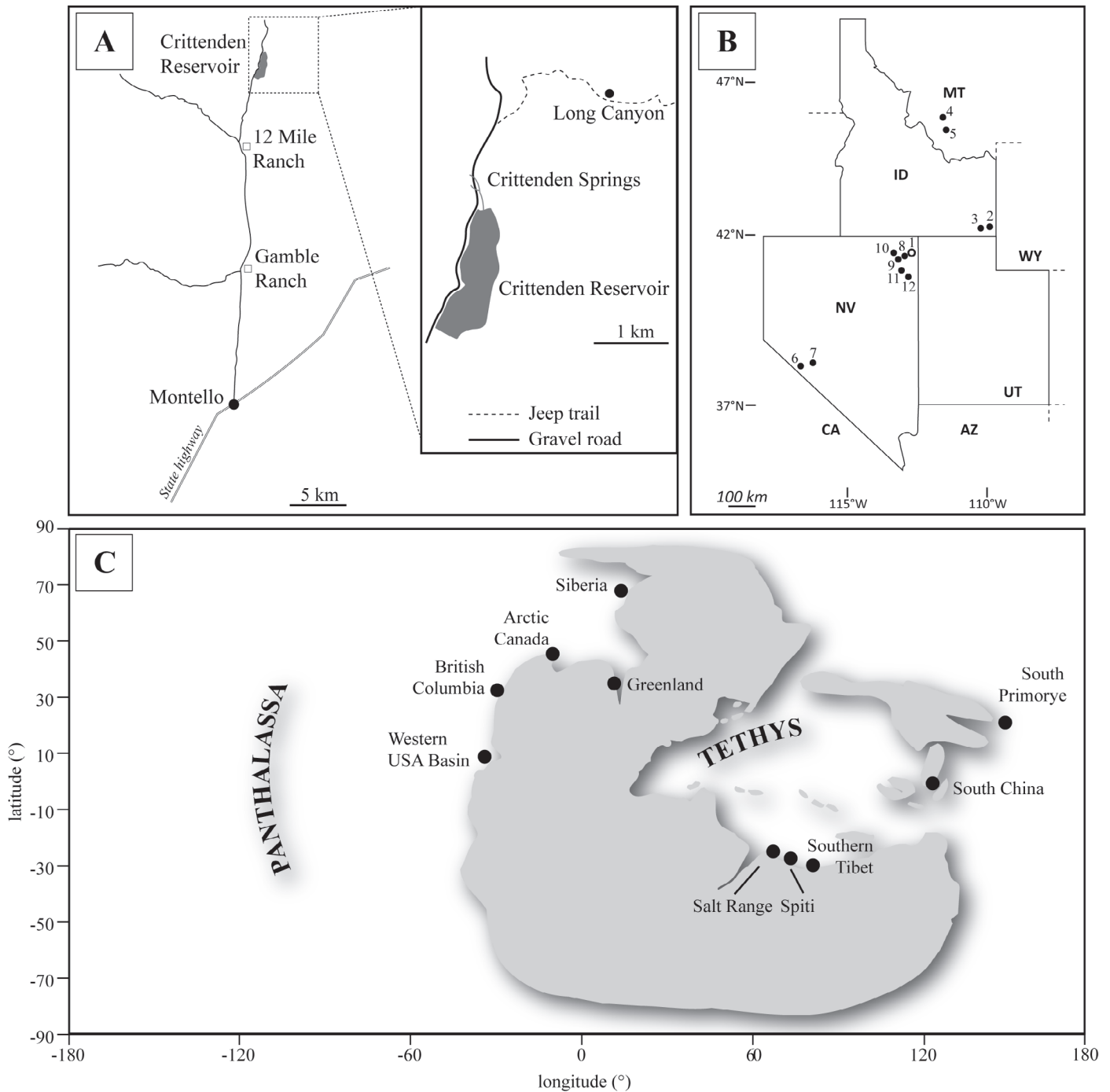
FIGURE 1. **A**, Generalized map showing location of the Griesbachian ammonoid and nautiloid sites in the Dinwoody Formation (indicated by black dot in Long Canyon) at Crittenden Springs. **B**, Location of Crittenden Springs area in relation to other western USA Dienerian and Griesbachian localities mentioned in text: 1) Crittenden Springs, 2) Montpelier Canyon, 3) Sleight Canyon, 4) Melrose, 5) Frying Pan Gulch, 6) Candelaria, 7) Willow Spring. Other Triassic exposures mentioned in text: 8) Immigrant Canyon, 9) Windemere Hills, 10) O'Neil Pass, 11) southern end of Pequop Range, 12) Dolly Varden Valley. **C.** Early Triassic paleoposition of the western USA basin in relation to other world-wide localities discussed in text. (A to C modified from Jenks and Brayard, 2018).

on a west-facing hillside (Fig. 2A-B) on the north side of Long Canyon, ~ 230 meters east-northeast of the original classic Crittenden Springs Smithian ammonoid site (Kummel and Steele, 1962; Jenks, 2007; Jenks et al., 2010; Jenks and Brayard, 2018; Maekawa and Jenks, in press). This general area is located ~32 km north of Montello, Elko County, Nevada, and ~ 2.3 km northeast of the abandoned ranch house at the north end of Crittenden Reservoir (Fig. 1A).

Dinwoody Formation: History and Depositional Basin Setting

The Dinwoody Formation, the oldest Triassic unit in the Cordilleran western USA basin, was named and defined by Blackwelder (1918), based on outcrops in Dinwoody Canyon on the northeastern side of the Wind River Mountains near Du Bois, Wyoming (Kummel, 1954; Paull, 1980). Deposited unconformably on Permian strata during a rapid Early Triassic
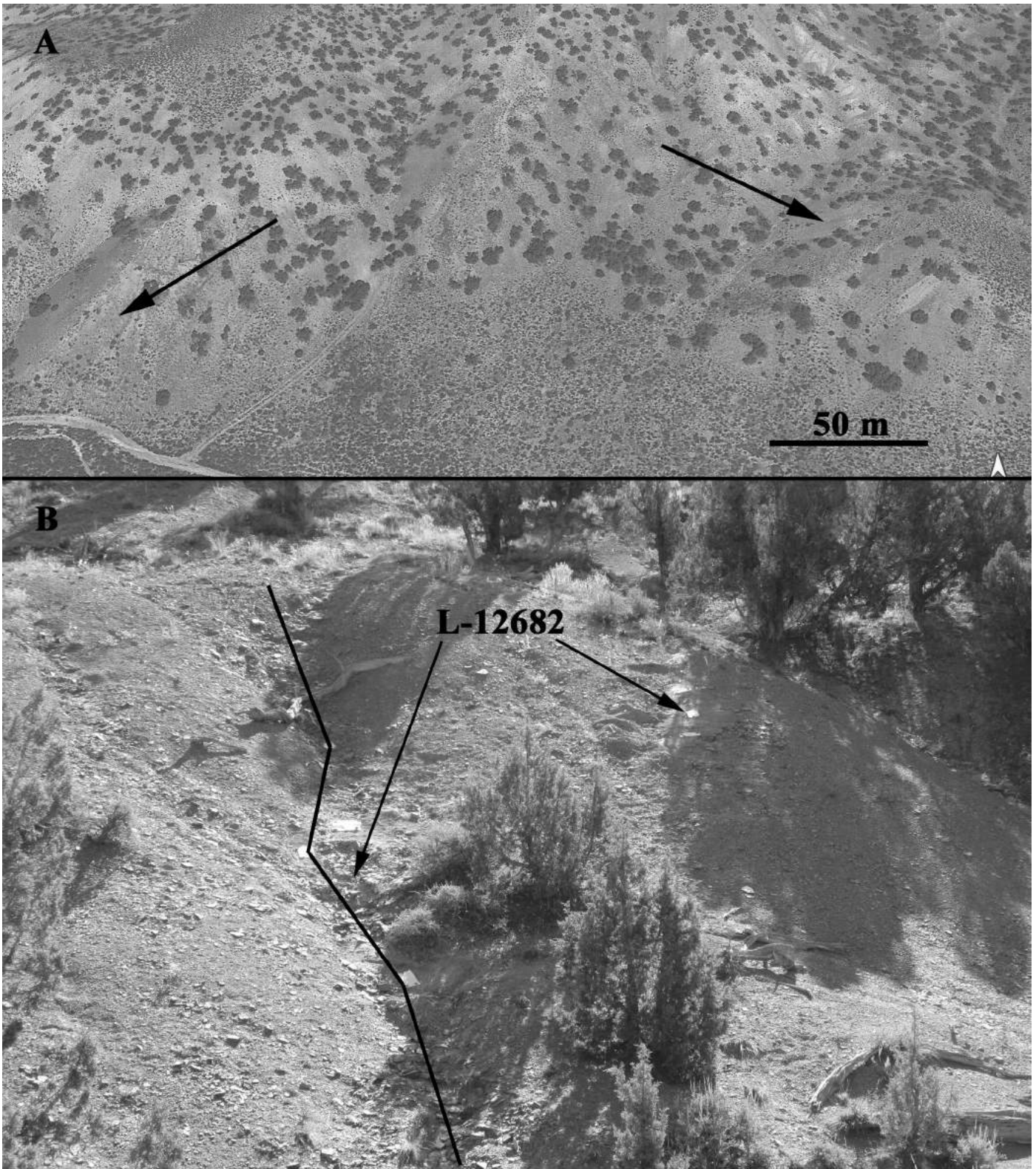
FIGURE 2. **A**, Google Earth image showing location of Griesbachian ammonoid and nautiloid site (right arrow) in relation to classic Smithian ammonoid site (left arrow) at Crittenden Springs. **B**, West-facing hillside with exposures of fossiliferous siltstone bed (NMMNH L-12682) in erosional channel and about 4 m to the south on same hillside. Slope of hillside more or less matches the dip angle of the beds.

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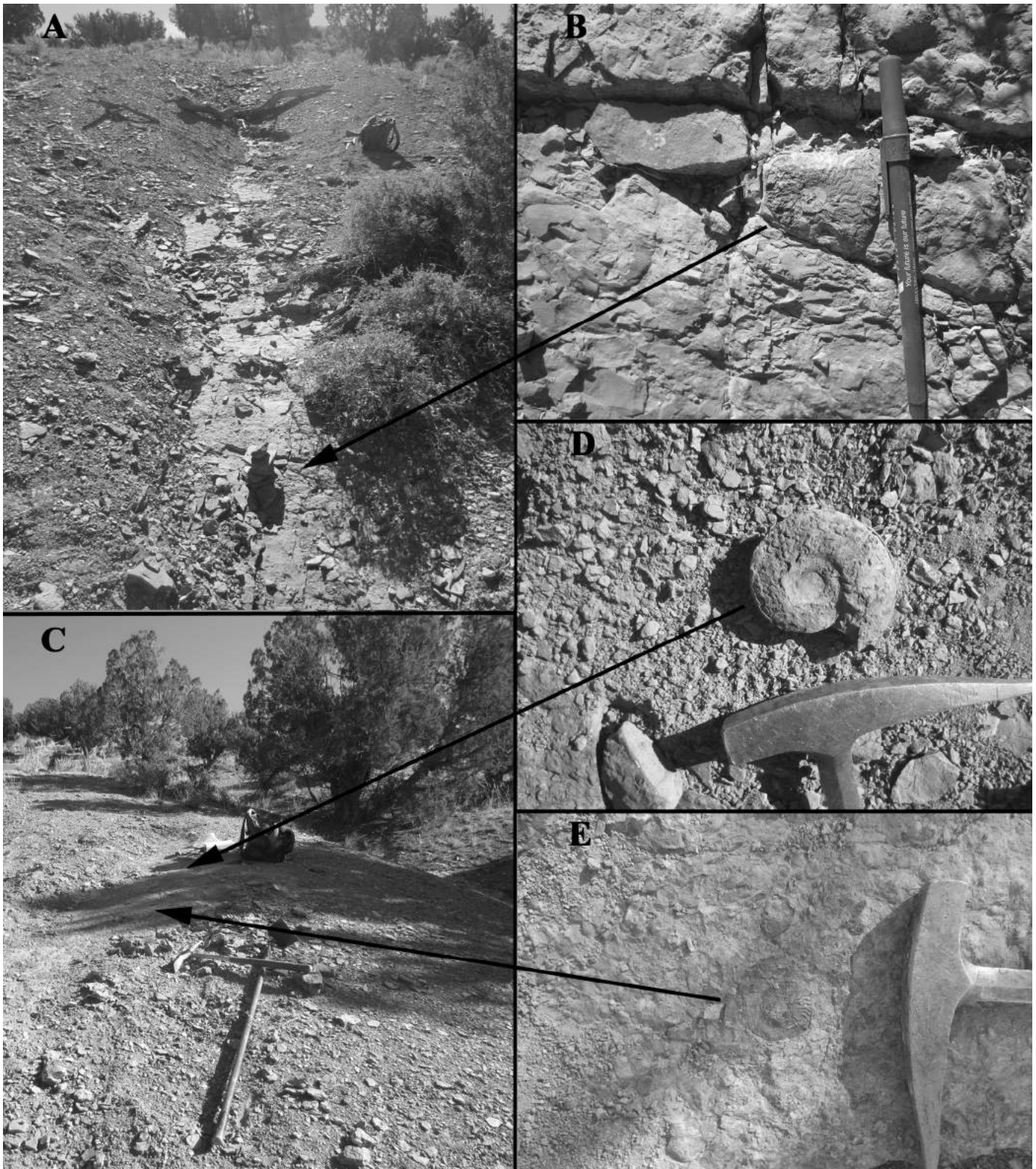
FIGURE 3. West-facing hillside with exposures of fossiliferous siltstone beds, in **A** and **C**. Ammonoid phragmocone in **B** (NMMNH P-81680, *Wordieoceras mullenae* n. sp.), arrow points to location in **A**. **D** (NMMNH P-81677, *Wordieoceras wordiei*), and **E** (poorly preserved specimen, not collected) illustrate type of preservation, i.e., heavily corroded upper surfaces.
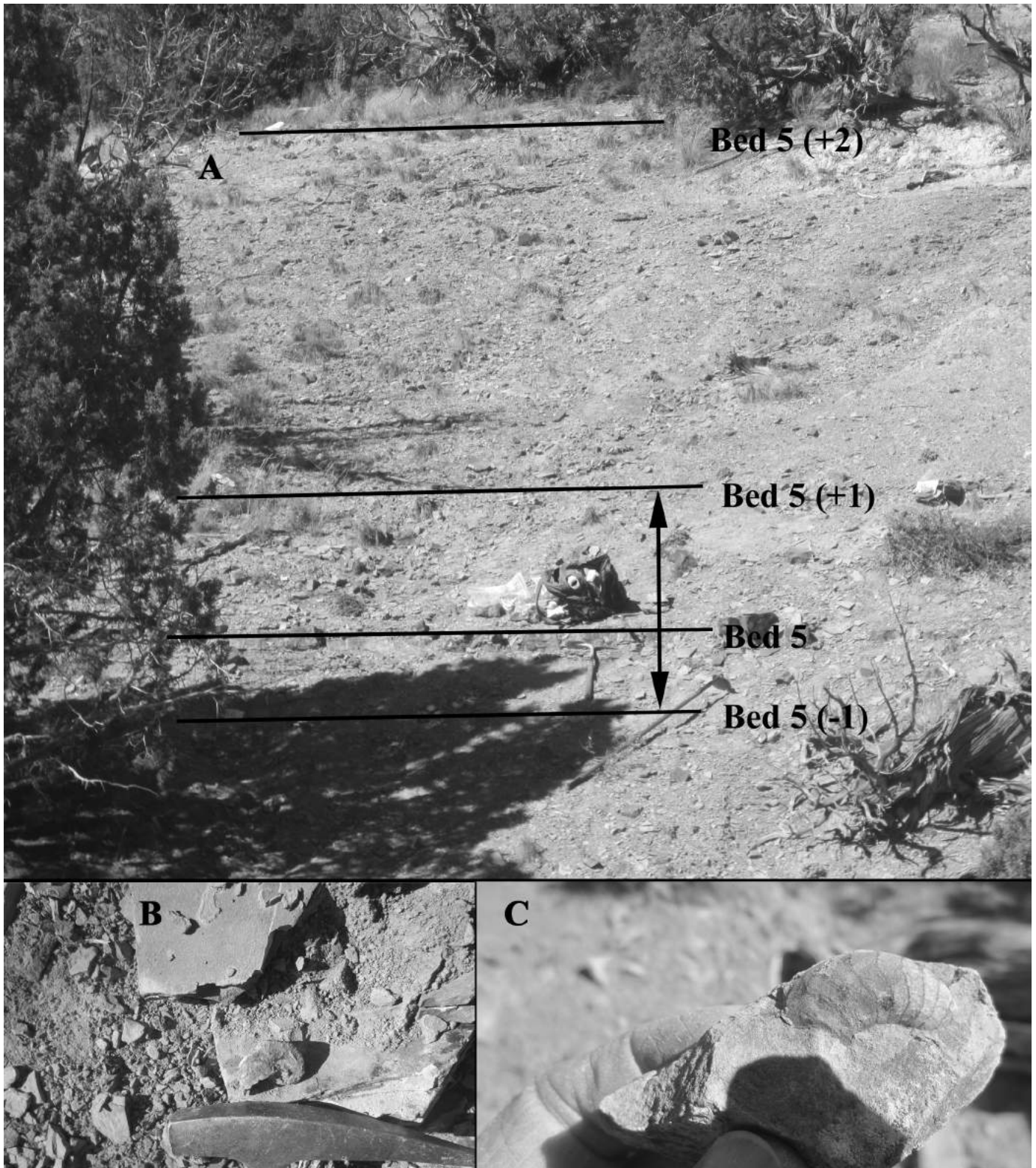
FIGURE 4. **A**, Gently sloping, east-facing hillside immediately west of ammonoid site with sampled beds demarcated. Nautiloids (five specimens) were found as float within the 2.5 m- thick interval indicated by double-ended arrow (locality NMMNH L-12683) between beds 5 (-1) and 5 (+1), e,g., in **B**, NMMNH P-81691, *Xiaohenautilus mulleni* n. sp. and **C**, NMMNH P-81692, *Xiaohenautilus mulleni* n. sp. Of these sampled beds, only 5 (+2), a silty limestone bivalve coquina, yielded conodonts.
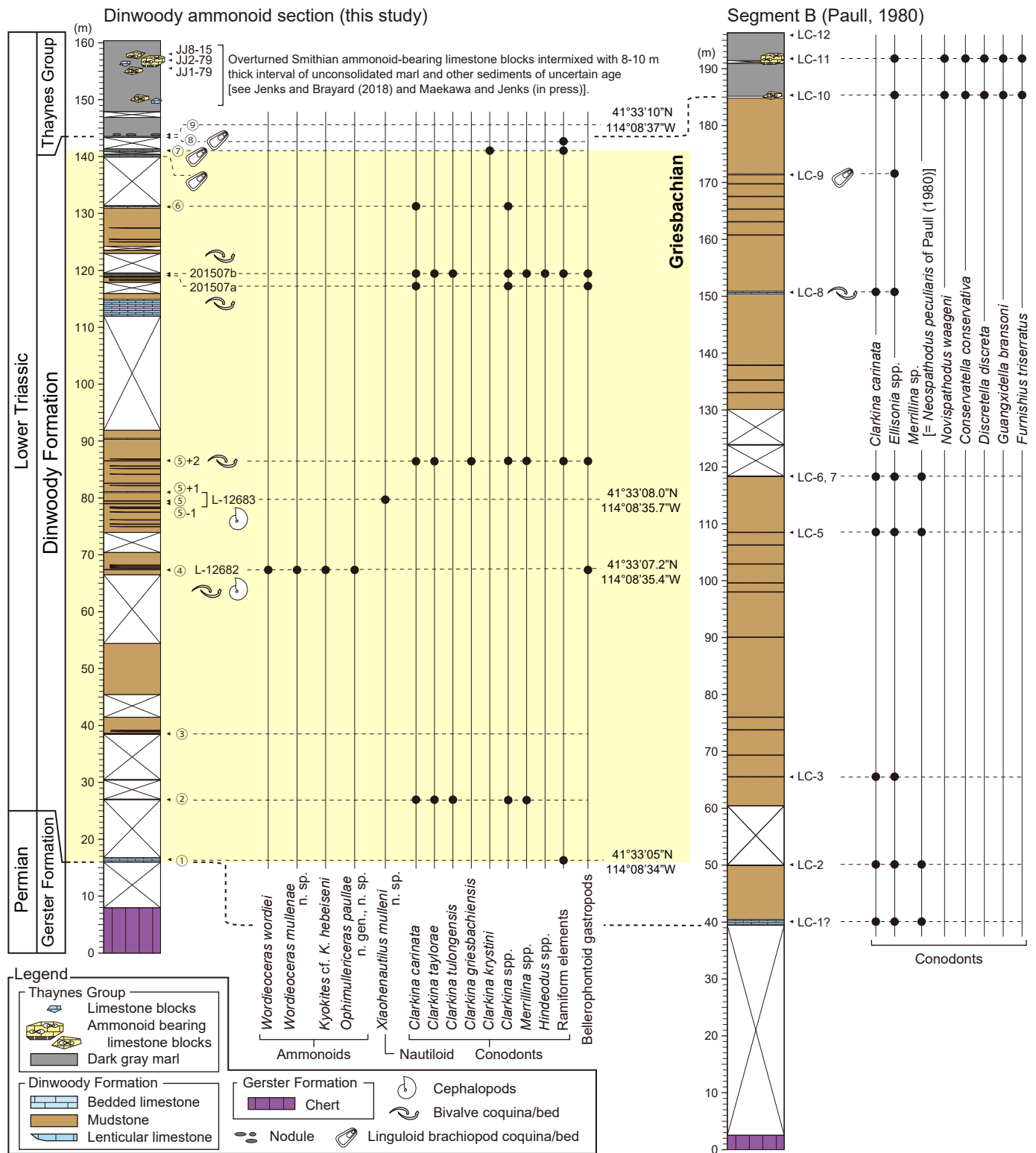
FIGURE 5. Columnar section showing stratigraphic occurrences of ammonoids, nautiloids, conodonts and bivalve/linguloid coquina beds in the Dinwoody Formation study section. Also shown is the Segment B columnar section, the upper part of Paull's (1980) composite section, which is located only ~140 m north of the present study section.

marine transgression (Newell and Kummel, 1942; Paull and Paull, 1994; Hofmann et al., 2013), the Dinwoody Formation is overlain conformably either by basal rocks of the Thaynes Group or by red beds of the Woodside Formation in the more easterly areas (Paull, 1980). Sediments of the Dinwoody Formation were deposited in the northern part of the Cordilleran western USA basin, an elongate epicontinental marine basin, whose axis extended in a northeasterly direction through east-central Nevada, northwestern Utah and southeastern Idaho (Silberling, 1973; Collinson and Hasenmueller, 1978; Paull, 1980). The Dinwoody sea, bounded on the south by an east-trending structural high that bisected the western USA basin, extended to the northeast through northeastern Nevada, south-central and southeastern Idaho, and then northward in a wide band along the Wyoming-Idaho border into southwestern Montana (Collinson and Hasenmuller, 1978; Wardlaw et al., 1979: Paull, 1980; Carr and Paull, 1983; Mullen, 1985; Caravaca et al., 2017). Initially, the eastern shore of the Dinwoody sea bordered on the edge of the craton, but it moved eastward during the Griesbachian transgression as far as the Big Horn Mountains in north-central Wyoming (Kummel, 1957; Collinson and Hasenmueller, 1978; Paull, 1980), before prograding back to the edge of the western USA basin during late Dienerian time (Collinson and Hasenmueller, 1978). According to Silberling (1973), the western boundary of the Dinwoody sea in northeastern Nevada probably shoaled against the Sonoma orogenic belt with an opening to the Panthalassa Ocean at some point along the margin, but very little is known about these orogenic sediments in the region due to the lack of outcrops (Hofmann et al., 2013).

Lithostratigraphic Divisions

Newell and Kummel (1942) informally divided the Dinwoody Formation in Wyoming into three lithostratigraphic units, i.e., the basal siltstone, the *Lingula* zone and the *Claraia* zone, but avoided extending this classification into other areas until its usefulness could be tested (Hofmann et al., 2013). Indeed, later work by Kummel (1954) in southeastern Idaho indicated that these subdivisions were not widely recognizable. Furthermore, Hofmann et al. (2013) in their survey of nine Dinwoody Formation sections in southwestern Montana, southeastern Idaho, western Wyoming and northern Utah, found that the three units were difficult to recognize and of little value other than in Wyoming. Lithologically, the Dinwoody Formation generally consists of an interbedded complex of olive-gray to tan, calcareous silty shale, brown to gray limestone and olive-drab, calcareous siltstone (Paull, 1980). The deeper water, shale facies component of these sediments accumulated in the Sonoma Foreland Basin during early Dinwoody deposition, whereas the siltstone and limestone facies buildup occurred during the later stages (Collinson and Hasenmueller, 1978; Mullen, 1985). Consequently, the Dinwoody Formation in the central part of the basin, which encompasses the Crittenden Springs area, is distinguished by a lower shaly unit and an upper siltstone and limestone unit (Mullen, 1985). Accordingly, Paull (1980) and Mullen (1985), both of whom extensively sampled the Dinwoody Formation in the Long Canyon area for conodonts, roughly divided the formation into two lithological units. The lower unit, consisting mainly of poorly exposed, olive-gray shales with a few thin, lenticular inter-beds of olive-grey, silty limestone, contains abundant compressed bivalves (*Claraia* sp.) in the lowermost portion of the shales (Mullen, 1985). Their upper unit, while generally more resistant, is comprised of thin to medium-bedded, gray calcareous siltstone and inter-bedded thin to massive-bedded gray limestone, most of which contain abundant bivalves and linguloid brachiopods (Mullen, 1985). Weathered surfaces in the upper unit vary widely in color from tan, gray, and brown to dark brown (Mullen, 1985).

Depositional Environment

In general, Paull (1980) based her interpretation of the depositional environment of these rocks (wackestone-type limestones as well as calcareous siltstones and shales) on the facies belts of Wilson's (1975) idealized carbonate model. That is, the rocks likely represent a neritic shelf facies with good current circulation and normal salinity, where water depth over the shelf was quite shallow, i.e., probably only tens of meters, but was below normal wave base, and sedimentation was fairly uniform (Wilson, 1975; Paull, 1980). A few bivalve coquina beds in the upper part of the formation hint at the existence of tidal bars or shoals rising above the general level of the sea floor (Wilson, 1975; Paull, 1980). Also indicative of a shelf environment is the thin to thick bedding style combined with the fairly wide range of rock colors resulting from variable oxidizing and reducing conditions; the presence of sedimentary structures, i.e., ripple marks and horizontal grazing traces, also supports this interpretation (Wilson, 1975; Paull, 1980). Kummel (1957), in his extensive faunal and lithofacies analysis of Lower Triassic formations in the middle Rocky Mountain region, also concluded that the Dinwoody Formation represents a shallow shelf facies (Paull, 1980).

Depositional Basin Outcrops

Outcrops of the Dinwoody Formation, which occur in all states originally covered by the Dinwoody sea (Fig. 1B), range in thickness from ~30 m at the type locality (as redefined by Newell and Kummel, 1942) to ~740 m near the depo-center in southeastern Idaho (Paull, 1980). In most outcrop areas, where the formation is overlain by the Thaynes Group (*sensu* Lucas et al., 2007), its uppermost limit is arbitrarily placed at the base of the *Meekoceras*-bearing lower limestone member (or equivalents) of the Thaynes Group (Paull, 1980). In the study area, however, the typical lower limestone member of the Thaynes Group is absent, and instead, the Dinwoody Formation is overlain by an 8-10 m thick interval of unconsolidated sediments of uncertain age (marls, thin-bedded, fractured siltstone debris and unfossiliferous limestone boulders), which encompasses the discontinuous and overturned Smithian ammonoid-bearing blocks for which the Crittenden Springs locality is well known (Jenks, 2007, Jenks et al., 2010; Jenks and Brayard, 2018; Maekawa and Jenks, in press). The Dinwoody Formation is not present in Triassic exposures to the west in the Windemere Hills (Wilkins Ranch section of Clark, 1957) or the O'Neil Pass area in the Snake Mountains (Clark, 1957; Paull and Paull, 1998) and is absent to the south in several measured sections, e.g., southern end of Pequop Range and Dolly Varden Valley (Scott, 1954; Hose and Repenning, 1959; Collinson et al., 1976; Carr, 1981; Mullen, 1985). Exposures in Immigrant Canyon in the Leach Range west of Montello represent the westernmost and southernmost outcrops of the Dinwoody Formation in Nevada.

Study Area Outcrops

Lower Triassic marine strata, consisting of the Dinwoody Formation (Griesbachian and Dienerian) and overlying Thaynes Group (Smithian and Spathian) crop out just north of the Long Canyon road and extend to the northeast for about 8 km, covering an area of about 33 km² (Clark, 1957; Mullen, 1985; Jenks and Brayard, 2018). Mullen (1985) mapped the entire area, differentiating the following units, in ascending order: Permian – undifferentiated, Dinwoody Formation, and Thaynes Group (*Meekoceras* limestone, black limestone, calcareous siltstone and limestone, and *Pentacrinus* limestone). By far, the calcareous siltstone and limestone unit of the Thaynes Group covers the majority of the mapped area, especially the central and northeastern portion. The area is heavily faulted, and, according to Mullen (1985), the Dinwoody Formation is in normal stratigraphic sequence with underlying Permian rocks at

only one location, which was chosen as the base of her measured section. Elsewhere in the area, Permian rocks are either in fault contact with the Dinwoody Formation, or the contact is covered (Mullen, 1985). Nearly all the important outcrops of the Dinwoody Formation are present within the southwestern portion of the area, over a span stretching from the Long Canyon road to a point ~4 km northeast of Long Canyon. A few additional outcrops are present farther north and northeast, but most are isolated, incomplete sections.

Location of Study Section and Measured Sections of Other Workers

Mullen's (1985) measured section (~395 m thick) is located ~3 km north of Long Canyon, whereas Paull's (1980) composite section (~305 m thick) consists of a 120 m thick lower part (segment A) located ~1.25 km north of Long Canyon and a 185 m thick upper part (segment B) located only ~0.28 km north of the Long Canyon road. In contrast, the thickness of the Dinwoody Formation in the immediate vicinity of the ammonoid discovery site at the extreme southern end of the outcrop area, only a short distance (~140 m) south of Paull's upper section, is merely ~135 m. Thus, a sizeable portion (40 to 50 m) of the Dinwoody Formation has been removed, most likely by concealed faulting, near the southern end of the outcrop area. The lithology, color and thickness of the various component beds of the formation can vary greatly within a relatively short distance along strike, plus the stratigraphic portion of the section that is covered varies widely in the area of the Permian/Dinwoody contact. These variances, combined with extensive faulting, much of which is concealed, make it extremely difficult to find and trace marker beds or correlate beds within the above described units, other than in a very general sense. Indeed, Paull (1985) commented regarding these difficulties and estimated that the lower and upper parts of her composite section could possibly overlap by as much as 20 meters.

Description of Ammonoid- and Nautiloid-Bearing Beds: Attitude and Topography

The newly discovered ammonoids are preserved in a westerly dipping, ~10 cm thick succession of calcareous shaly siltstone beds (each 2-3 cm thick) exposed on a west-facing hillside (Fig. 2B), where the dip of the beds more or less matches the slope of the hill. Over time, meteoric water has eroded the softer overlying siltstone beds and shales, exposing the fossiliferous beds in stair-step fashion in a narrow erosional channel; ammonoids appear to be more abundant and better preserved in the lowermost or primary bed of the succession, which is exposed near the bottom of the hill. This particular bed is also exposed in a relatively large patch (~4 m²) on the same hillside about 4 m south of the channel (Fig. 2B), and it is from this exposure that the majority of the specimens have been collected. Compared to the abundance of very poorly preserved bivalves on these surfaces, ammonoids are quite rare, but they usually are readily visible (Fig. 3B, D, E) because their spiral form, deeply corroded phragmocones and reddish-brown color tend to make them conspicuous in contrast to the irregular surface formed by the bivalves.

Indeed, given the rarity of ammonoids in the Dinwoody Formation, this discovery never would have occurred had it not been for the concordance between the topographic slope and the attitude of these fossiliferous beds on this relatively small hillside (~250 m²). Efforts to expose more of the primary fossiliferous bed by manually removing the overlying shales and siltstone beds have resulted in the discovery of a few additional specimens, but the excessive amount of generated dust tends to obscure newly exposed specimens, whose discovery must await dust-cleansing rain storms. In contrast, the coiled nautiloids were found as float about 15 m west of the ammonoid site, on a gentle, east-facing slope, just across the small gulley at the foot of the ammonoid-containing hillside. These float specimens occur within a ~2.5 m interval (fossil locality JJ6-19, Fig. 5) located ~7 m stratigraphically above the ammonoid level; to date, five specimens have been found between siltstone beds designated as 5(-1) and 5(+1) (Figs. 4, 5).

AMMONOID AND NAUTILOID PRESERVATION

Ammonoids from the primary productive bed (NMMNH L-12682; Fig. 5) mainly consist of complete phragmocones, mostly without distortion or compaction, together with very short portions (less than ¼ whorl) of body chambers, most of which are badly distorted or crushed. The upper surfaces of all phragmocones are corroded to varying degrees, some quite deeply (Fig. 3B, D), whereas the bottom surfaces of about half of the specimens are generally free of corrosion, except for the test, which is usually corroded so that shell features, e.g., growth lines, are not preserved. On many specimens, the nature of the ventral surface (rounded, tabulate, etc.) has also been adversely affected by corrosion for much of the circumference. In some cases, the shell material on the bottom surfaces together with adhering siltstone can be removed with an air pneumatic tool, revealing well-preserved suture lines. As with the ammonoids, nautiloids usually consist of either complete or partial phragmocones, but the preservation of our five float specimens ranges from very poor with some lateral distortion and severe corrosion, to fairly good with well-preserved suture lines.

INDUAN AMMONOID BIOSTRATIGRAPHY

Western USA Basin

Until now, virtually nothing was known regarding Griesbachian ammonoids in this region, other than for a brief report by Newell and Kummel (1942, pl. 2, figs. 6 and 7) in which, after an extensive survey of some 20 measured sections in Wyoming, Idaho and Montana, they were able to document the occurrence of only two poorly preserved, fragmental Griesbachian ammonoids, tentatively identified as *Discophiceras subkyokticum* and *Metophiceras subdemissum,* from the Dinwoody Formation at Montpelier Canyon, Idaho and Melrose, Montana, respectively. Beyond this report, there are no other documented occurrences of Griesbachian ammonoids from the Dinwoody Formation.

Ware et al. (2011) documented a long known but never illustrated, well preserved late middle and early late Dienerian ammonoid fauna that includes the *Ambites lilangensis* assemblage as well as two additional but informal ammonoid horizons from the Candelaria Formation near the old "ghost town" of Candelaria in southwestern Nevada. The late middle Dienerian *A. lilangensis* assemblage, informally termed the "*Proptychites* beds", includes *P. haydeni*, *P. pagei*, "*Koninckites*" aff. *kraffti* and *Mullericeras spitiense* as well as the eponymous taxon (Ware et al., 2011). Poole and Wardlaw (1978) mentioned an additional Candelaria Formation locality containing a very poorly preserved Dienerian ammonoid fauna near Willow Spring in Nye County, Nevada, about 80 km northeast of the Candelaria locality. This fauna has not been studied due to its poor preservation, but it is assumed to be more or less equivalent to that of the Candelaria locality. And, finally, Kummel (1954) mentioned the occurrence of two poorly preserved "Gyronitan" (=Dienerian) ammonoid faunas in succession in the Dinwoody Formation at Frying Pan Gulch in southwestern Montana, containing specimens identified as *Prionolobus* and *Koninckites* in the lower horizon and *Kymatites*, *Koninckites* and *Xenodiscoides* in the upper horizon, but he neither illustrated these specimens nor provided precise collection locations. These three localities essentially represent all that is known regarding Dienerian ammonoids within the western USA basin.

Mid-Paleolatitude Eastern Panthalassa

Documented mid-paleolatitude Griesbachian ammonoid occurrences in eastern Panthalassa are essentially nonexistent except for an obscure report by Warren (1945) of flattened ammonoids in the Sulphur Mountain Member of the Spray River Formation in Alberta, Canada. More specifically, these ammonoids occur in close stratigraphic proximity to beds containing the bivalve *Claraia stachei*, which is generally considered to straddle the Griesbachian-Dienerian boundary (Kummel, 1954; Ware et al., 2011). According to Kummel (1954), Warren (1945) thought the ammonoids represented the genera *Ophiceras*, *Proptychites* and *Otoceras*, but the specimens were never illustrated and, given their flattened preservation, even their identification at the generic level is questionable.

Boreal Realm

In contrast, Griesbachian ammonoid biostratigraphy in the Boreal Realm is fairly well documented from more or less correlative sections (Fig. 6) in eastern Panthalassa, i.e., Arctic Canada (Tozer, 1994a), Eastern Greenland (Spath, 1930, 1935; Bjerager et al., 2006), Svalbard (Weitschat and Dagys, 1989) and northeastern Siberia (Dagys and Weitschat, 1993; Dagys and Ermakova, 1996). The Griesbachian in these areas generally consists of the *Otoceras concavum*, *Otoceras boreale*, *Ophiceras commune* and *Bukkenites strigatus* or *B. rosenkrantzi* Zones or equivalents thereof, in ascending order (Bjerager et al., 2006, fig. 6). Zonal correlation schemes in East Greenland and northeastern Siberia include *Wordieoceras decipiens* (=*W. wordiei*) in the late or latest Griesbachian, respectively (Bjerager et al., 2006). Although the East Greenland zonal correlation scheme of Bjerager et al., (2006) is shown in the correlation chart (Fig. 6), it is anticipated that extensive studies by Ware (ongoing work) will eventually result in significant modification to this succession. Additionally, the five-fold, Siberian Griesbachian zonal scheme of Dagys and Ermakova (1996) has been reduced to a four-fold succession with the elimination of the *Tompophiceras pascoei* Zone by Zakharov et al. (2020). Also, it should be noted that both Ware et al. (2018a) and Dai et al. (2019) have slightly modified the zonation of Arctic Canada by placing the *Bukkenites strigatus* Zone in the lowermost Dienerian. Furthermore, when the IUGS formally defined the base of the Induan based on the lowest occurrence of the conodont *Hindeodus parvus* at the Meishan section, South China (Yin et al., 2001), the traditional base of the Griesbachian, i.e., the FAD of *Otoceras*, effectively became part of the Permian (Jenks et al., 2015). This change has not been widely accepted by Triassic workers (e.g., Tozer, 2003; Shevyrev, 2006), especially given that the scarcity and poor preservation of ammonoids in the Meishan section (Jenks et al., 2015) essentially precludes their use for authenticating the conodont-based boundary placement. Consequently, considerable debate still exists regarding the placement of the PTB in Arctic ammonoid zonations. However, we choose to follow Tozer's (1967) definition of the Griesbachian, with the *Otoceras concavum* or *Hypophiceras trivale* Zone marking the base.

Northern Indian Margin

According to Ware et al. (2018a), the Griesbachian is not well represented in the Salt Range, with ammonoids being rare and generally poorly preserved. Consequently, it is difficult to correlate their three regional biostratigraphical subdivisions, i.e., *Hypophiceras* cf. *H. gracile*, *Ophiceras connectens* and ?*Ophiceras sakuntala*, with other NIM areas (Ware et al., 2018a). Nevertheless, Ware et al. (2018a) described two new latest Griesbachian/earliest Dienerian taxa from the Nammal Nala section, upon which one of the present studied taxa is based, i.e., *Kyoktites* cf. *K. hebeiseni*. Krystyn et al. (2004, 2007) proposed a somewhat more definitive zonal scheme for the Spiti Valley area, i.e., the *Otoceras woodwardi*, *Ophiceras tibeticum* and *Discophiceras* Zones, but because they did not provide sufficient explanations and taxonomic definitions as well as illustrations, its usefulness for correlational purposes is uncertain (Ware et al., 2018a). Zhang et al. (2017) documented Griesbachian and Dienerian ammonoid occurrences from Qubu in the Mt. Everest area, southern Tibet; zonation for the Griesbachian in this area includes the basal *Otoceras woodwardi* Zone and overlying *Ophiceras tibeticum* Zone.

South China

For the most part, Griesbachian faunas from the low-paleolatitude South China Block are not well known, primarily because of poor ammonoid preservation at most localities. Furthermore, confirmed reports of earliest Griesbachian *Otoceras* or equivalent faunas are as yet unknown (Brühwiler et al., 2008; Dai et al., 2019). A supposed early Griesbachian "*Hypophiceras* fauna" together with ?*Otoceras* sp. was reported from the Meishan section by Wang (1984), but the poor preservation of these specimens has cast serious doubt on the accuracy of these attributions, and there is some question as to whether they are even of Triassic age (Tozer, 1994b; Shevyrev, 2006; Brühwiler et al., 2008). In contrast to the poor preservation in most areas, Brühwiler et al. (2008) and Dai et al. (2019) have documented fairly well-preserved Griesbachian and Dienerian ammonoid faunas from northwestern Guangxi/southern Guizhou, South China, respectively. Brühwiler et al. (2008) collected small, late Griesbachian ophiceratid specimens from the Luolou Formation at Shanggan, Guangxi that they suspected were juveniles of *O. sinense*, but because they found no adult shells, they illustrated their specimens in open nomenclature as *Ophiceras* sp. indet.

Dai et al. (2019) collected numerous Griesbachian (and Dienerian) ammonoids from the Gujiao section, a well-exposed outcrop of the Daye Formation created by new highway construction about 20 km southeast of Guiyang, the capital of Guizhou Province. Late Griesbachian ammonoids are placed into two informal subdivisions, i.e., the *Ophiceras medium* beds and the overlying *Jieshaniceras guizhouense* beds, whose age is problematic (Dai et al., 2019). Taxa from the *J. guizhouense* beds include *Vishnuites pralambha*, *Mullericeras gujiaoense* and *Proptychites* sp. indet. While *Ophiceras medium* is definitely of late Griesbachian age, taxa from the overlying *J. guizhouense* beds are also considered to be of Dienerian age at other localities, e.g., *V. pralambha* from Guangxi, *J. guizhouense* from Guizhou, and *Mullericeras* from Nevada (Brühwiler et al., 2008; Dai et al., 2019). According to Dai et al. (2019) and Ware (ongoing work), the age of the *J. guizhouense* beds and, for that matter, the Griesbachian/Dienerian boundary itself is poorly constrained if based solely on ammonoids. On the other hand, conodonts are known to have undergone a significant change at this boundary (Orchard, 2007; Brosse et al., 2017; Dai et al., 2019), and taxa contained in the beds from which Brühwiler et al. (2008) collected *J. guizhouense* clearly demonstrate that the beds are of late Griesbachian age.

South Primorye

Shigeta and Zakharov (2009) documented a succession of abundant and well-preserved Griesbachian, Dienerian and early to middle Smithian ammonoid faunas from the Lazurnaya Bay and Zhitkov formations at Abrek Bay, South Primorye. The Griesbachian portion of these bedrock-controlled collections includes ammonoids belonging to the late Griesbachian *Lytophiceras* Zone and part of the overlying *Gyronites subdharmus* Zone, as well as several nautiloid taxa (Shigeta and Zakharov, 2009). Some controversy surrounds the possible designation of the lower portion of the *G. subdharmus* Zone as latest Griesbachian (see Dai et al., 2019, fig. 18), but these beds contain ammonoid co-occurrences not seen before in other

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		Western USA Basin	Northern Indian Margin	South China	South Primorye	Verkhoyansk Basin (Siberia)	Arctic Canada	East Greenland
		Newell & Kummel, 1942; Kummel, 1954; Ware et al., 2011; this work	Krystyn et al., 2004, 2007; Ware et al., 2015, 2018	Brayard & Bucher 2008; Brühwiler et al., 2008; Dai et al., 2018	Zakharov, 1999; Shigeta & Zakharov, 2009; Shigeta, ongoing work	Dagys & Weitschat, 1993; Dagys & Ermakova, 1996; Zakharov et al., 2020	Tozer 1994	Bjerager et al., 2006
DIENERIAN	late		Aw. awani UAZ					
			Ko. vetustus UAZ			Ki.? korostelevi Zone		
			Ki. davidsonianus UAZ	Ci. sp. indet. beds	Co. spitiense Zone	V. turgidus Zone	V. sverdrupi Zone	
		V. meridialis beds	V. meridialis UAZ			V. sverdrupi Zone		
	middle	Ambe. lilangensis beds	Ambe. lilangensis UAZ	Ambe. bjerageri beds				
			Ambe. superior UAZ					
		Ambe. subradiatus beds	Ambe. discus UAZ		"Ambo. fuliginatus" Zone		Pr. candidus Zone	
			Ambe. bojeseni UAZ	Ambe. radiatus beds				
			Ambe. atavus UAZ					
	early		Gy. frequens UAZ					
			Gy. plicosus UAZ		Gy. subdharmus Zone		B. strigatus Zone	B. rosenkrantzi Zone
			Gy. dubius UAZ					
GRIESBACHIAN	late	W. wordiei beds	Discophiceras Zone	J. guizhouense beds	Lytophiceras Zone	W. decipiens beds	Op. commune Zone	W. decipiens Zone
		Op. tibeticum Zone	Op. medium beds			T. morpheos Zone		Op. commune Zone
	early	M. subdemissum beds*	Ot. woodwardi Zone			Ot. boreale Zone	Ot. boreale Zone	M. subdemissum Zone
								M. martini Zone
						Ot. concavum Zone	Ot. concavum Zone	M. triviale Zone

Abbreviations of genera

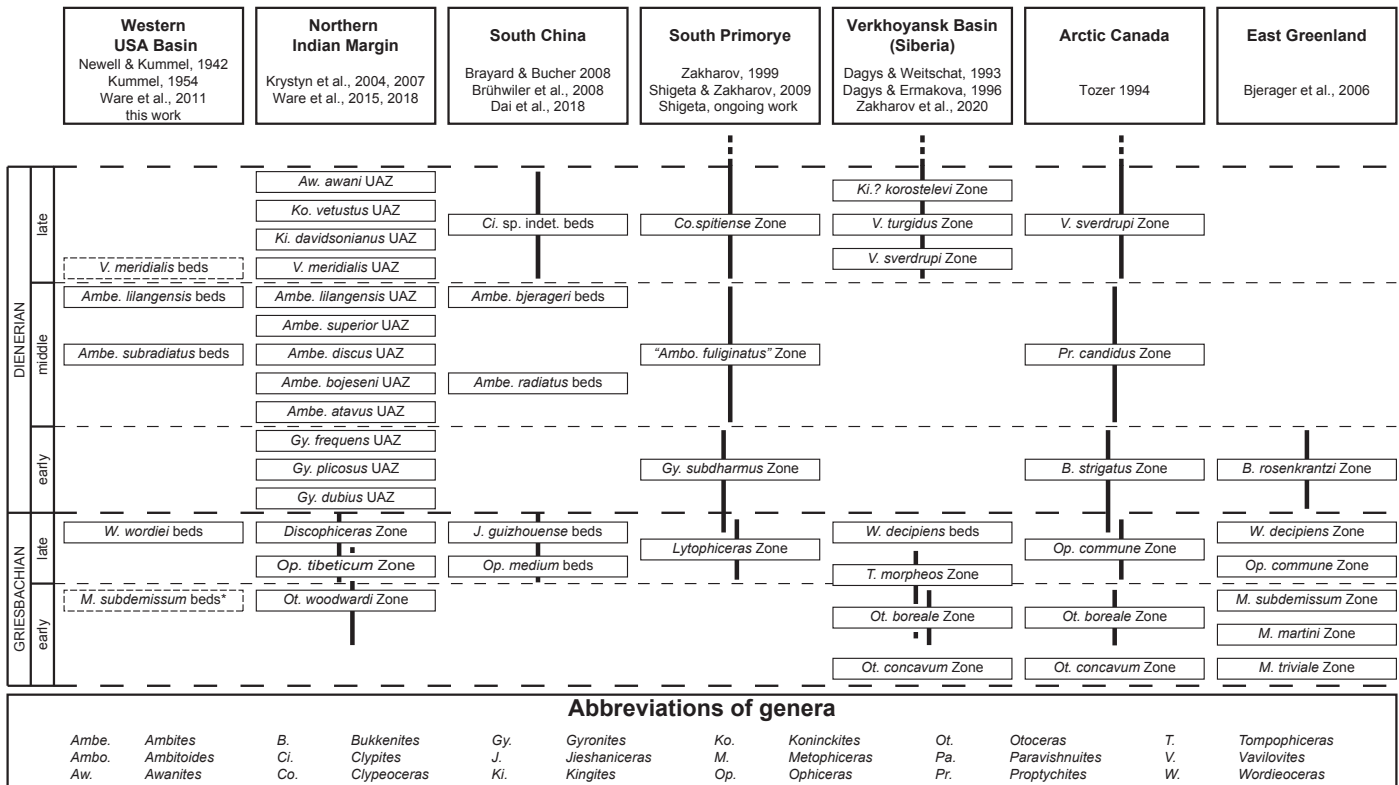|								
Ambe.	Ambites	B.	Bukkenites	Gy.	Gyronites	Ko.	Koninckites	Ot.	Otoceras	T.	Tompophiceras
Ambo.	Ambitoides	Ci.	Clypites	J.	Jieshaniceras	M.	Metophiceras	Pa.	Paravishnuites	V.	Vavilovites
Aw.	Awanites	Co.	Clypeoceras	Ki.	Kingites	Op.	Ophiceras	Pr.	Proptychites	W.	Wordieoceras

FIGURE 6. Induan ammonoid zonation of the western USA basin and correlation with other global occurrences. Bold vertical black bars represent uncertain correlation. Dashed line boxes encompassing *Vavilovites meridialis* beds and *Metophiceras subdemissum* beds of western USA basin represent uncertain stratigraphic occurrences within late Dienerian and early Griesbachian, respectively. Similarly, asterisk marking *M. subdemissum* beds denotes uncertain ammonoid identification. Note: Ongoing work by Ware is expected to significantly modify the zonation of Bjerager et al., (2006) for East Greenland. UAZ = Unitary Association Zone.

localities that lend credence to this designation. Ongoing work by Shigeta et al. is expected to further resolve this issue.

In summary, world-wide Griesbachian ammonoid distribution (Fig. 6) generally includes the *Otoceras* and overlying *Ophiceras* faunas or equivalents thereof, even though the *Otoceras* faunal record in the Tethyan Realm is not as complete as in the Boreal Realm (e.g., Brühwiler et al., 2008). *Ophiceras* and its various species are generally considered to be cosmopolitan taxa that range throughout the upper Griesbachian (Shevyrev, 2001; Brühwiler et al., 2008). Some areas, e.g., NIM, East Greenland, Arctic Canada, are characterized by expanded sections that exhibit much higher faunal resolution. Nevertheless, this general similarity in ammonoid faunas and succession, irrespective of paleolatitude, tends to reinforce the concept of weak latitudinal diversity gradients following the end-Permian extinction (Brayard et al., 2006, 2009; Brühwiler et al., 2008). And, the newly reported late Griesbachian ammonoid assemblage from the Dinwoody Formation at Crittenden Springs, which represents the first documented occurrence of *Wordieoceras wordiei* and two additional Boreal taxa in the low paleolatitudes, provides convincing evidence of this concept.

EARLY TRIASSIC NAUTILOID BIOSTRATIGRAPHY

Until now, reports of coiled nautiloids from the Dinwoody Formation are even rarer than ammonoids, consisting of only two specimens. Kummel (1953, p. 53, pl. 6, figs. 5, 6) described a new taxon (*Grypoceras milleri*) based on one poorly preserved, incomplete specimen found in the western part of Sleight Canyon, west of Paris, Idaho. He also mentioned, but did not illustrate a very large fragment of a nautiloid body chamber from Montpelier Canyon, Idaho, whose original shell he estimated to be ~30 cm in diameter (Kummel, 1953). Muller and Ferguson (1939) listed *Grypoceras* cf. *G. brahmanicum* (Griesbach) from the Candelaria Formation in southwestern Nevada. Beyond these three reports, no other Griesbachian or Dienerian coiled nautiloids have been reported from eastern Panthalassa until now. It is somewhat surprising that nautiloids have not been reported from British Columbia and/or Arctic Canada, given the relatively large Induan ammonoid collections amassed over the years by F. McClearn and E.T. Tozer, respectively.

In contrast, the record of Induan coiled nautiloids in the Tethys and Boreal northeastern Siberia is considerably richer. Griesbach (1880) and Diener (1895, 1897) reported nautiloids, e.g., *Grypoceras brahmanicum* (Griesbach) and *Pleuronautilus* sp. indet, from several areas in the Himalayas, but one of the more prolific sites, Shalshal Cliff, which is badly in need of restudy, cannot be accessed because of its location in a geopolitically sensitive area. Although Induan nautiloids are not well known in South China, Xu (1988) erected a new genus, *Xiaohenautilus*, from the late Griesbachian/early Dienerian in the Guizhou-Hubei area to which he attributed two species, i.e., *X. sinensis* and *X. huananensis*. Shigeta and Zakharov (2009) reviewed the recovery of nautiloids in the Early Triassic and documented the occurrence of well-preserved specimens attributed to five species (belonging to three genera) in succession throughout ~45 m of Griesbachian and Dienerian sediments in the Abrek Bay section of South Primorye, Russia. These authors suggest that these five taxa may belong to the same evolutionary lineage within the Grypoceratidae (Shigeta and Zakharov, 2009). Indeed, given the relative scarcity of nautiloid occurrences, the Abrek Bay section likely represents the best documented late Griesbachian/early Dienerian nautiloid succession in the world. One of these taxa, *Xiaohenautilus abrekensis,* is similar to the present specimens.

Sobolev's (1989, 1994) work in Boreal northeastern Siberia aptly demonstrates that this region contains by far the most complete record of Triassic nautiloids known worldwide. According to Sobolev (1994), nautiloid occurrences are not all that common, but they occur throughout nearly the entire Triassic. This statement is well supported by the ~ 50 sites shown on the nautiloid locality map of northeastern Asia (Sobolev, 1994, fig. 1). Nautiloid diversity and abundance in the Boreal Realm remained relatively low throughout the Griesbachian, consisting only of two local P/T extinction event survivors, i.e., the liroceratid genus *Tomponautilus*, which is a probable descendant of the late Permian genus *Permonautilus*, and the late Permian genus *Tainionautilus* (Sobolev, 1994). Nautiloids completely disappeared from the Boreal fossil record during the Dienerian and early Smithian, but orthoconic nautiloids migrated from the Tethys and dominated the middle and late Smithian (Sobolev, 1994) of northeastern Asia. The Spathian witnessed an explosive radiation of tainoceratids in the Tethyan Realm, some of which also migrated to northeastern Asia and gave rise to the genus *Phaedrysmocheilus*, on whose evolution Sobolev (1994) based a biostratigraphic scheme with extremely high resolution for northeastern Siberia. Nautiloids continued to diversify almost without interruption throughout the Middle and Late Triassic, and this resultant diversity enabled Sobolev (1994) to develop a nautiloid-based biostratigraphic scheme for northeastern Siberia consisting of 19 zones with nearly as much resolution and correlation usefulness as the ammonoid-based scheme. Indeed, a portion of Sobolev's (1994) Spathian biostratigraphic scheme can be correlated with the early Spathian *Columbites* beds of southeastern Idaho from which Brayard et al. (2019) recently illustrated two nautiloid taxa, i.e., *Trematoceras* sp. indet. and *Phaedrysmocheilus idahoensis*.

GRIESBACHIAN CONODONT BIOSTRATIGRAPHY AT CRITTENDEN SPRINGS

Conodont biostratigraphy of the Dinwoody Formation in the Crittenden Springs area has been studied by numerous workers, beginning with Clark (1957) and culminating with Paull (1980), Carr and Paull (1983) and Mullen (1985). According to the latter three studies, conodonts within the Dinwoody Formation can be divided into five zones, in ascending order: the *Hindeodus typicalis* Zone, *Isarcicella isarcica* Zone, *Neogondolella carinata* Zone, *Neospathodus kummeli* Zone, and *Neospathodus dieneri* Zone. The interval from the *H. typicalis* Zone to the *Ng. carinata* Zone, and the *Ns. kummeli* and *Ns. dieneri* zones are generally considered to be indicative of the Griesbachian and Dienerian, respectively (Sweet et al., 1971; Mullen, 1985). In particular, the *Isarcicella isarcica* Zone generally indicates an early to middle Griesbachian age (Orchard, 2007).

According to Paull (1980), both the *Hindeodus typicalis* and *Isarcicella isarcica* Zones are recognized in segment A, (~1.25 km north of the Long Canyon road), which represents the lowest part of the Dinwoody Formation. In contrast, only a few index conodonts, e.g., *Neogondolella carinata* (= *Clarkina carinata*) were reported from segment B (Fig. 5), ~280 m north of the Long Canyon road. Paull (1980) stated that the upper 33 m interval of segment B was assignable to the upper Dienerian, because of the presence of a few lenticular limestone beds containing numerous linguloid brachiopods. However, it should be noted that no age-diagnostic conodonts were reported from this particular interval of segment B.

The ammonoid/nautiloid study section is located ~140 m north of the Long Canyon road, which is only ~140 m south of segment B. Sampling efforts in the study section yielded eight conodont species belonging to three genera, i.e., *Clarkina*, *Hindeodus*, and *Merrillina*, from six limestone beds (Fig. 5; Fig. 14). These three genera are Permian conodont relics that rapidly diversified in the Early Triassic (e.g., Orchard, 2007).

Most importantly, the various species of *Hindeodus* are limited to the Griesbachian. More specifically, the study section yielded *Hindeodus* sp., *Merrillina* sp., and several species of *Clarkina*, i.e., *C. carinata*, *C. taylorae*, *C. tulongensis*, *C. griesbachiensis*, and *C. krystini*. *Clarkina krystini*, a late Griesbachian conodont, was collected from Loc. 7, a linguloid brachiopod limestone bed (Fig. 5). Furthermore, the basal Dienerian index conodont, i.e., *Sweetospathodus kummeli*, was not found in the studied section, and it was not reported from segment B. Based on the above conodont evidence, it is concluded therefore, that nearly all of the Dinwoody Formation of the studied section is middle to late Griesbachian in age. The following taxa are illustrated in Fig. 14: *Clarkina carinata* (Clark), *C. griesbachiensis* (Orchard), *C. tulongensis* (Tian), *Merrillina* sp., and *Hindeodus* sp. (Table 2).

SYSTEMATIC PALEONTOLOGY

Systematic descriptions are mainly based on the classification scheme of Tozer (1981, 1994a), but modifications by Ware et al. (2018a, b) are incorporated. Morphological measurements are expressed using the four classic geometrical parameters of the shell: diameter (D), whorl height (H), whorl width (W) and umbilical diameter (U). Absolute values of H and U are plotted versus diameter, as are the ratios H/D and U/D. Whorl width (W) measurements are not included in ammonoid scatter diagrams because of varying degrees of corrosion on upper surfaces. Terminology used to express shell size, umbilical width and type of coiling (whorl involution) is taken from Haggart (1989, table 8.1). All specimens are reposited in the New Mexico Museum of Natural History and Science (NMMNH) in Albuquerque.

Class CEPHALOPODA Cuvier, 1797
Order CERATITIDA Hyatt, 1884
Superfamily MEEKOCERATOIDEA Waagen, 1895
Family OPHICERATIDAE Arthaber, 1911
Genus *Wordieoceras* Tozer, 1971
Type species: *Vishnuites wordiei* Spath
***Wordieoceras wordiei* (Spath)**
Figure 7A-B'

1930 *Vishnuites wordiei* Spath, p. 31, pl. 2, figs. 11a, b (holotype).
1930 *Vishnuites decipiens* Spath, p. 31, pl. 3, figs. 2a-g; pl. 4, figs. 2a, b.
1935 *Vishnuites wordiei* Spath, p. 41, pl. 4, figs. 5a, b; pl. 12, figs. 2a, b.
1935 *Vishnuites decipiens* Spath, p. 41, pl. 4, figs. 4a, b; pl. 9, figs. 3a, b; pl. 10, figs. 2-5; pl. 12, figs. 1a, b; pl. 13, figs. 4, 7.
1967 *Ophiceras decipiens* (Spath), Tozer, p. 16, 17, 51, 52 and 54.
1971 *Wordieoceras wordiei* (Spath), Tozer, p. 1031.
1987 *Vishnuites domokhotovi* Zakharov and Rybalka, p. 36, pl. II, fig. 5.
1994 *Wordieoceras wordiei* (Spath), Tozer, p. 58, pl. 5, figs. 1-3; pl. 6, figs. 1-3; pl. 7, figs. 1-4.
1996 *Wordieoceras decipiens* (Spath), Dagys and Ermakova, p. 416, pl. 11, figs. 1,2,4,5.
2006 *Wordieoceras wordiei* (Spath), Bjerager et al., p. 640, fig. 5;
2006 *Wordieoceras decipiens* (Spath), Bjerager et al., p. 640, fig. 5; fig. 8, j-k; p. 644, 646.
non 2007 *Wordieoceras* aff. *wordiei* (Spath), Mu et al., p. 862, figs. 6.7, 6.9, 6.11, 7.1, 7.2, 8.
non 2009 *Wordieoceras* cf. *wordiei* (Spath), Shigeta and Zakharov, p. 68, pl. 50, figs. 12-15.
2015 *Wordieoceras wordiei* (Spath), Jenks et al., p. 343, fig. 13.3, i-j, GSC28060.

Material: Eight measured specimens consisting of complete phragmocones with very short body chamber fragments, ranging
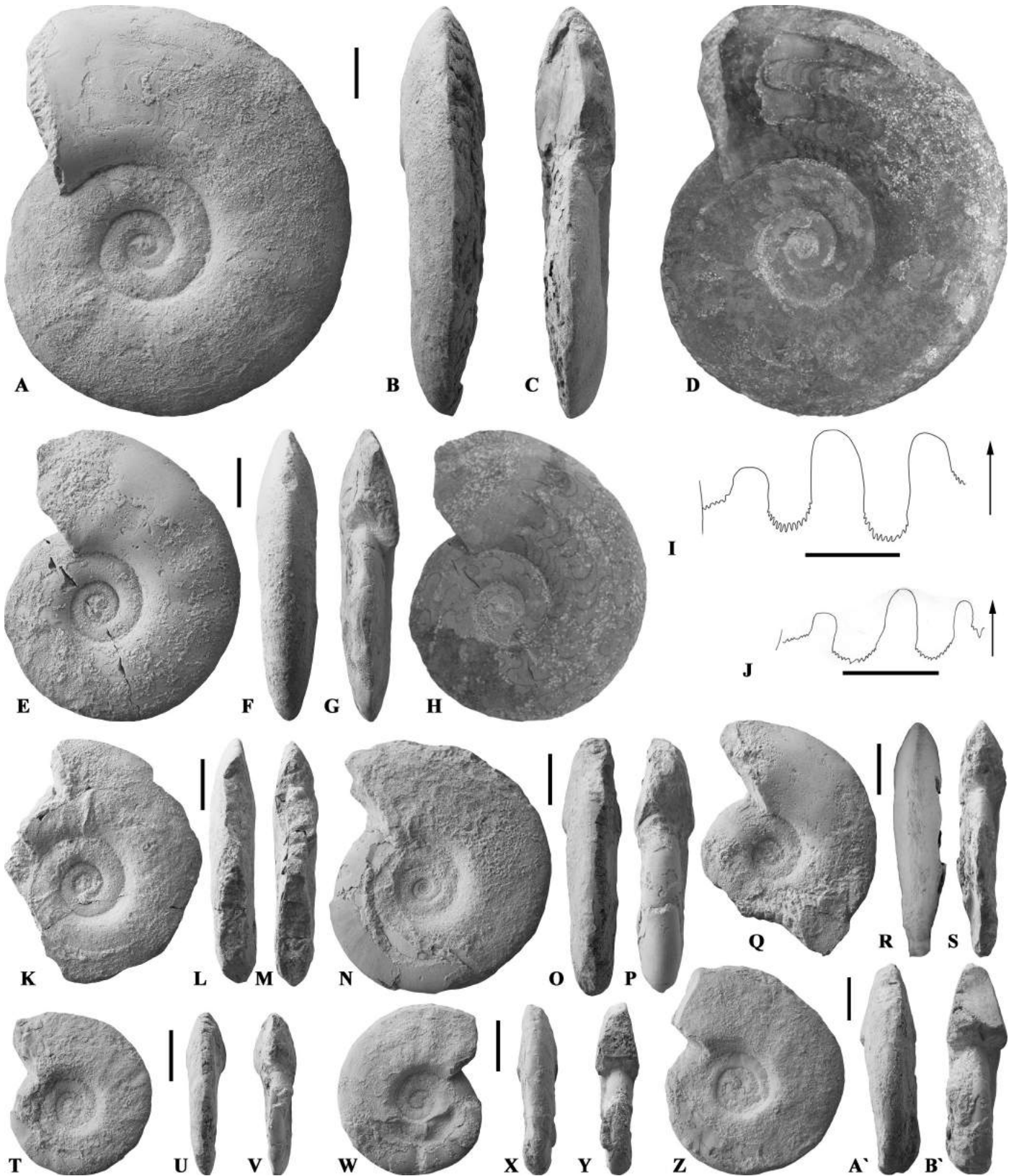
12

FIGURE 7. *Wordieoceras wordiei* (Spath). **A-D**, NMMNH P-81677, in **A**, lateral, **B**, ventral, **C**, apertural views, and **D**, unwhitened lateral view showing suture lines. **E-H**, NMMNH P-81672, in **E**, lateral, **F**, ventral, **G**, apertural and **H**, unwhitened lateral view showing suture lines. **I-J**, suture lines, in **I**, NMMNH P-81677, H = 32 mm, **J**, NMMNH P-81672, H = 23 mm. **K-M**, NMMNH P-81673, in **K**, lateral, **L**, ventral and **M**, apertural views. **N-P**, NMMNH P-81675, in **N**, lateral, **O**, ventral and **P**, apertural views. **Q-S**, NMMNH P-81674, in **Q**, lateral, **R**, ventral and **S**, apertural views. **T-V**, NMMNH P-81679, in **T**, lateral, **U**, ventral and **V**, apertural views. **W-Y**, NMMNH P-81676, in **W**, lateral, **X**, ventral and **Y**, apertural views. **Z-B'**, NMMNH P-81678, in **Z,** lateral, **A'**, ventral and **B'**, apertural views. All scale bars = 1 cm.

in diameter from ~29 to ~86 mm, NMMNH P-81672 (Fig. 7E-H, J), NMMNH P-81673 (Fig. 7K-M), NMMNH P-81675 (Fig. 7N-P), NMMNH P-81674 (Fig. 7Q-S), NMMNH P-81676 (Fig. 7W-Y), NMMNH P-81677 (Fig. 7A-D, I), NMMNH P-81678 (Fig. 7Z-B') and NMMNH P-81679 (Fig. 7T-V). All are illustrated.

Description: Small to medium sized, fairly evolute, compressed shell with convex flanks converging gently to highly variable venter with/without distinct shoulders, that varies from narrowly rounded on some specimens to fastigate with distinct bordering shoulders to nearly acute on others. Maximum whorl width occurs at ~ 40% of whorl height. Flank contour broadly convex from top of umbilical shoulder to point of maximum whorl width, then converging more rapidly to venter, forming a sub-trigonal to ovoid whorl section. Venter tends to become slightly more fastigate in an apertural direction on present specimens. Umbilicus moderately wide (U/D avg, 0.31) and fairly shallow with low, moderately inclined (~45°) wall and barely perceptible, broadly rounded shoulders. Ornamentation cannot be accurately assessed because test on most specimens is corroded, and body chambers are not preserved. One specimen (NMMNH P-81672) exhibits barely perceptible, distant, broad fold-type ribs on the last quarter whorl of the phragmocone, and it is assumed this feature would become more prominent on the body chamber, if preserved. Suture line somewhat typical of ophiceratids, with deep first lateral lobe and relatively high median saddle. Lobes well denticulated.

Measurements: See Table 1.

Discussion: As pointed out by Tozer (1994a), this taxon exhibits an extremely wide range of intraspecific variation in terms of both whorl morphology and ornamentation, and it is obvious that much of this expanded variation results from his inclusion of *Vishnuites decipiens* Spath, 1930, in synonymy with *W. wordiei* Spath, 1930. The present specimens fit well within this variation, as is evident in the box plot comparison of the Nevada specimens with those from Arctic Canada, East Greenland and Siberia (Fig. 10). According to Tozer (1994a) many Canadian specimens exhibit blunt ribbing, mainly on the phragmocone, but also occasionally on the body chamber. In contrast, ribbing is not reported on any of the specimens from East Greenland and Siberia (Spath, 1930, 1935; Dagys and Ermakova, 1996), and only one of the present specimens exhibits very weak, blunt ribbing near the end of its phragmocone. Nearly all specimens exhibit a fastigate venter, but this feature is also highly variable, in that the degree to which the gabled venter is obvious varies widely. Unlike specimens from Nevada and East Greenland, most Canadian specimens retain nearly complete, well preserved body chambers, and Tozer (1994a) commented that, while most specimens maintain an obvious fastigate venter throughout ontogeny, a few specimens transition to a nearly rounded or fastigate venter with barely perceptible angularity.

Not only does the present study represent the first report of late Griesbachian ammonoids from low-paleolatitude eastern Panthalassa, but it is also the first documented low-paleolatitude occurrence of clearly identified *Wordieoceras*, until now known only from the late Griesbachian of the Boreal Realm. This discovery thus suggests a more cosmopolitan occurrence for this taxon. Zakharov and Mu in Mu et al. (2007) described two late Griesbachian taxa, i.e., *Wordieoceras* aff. *W. wordiei* and *Wordieoceras guizhouensis*, from the lower part of the Daye Formation at Guiding, South China, but Brühwiler et al. (2008) disputed this assignment and erected a new proptychitid genus, i.e., *Jieshaniceras*, with *"W". guizhouensis* as the type species and also synonymized *"W".* aff. *W. wordiei* with the new taxon. Shigeta and Zakharov (2009) assigned a single specimen from Abrek Bay, South Primorye, to *Wordieoceras* cf. *W. wordiei*, but its whorl parameters clearly do not match *Wordieoceras,* and Shigeta (ongoing work) indicates the specimen likely represents

a new genus and species.

Dagys and Ermakova (1996) established a new species, i.e., *Wordieoceras tompoense*, from the Decipiens Zone of the eastern Verkhoyansk area, Siberia. While the inner whorls of this taxon bear some resemblance to the present specimens (see Dagys and Ermakova, text-fig. 11, p. 418), it differs significantly upon reaching large mature size with its much inflated whorl section (W/D, 0.32 vs. 0.23) and much more involute coiling (U/D, 0.21 vs. 0.31). It should be noted, however, that the W/D measurements provided by Dagys and Ermakova (1996) represent only specimens in excess of 64 mm in diameter, which is considerably larger than most of our specimens. Zakharov and Rybalka (1987) erected a new species *Vishnuites domokhotovi* from Eastern Verkhoyansk that was later synonymized with *W. decipiens* by Dagys and Ermakova (1996). This new taxon, based on a single, small fragmental specimen (D = 21 mm), is poorly illustrated, but the features of its whorl, e.g.., fastigate venter, appear similar to the smaller present specimens.

The type specimen of *Vishnuites pralambha* Diener, 1897, from Shalshal Cliff, Kashmir, exhibits a superficial resemblance to at least one of the present specimens, i.e., NMMNH P-81677, but this taxon is much more compressed, and considerable confusion exists as to its taxonomy and stratigraphic distribution at Shalshal Cliff, as well as its relationship to specimens from South China (Brühwiler et al., 2008; Dai et al., 2019). Dai et al. (2019) emphasized the need for both a reinvestigation of the Shalshal Cliff site, located in a geopolitically sensitive area between India and China, and a thorough revision of the various *Vishnuites* taxa from central Himalaya and South China.

Occurrence: Found in a 2-3 cm thick siltstone bed represented by locality number NMMNH L-12682, ~75 m below the top of the Dinwoody Formation.

Wordieoceras mullenae n. sp.
Figure 8A-M

1935 *Vishnuites decipiens* var. *discoidea*, Spath, p. 44, pl. XII, fig. 1; pl. XIII, fig. 4. Not pl. X, fig. 5.

Type series: Four specimens: Holotype, specimen NMMNH P-81680 (Fig. 8A-C, M), paratypes, three specimens: NMMNH P-81681 (Fig. 8G-I), NMMNH P-81682 (Fig. 8D-F), NMMNH P-81683 (Fig. 8J-L). Type series reposited in the NMMNH.

Etymology: Named in honor of Donna M. Mullen of Denver, Colorado.

Diagnosis: Fairly small, very involute compressed shell with sub-trigonal whorl section characterized by convex flanks converging to narrowly rounded to fastigate venter with barely perceptible angularity. Fairly narrow umbilicus with inclined wall and well-rounded shoulder. Maximum whorl width at ~30% of whorl height or top of umbilical shoulder. No visible ornamentation except for a barely perceptible, broad fold-type rib on the holotype, near the end of the phragmocone.

Description: Fairly small, fairly involute compressed shell with gently convex flanks converging to narrowly rounded venter without distinct ventral shoulders. Maximum whorl width occurs at 40 to 45% of whorl height. Flank contour broadly convex from top of umbilical shoulder to point of maximum whorl width, then converging more rapidly to venter, forming a high-whorled, sub-trigonal whorl section. Fairly narrow umbilicus (U/D avg, 0.20) with low, moderately steep wall and barely perceptible, broadly rounded shoulders. No obvious ornamentation on paratypes, but holotype bears one barely perceptible, broad fold-type rib near end of phragmocone. Suture line with relatively low, broadly rounded saddles, fairly wide, well denticulated first lateral lobe, finely denticulated 2nd lateral lobe and short auxiliary series with weak indentations.

Measurements: See Table 1.

Discussion: At first glance, *Wordieoceras mullenae* n. sp. appears similar in whorl morphology to the *W. wordiei*
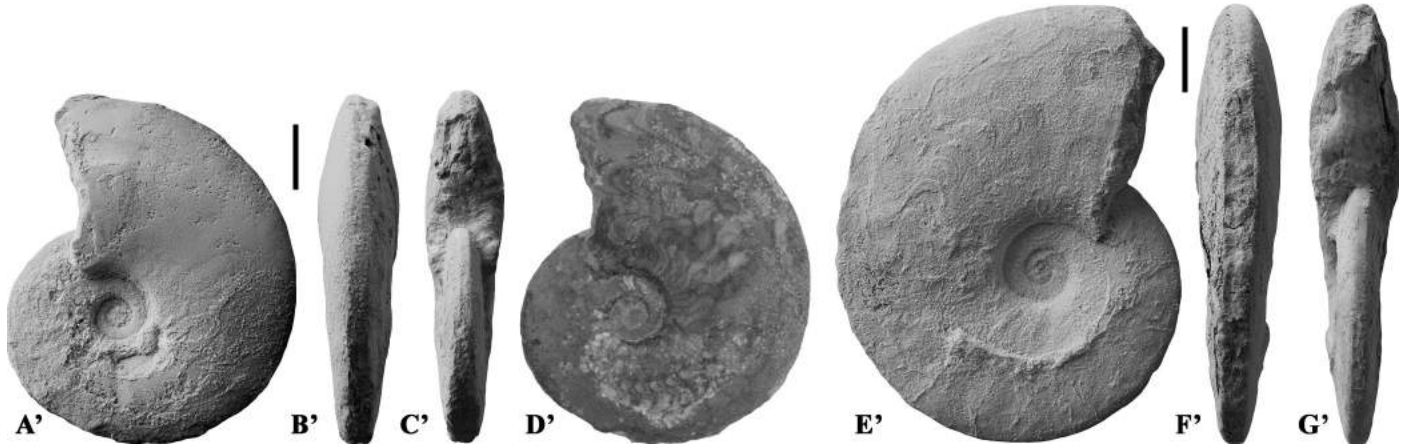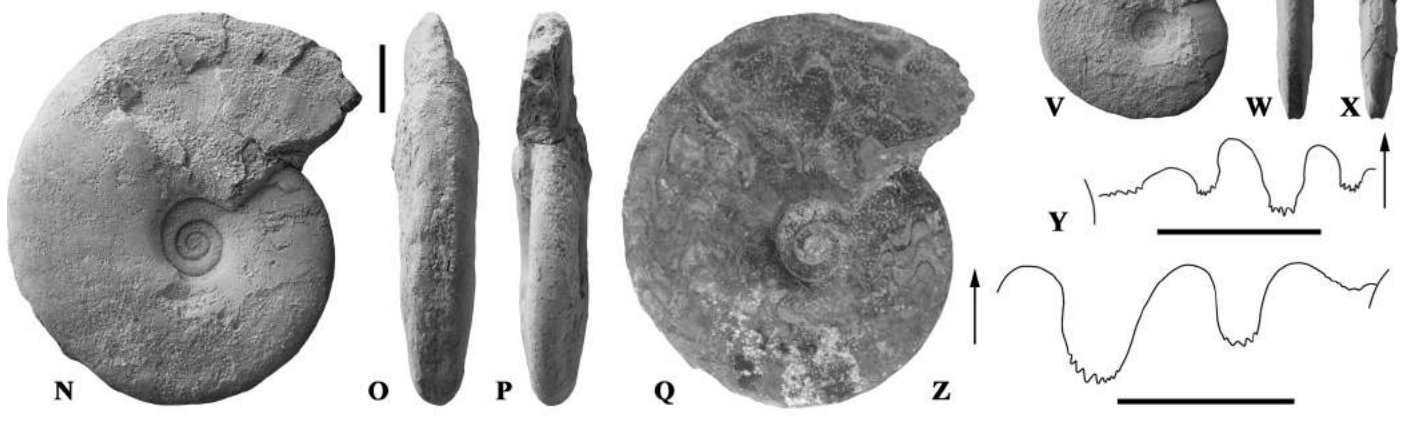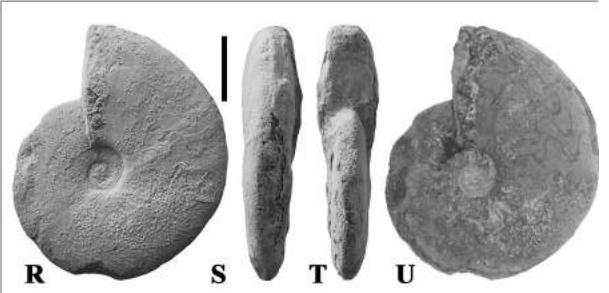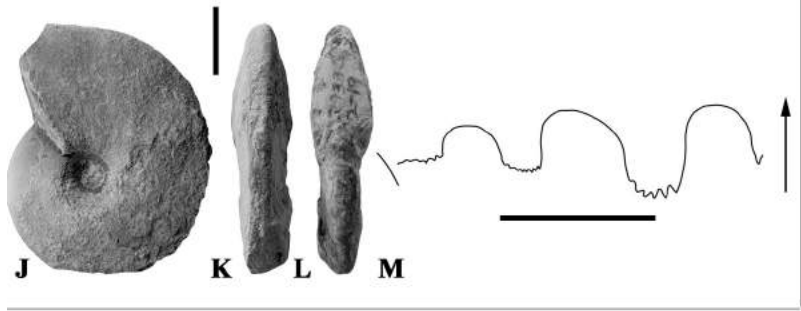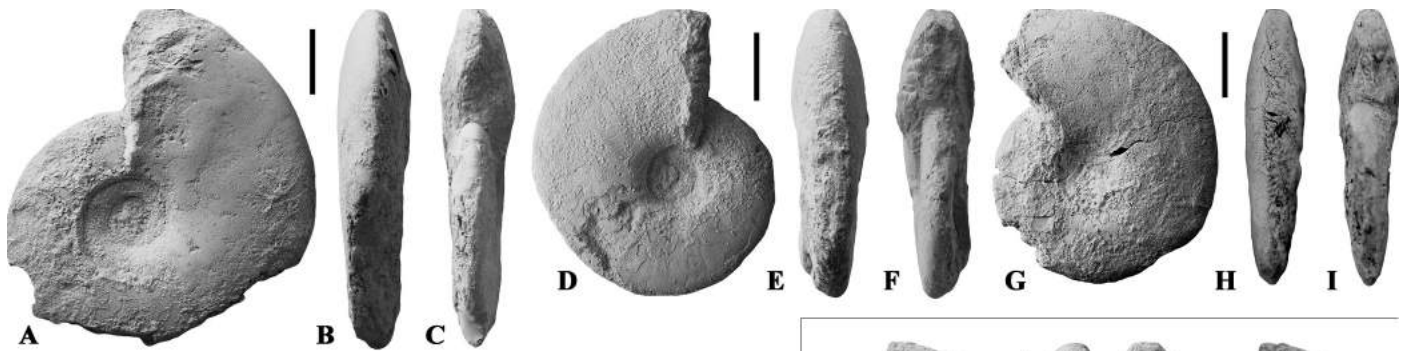
FIGURE 8. (facing page) **A-M**, *Wordieoceras mullenae* n. sp. **A-C**, NMMNH P-81680, holotype, in **A**, lateral, **B**, ventral and **C**, apertural views. **D-F**, NMMNH P-81682, paratype, in **D**, lateral, **E**, ventral and **F**, apertural views. **G-I**, NMMNH P-81681, paratype, in **G**, lateral, **H**, ventral and **I**, apertural views. **J-L**, NMMNH P-81683, paratype, in **J**, lateral, **K**, ventral and **L**, apertural views. **M**, suture line, NMMNH P-81680, H = 24 mm. **N-Z**, *Kyoktites* cf. *K. hebeiseni* Ware and Bucher. **N-Q**, NMMNH P-81688, in **N**, lateral, **O**, ventral, **P**, apertural views, and **Q**, unwhitened lateral view showing suture lines. **R-U**, NMMNH P-81690, in **R**, lateral, **S**, ventral, **T**, apertural views, **U**, unwhitened lateral view showing suture lines. **V-X**, NMMNH P-81689, in **V**, lateral, **W**, ventral and **X**, apertural views. **Y-Z**, suture lines, in **Y**, NMMNH P-81690, H = 17 mm, **Z**, NMMNH P-81688, H=23 mm. **A'-G'**, *Ophimullericeras paullae* n. gen., n. sp. **A'-D'**, NMMNH P-81684, paratype, in **A'**, lateral, **B'**, ventral, **C'**, apertural views and **D'**, unwhitened lateral view showing suture lines. **E'-G'**, NMMNH P-81687, holotype, in **E'**, lateral, **F'**, ventral (sub-tabulate venter preserved near end of phragmocone) and **G'**, apertural views. All scale bars = 1 cm.

specimens from Crittenden Springs, but as is evident from the plot of U/D and H/D for the two taxa (Fig. 9), *W. mullenae* n. sp. is clearly more involute and well differentiated from *W. wordiei*.

Spath (1935) attributed three specimens from East Greenland to *Vishnuites decipiens* var. *discoidea*, two of which exhibit very similar coiling geometry and whorl parameters to *W. mullenae* n. sp. It is clear from Spath's illustrations (pl. XII, fig. 1; pl. XIII, fig. 4) and measurements that these specimens are much more involute than *V. decipiens* and are very close to the present specimens. Thus, they are herein placed in synonymy with *W. mullenae* n. sp.

Wordieoceras mullenae n. sp. is much closer to *W. tompoense* Dagys and Ermakova in terms of coiling geometry (U/D avg, 0.20 vs. 0.21) than *W. wordiei*, and its whorl width is closer to the inner whorls of *W. tompoense*. But, again, the specimens for which these authors provided measurements are much larger than the present specimens, and their mature whorls are much more inflated (W/D avg. 0.32 vs. 0.23). It is unlikely that the body chambers of *W. mullenae* n. sp., if preserved, would exhibit such inflation, even at larger diameters.

The suture line of *Wordieoceras mullenae* n. sp. (Fig. 8M), with its shallower lobes and longer saddles, contrasts somewhat with that of *W. wordiei*, but according to Ware (ongoing work), this slight deviation is not all that uncommon and simply represents intraspecific variation. Spath (1930, 1935) and Tozer (1994a) both show similar divergences in ophiceratids, and some specimens from East Greenland also exhibit the same variation.

Occurrence: Found in a 2-3 cm thick siltstone bed represented by locality number NMMNH L-12682, ~75 m below the top of the Dinwoody Formation.

Genus *Kyoktites* Ware and Bucher 2018
Kyoktites cf. *K. hebeiseni* Ware and Bucher 2018
Figure 8N-Z

2018a *Kyoktites* cf. *H. hebeiseni* Ware et al., p. 37, pl. 2, figs. 5-8.

Material: Three measured specimens, NMMNH P-81688 (Fig. 8N-Q, Z), NMMNH P-81689 (Fig. 8V-X), NMMNH P-81690 (Fig. 8R-U, Y), consisting of complete phragmocones ranging in diameter from ~32 to 55 mm, two of which include very short body chamber fragments. One specimen (NMMNH P-81688) includes ~1/4 whorl of badly distorted/crushed body chamber. Two specimens (NMMNH P-81688 and NMMNH P-81690) are fairly well preserved with exposed suture lines. NMMNH P-81689 is poorly preserved with corrosion affecting both sides. All are illustrated.

Description: Fairly small, very involute, compressed, platyconic shell with very slightly convex, sub-parallel flanks that converge very slightly to well-rounded venter without distinctive shoulders. Maximum whorl width occurs at 40-45% of whorl height. Flank contour broadly convex from top of umbilical shoulder to point of maximum whorl width, then converging very gently in a sub-parallel manner to a rounded venter. Whorl section is sub-quadrate. Fairly narrow, shallow umbilicus (U/D avg. 0.19) with steep, nearly vertical wall and narrowly rounded shoulders. No visible ornamentation. Suture line with shallow, well-developed ventral lobe, deep first lateral lobe and shallow second lateral lobe, both well denticulated. Elongated first and second lateral saddles and broad but low third lateral saddle. Short auxiliary series with several small indentations.

Measurements: See Table 1.

Discussion: *Kyoktites hebeiseni* and *K.* cf. *K. hebeiseni* were erected by Ware and Bucher (2018a) based on three fairly well preserved specimens (one from the Nammal Nala section and two from the Amb section) from condensed horizons of latest Griesbachian/earliest Dienerian age in the Salt Range, Pakistan. In terms of whorl geometry, the present specimens fit well within *K. hebeiseni*, but the type specimen exhibits weak sigmoidal ribbing on the lower half of the flank. The present specimens bear no such ornamentation, and since the taxon is based on only one specimen, nothing is known regarding its range of intraspecific variation. Hence, we prefer to place our specimens in open nomenclature. The suture line of specimen NMMNH P-81690 is very similar to *K. hebeiseni*, and there is little doubt this specimen is correctly attributed. However, the suture line of the largest specimen, NMMNH P-81688, is problematic in that it does not exhibit the low, wide third lateral saddle typical of the taxon. The height of this particular saddle on NMMNH P-81688, which is about the same as the second lateral, is considerably higher than that of the holotype, and it is missing most of the lower part of the dorsal side of the saddle wall. Essentially, it merges without a clear boundary with the weakly indented auxiliary series. Taken as a whole, this suture line more closely matches that of the early Dienerian taxon *Ghazalaites roohii* Ware and Bucher (2018a) with its asymmetrical third lateral saddle, but this taxon's whorl geometry is significantly different. Basically, the inner whorls of *G. roohii* are much more involute, with a nearly closed umbilicus, and these are then followed by very distinctive egressive coiling. In addition, its flanks are not sub-parallel, but instead are convex, converging toward the venter.

We choose to attribute specimen NMMNH P-81688 to *Kyoktites* cf. *K. hebeiseni* with some reservation. It is possible that this divergence in the suture line is due to extreme intraspecific variability, but additional specimens would be needed to quantify this speculation. According to Ware (ongoing work), this part of the suture line in some ophiceratids/gyronitids can often exhibit significant variability. In addition, a pathological cause for this discrepancy cannot be ruled out, even though there is no obvious evidence of sub-lethal shell damage in the immediate area where the suture line was drawn. However, there is a slight but sudden increase in whorl width near the umbilical margin at about 10 adapical septa removed, but it is impossible to determine if this change is pathological or caused by post-burial compaction.

The present specimens are also similar to the *Kyoktites* cf. *K. hebeiseni* specimen from the Amb section (Ware et al., 2018a, pl. 2, figs. 5-7), but they differ primarily by their slightly more involute coiling (U/D-0.19 vs. 0.24, respectively).

Occurrence: Found in a 2-3 cm thick siltstone bed represented by locality number NMMNH L-12682, ~75 m below the top of the Dinwoody Formation.

TABLE 1. Measurements. Note: Width measurements for all ammonoids slightly affected by corrosion.

Location	Taxon	Specimen No.	D (mm)	W	H	U	W/D	H/D	U/D
AMMONOIDS									
Crittenden Spr.	*Wordieoceras wordiei*	P-81672	54.4	11.9	22.3	17.7	0.22	0.41	0.33
"	"	P-81673	49.8	11.5	18.7	17.0	0.23	0.38	0.34
"	"	P-81674	34.8	8.3	14.4	10.0	0.24	0.41	0.29
"	"	P-81675	44.1	9.6	18.3	13.2	0.22	0.41	0.30
"	"	P-81676	28.7	6.5	11.4	8.2	0.23	0.40	0.29
"	"	P-81677	86.2	16.3	32.7	29.6	0.19	0.38	0.34
"	"	P-81678	36.6	9.4	14.8	11.5	0.26	0.40	0.31
"	"	P-81679	33.6	8.4	13.2	10.5	0.25	0.39	0.31
Arctic Canada (Tozer, 1994)	"	28060	121	25.4	44.8	43.6	0.21	0.37	0.36
"	"	28059	73	18.3	32.1	21.2	0.25	0.44	0.29
"	"	28062	96	26.9	44.2	27.8	0.28	0.46	0.29
"	"	28067	27	7.8	11.3	7.8	0.29	0.42	0.29
"	"	28065	59	14.8	23.0	20.1	0.25	0.39	0.34
"	"	28066	65	13.7	26.0	20.8	0.21	0.40	0.32
East Greenland (Spath, 1930,1935)	"	Holotype	57	15.4	22.8	18.8	0.27	0.40	0.33
"	*W. decipiens*	Holotype	44	12.8	19.8	11.9	0.29	0.45	0.27
"	"	Pl. 10, 3	54	13.0	21.6	17.8	0.24	0.40	0.33
"	"	Pl. 9, 3	62	14.9	26.7	21.1	0.24	0.43	0.34
"	"	Pl. 13, 7	55	11.6	23.1	16.0	0.21	0.42	0.29
"	"	No. 357d	60	13.2	27.6	16.8	0.22	0.46	0.28
Siberia (Dagys & Ermakova, 1996)	*W. decipiens*	921/99	64	16.7	26.7	19.0	0.26	0.42	0.30
"	"	921/102	67	17.0	25.5	23.0	0.26	0.45	0.34
Crittenden Spr.	*W. mullenae* n. sp.	P-81680, holotype	47.9	9.2	22.6	9.7	0.19	0.47	0.20
"	"	P-81681, paratype	40.9	9.0	19.4	8.6	0.22	0.47	0.21
"	"	P-81682, paratype	39.2	10.1	18.6	9.0	0.26	0.47	0.23
"	"	P-81683, paratype	34.3	7.9	17.1	5.5	0.23	0.50	0.16
"	*O.* n. gen., *paullae* n. sp.	P-81684, paratype	49.1	11.1	23.5	9.3	0.23	0.48	0.19
"	"	P-81685, paratype	46.7	9.1	22.2	10.7	0.19	0.48	0.23
"	"	P-81686, paratype	55.7	11.9	27.7	10.7	0.21	0.50	0.19
"	"	P-81687, holotype	65.5	12.8	31.7	12.5	0.20	0.48	0.19
"	*K.* cf. *K. hebeiseni*	P-81688	54.6	12.5	24.8	11.3	0.23	0.45	0.21
"	"	P-81689	32.3	6.5	15.8	6.2	0.20	0.49	0.19
"	"	P-81690	38.4	8.1	17.7	7.0	0.21	0.46	0.18
NAUTILOIDS									
"	*X. mulleni* n. sp.	P-81691, paratype	40.8	19.0	20.5	10.1	0.47	0.50	0.25
"	"	P-81692, paratype	25.8	13.2	13.6	7.4	0.51	0.53	0.29
"	"	P-81693, holotype	49.4	19.0	21.5	14.9	0.38	0.44	0.30
"	"	P-81694, paratype	59.7	29.3	31.2	13.0	0.49	0.52	0.22
"	"	P-81695, paratype	47.1	28.8	22.5	11.5	0.61	0.48	0.24

Gray highlight – excessive corrosion, measurement estimated.

Family MULLERICERATIDAE Ware et al., 2011
Genus *Ophimullericeras* n. gen.

Type species: *Ophimullericeras paullae* n. gen., n. sp.
Composition of the genus: Type species only.
Etymology: A combination of the genus names *Ophiceras* and *Mullericeras*, to emphasize that it represents a transitional form between Ophiceratidae and Mullericeratidae.

Diagnosis: Small to medium sized, fairly involute, compressed Mullericeratidae with slightly convex flanks converging to tabulate venter with angular shoulders on inner whorls, which transitions to a broadly rounded venter without distinct shoulders at end of phragmocone. Umbilicus fairly narrow and moderately deep with steeply (~75°) inclined wall and gently rounded but distinct shoulders.

Discussion: Erected by Ware et al. (2011), the family Mullericeratidae, whose original diagnosis included Hedenstroemidae-like shells without adventitious lobes and saddles, consisted of one middle Dienerian genus, *Mullericeras*, which included two species, i.e., *M. spitiense* and *M. fergusoni*, from the Candelaria Formation of Nevada. Both taxa exhibit relatively compressed, very involute shells with tabulate venters. Ware et al. (2018a) then emended the diagnosis to include involute, tabulate, platyconic shells with a suture line composed of a long auxiliary series and no adventitious element in the ventral lobe, and expanded the composition of the family to include *Ussuridiscus* Shigeta and Zakharov, 2009. Some of the taxa included in these two genera by Ware et al. (2018a), i.e., *U. ventriosus* and *M. indusense*, exhibit close similarity with the present specimens, but these two forms are characterized by a tabulate venter on the body chamber and a vertical to slightly overhanging umbilical wall that contrasts with the steep wall of the present specimens. Dai et al. (2019) erected one new late Griesbachian species of *Mullericeras*, i.e., *M. gujiaoense* from Guizhou, South China, but its umbilicus is nearly closed, its venter remains tabulate on the body chamber, and the indentations of it lobes and auxiliary series are irregular.

These three taxa differ from other forms of the genus in that they are more openly coiled, with coiling geometry and umbilical width of some specimens, e.g., *M. indusense* (see Ware et al., 2018a, pl. 28, figs. 1-9), nearly identical to that of the present specimens. However, there is one significant characteristic that is typical of not only these three species but of all *Mullericeras* taxa (and *Ussuridiscus* as well), regardless of coiling geometry – they all maintain a tabulate venter throughout ontogeny. This feature is in contrast with *Ophimullericeras paullae* n. gen., n. sp., whose inner whorls exhibit a tabulate venter with angular shoulders that transition to a broadly rounded venter at the end of the phragmocone. It is not unreasonable to postulate that this transition would continue to a well-rounded venter had the body chamber been preserved. Furthermore, the present specimens' oblique umbilical wall differs from other genera of the family. Thus, we consider these differences to be sufficient justification to erect the new genus *Ophimullericeras.*

Apart from Mullericeratidae, the present specimens are very close to some involute Ophiceratidae of similar age, e.g., *Discophiceras*, *Kyoktites*, from which they differ mostly by their ventral features, tabulate on inner whorls (Ophiceratidae typically have a rounded or occasionally acute venter) and their steeper umbilical wall. We therefore consider the present specimens to be a transitional form between the Ophiceratidae and Mullericeratidae, and furthermore, because of their tabulate early whorls, we opt to place them within the Mullericeratidae. It is recognized that the architecture of the present specimens' relatively simple suture line may be closer to some forms of Ophiceratidae, e.g., *Kyoktites hebeiseni* Ware and Bucher (2018, p. 37, pl. 2, fig. 4), with its wide, elongated first and second lateral saddles, deep first lateral lobe, shallow second lateral lobe, and relatively short auxiliary series. Both taxa lack an adventive

series, but the third lateral saddle of *O. paullae* n. gen., n. sp. appears to be significantly higher. In short, this similarity in suture lines between *O. paullae* n. gen., n. sp. and Ophiceratidae is considered to be less significant than the difference in whorl geometry, i.e., the distinctively tabulate inner whorls.

Ophimullericeras paullae n. sp.
Figures 8A'-G', 11A-H

?1935 *Ophiceras* (*Lytophiceras*) *dubium* Spath, p. 26, pl. 2, figs. 4a-d; pl. 11, figs. 8a, b; pl. 12, figs. 7a-c; pl. 13, figs. 11-12; pl. 14, figs. 4, 5.

Type series: Four specimens consisting of complete phragmocones without body chambers: Holotype, specimen NMMNH P-81687 (Fig. 8E'-G', 11H); paratypes, three specimens: NMMNH P-81686 (Fig. 11A-C), NMMNH P-81684 (Fig. 8A'-D', 11G), NMMNH P-81685 (Fig. 11D-F).
Etymology: Named in honor of Dr. Rachel Paull of Denver, Colorado.
Diagnosis: As for the genus.
Description: Medium sized (diameter complete phragmocone = 65 mm, estimated diameter complete shell ~100 mm) fairly involute, compressed (W/D = 20%, W/H = 40%) shell with slightly convex flanks gently converging to venter that transitions from tabulate with angular shoulders on inner whorls to sub-tabulate or broadly rounded, without distinct shoulders at end of phragmocone. Because of corrosion in ventral region, this transitional feature is preserved on only two specimens (Figs. 8E'-G',11A-C), and it is assumed that the venter would transition from sub-tabulate or broadly rounded to well-rounded or circular on body chambers if preserved. Maximum whorl width occurs at ~ 35 to 40% of whorl height. Flank contour broadly convex from top of umbilical wall to point of maximum width, then gradually converges to ventral area, forming compressed sub-trapezoidal whorl section. Umbilicus fairly narrow and moderately deep with steeply (~75°) inclined wall and gently rounded but distinct shoulders. One specimen (NMMNH P-81687, holotype) preserves the umbilical seam of its body chamber, which exhibits a slight egression. No apparent ornamentation. Suture line simple with rather broad lobes and saddles, moderately wide ventral lobe without adventitious series, broadly rounded lateral saddles of approximately equal size, lateral lobes and auxiliary series with small regular indentations, and no auxiliary lobe.
Measurements: See Table 1.
Discussion: *Ophimullericeras paullae* n. gen., n. sp. resembles the nine variable, relatively small ophiceratid specimens that Spath (1935) described and illustrated as *Ophiceras* (*Lytophiceras*) *dubium* from the Upper *Vishnuites* and Lower *Proptychites* beds (late Griesbachian–early Dienerian) of East Greenland. These specimens differ in that, according to Spath (1935), they exhibit various degrees of egressive coiling, some are slightly more inflated than others, and their umbilical wall is more oblique and less differentiated. Spath's specimens are poorly illustrated, and it is difficult to assess the amount of egression and inflation present in each specimen. Spath (1935) stated that some of the specimens exhibit a "truncated" venter on the inner whorls that transitions to more rounded on the adult body chamber, but this transition is not apparent on all specimens, in particular the holotype (Spath, 1935, pl. XIV, figs. 5a, b).

Because of these variations, we strongly suspect that these specimens comprise an inadvertently mixed collection from different horizons, with some being true ophiceratids, while others may belong to Mullericeratidae. All Spath's (1930, 1935) East Greenland material was collected by others, and much of it was collected as float, some of which came from sections greatly affected by solifluction (D. Ware, ongoing work). We therefore prefer to erect a new species for the present specimens, and we
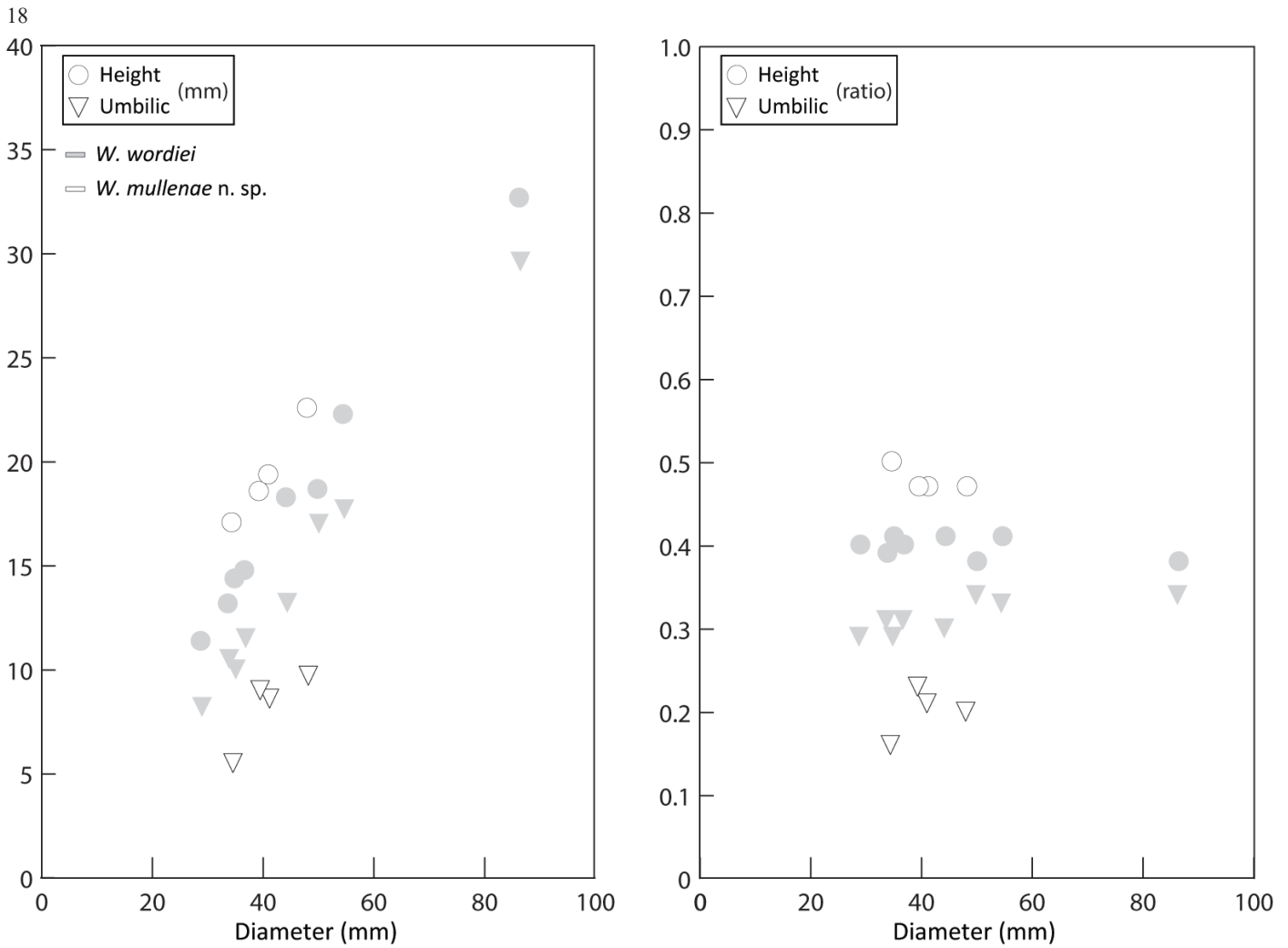
FIGURE 9. Scatter diagram comparison of H and U, and H/D and U/D for *Wordieoceras wordiei* (Spath) (gray-shaded circles and triangles) and *Wordieoceras mullenae* n. sp. (white circles and triangles).
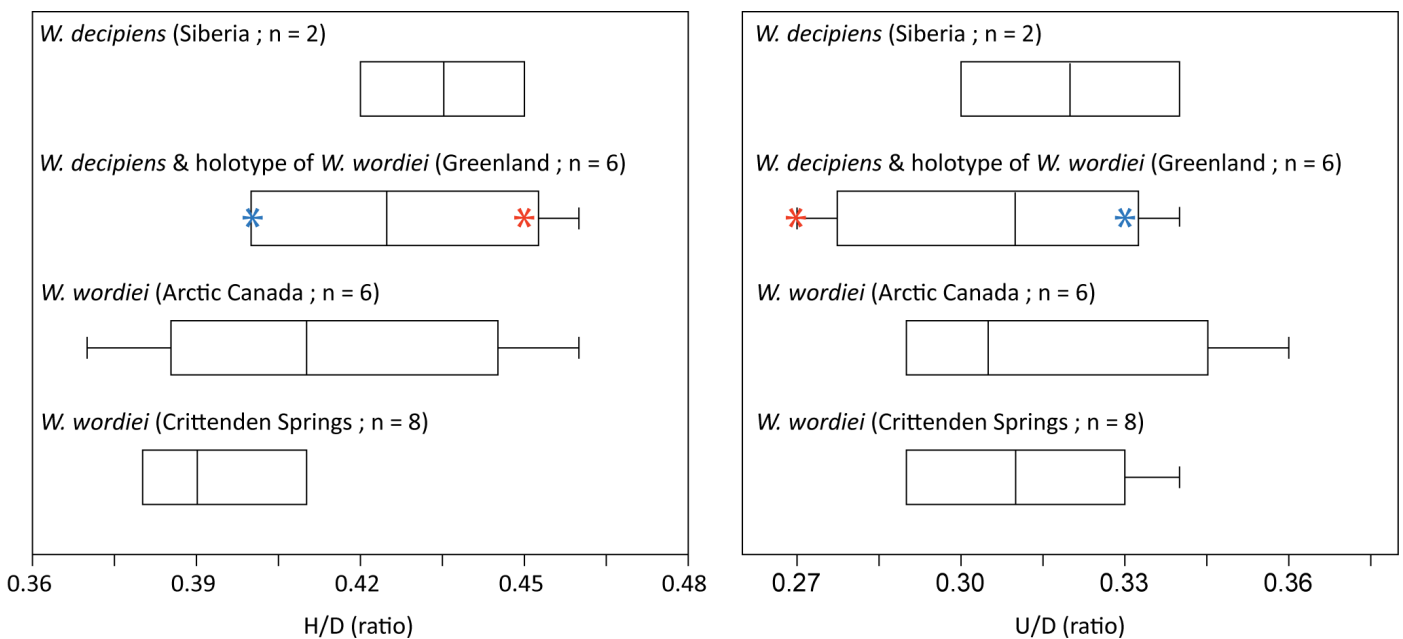

FIGURE 10. Box plot comparison of H/D and U/D for *Wordieoceras wordiei* (Spath) *vs.* specimens from Arctic Canada, East Greenland and Siberia. Asterisks indicate values for holotypes of *W. wordiei* (blue) and *W. decipiens* (red).
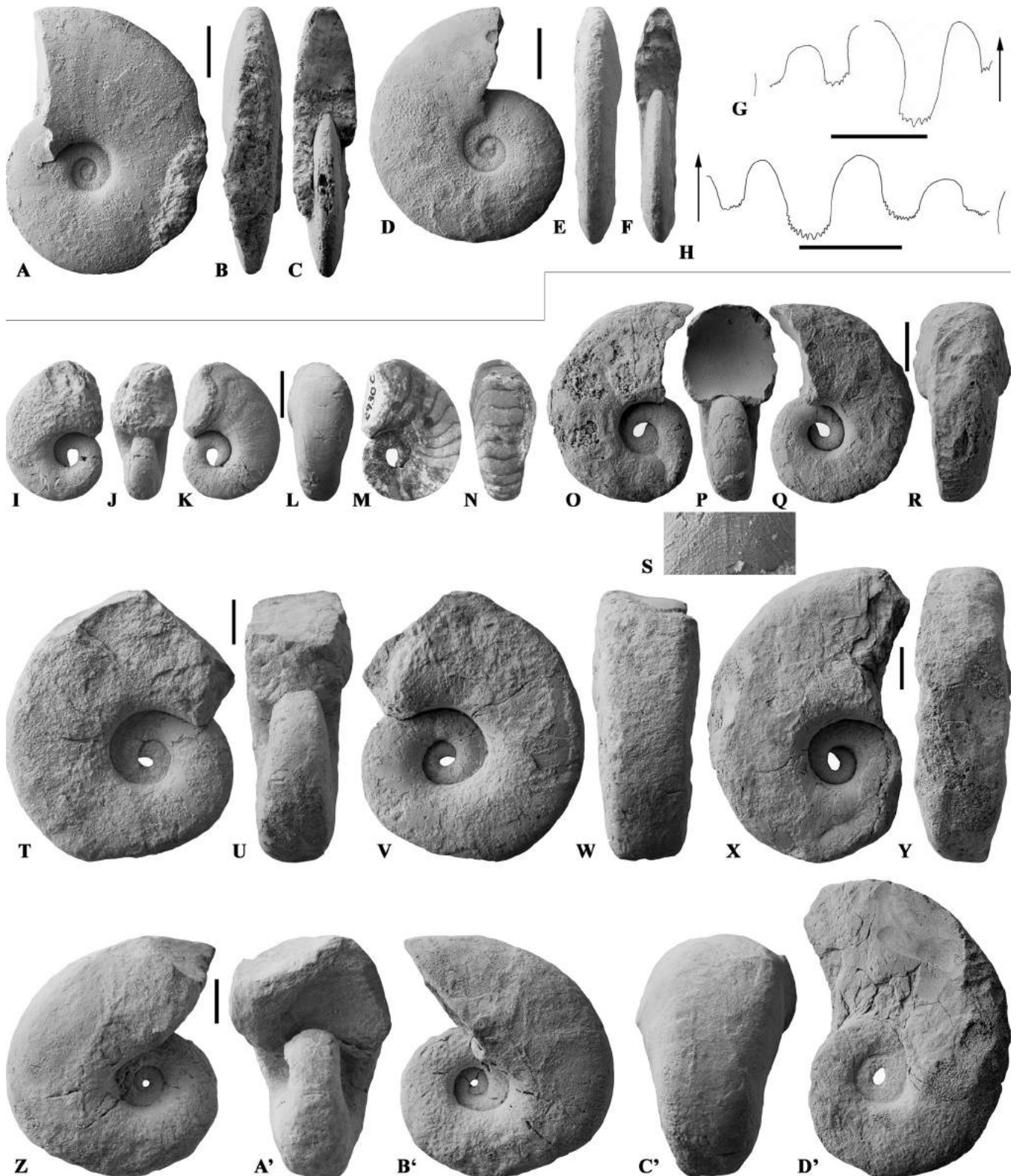
FIGURE 11. **A-H**, *Ophimullericeras paullae* n. gen., n. sp. **A-C**, NMMNH P-81686, paratype, in **A**, lateral, **B**, ventral (sub-tabulate venter preserved near end of phragmocone) and **C**, apertural views. **D-F**, NMMNH P-81685, paratype, in **D**, lateral, **E**, ventral and **F**, apertural views. **G-H**, suture lines, in **G**, NMMNH P-81684, H = 26 mm, **H**, NMMNH P-81687, H = 29 mm. **I-D'**, *Xiaohenautilus mulleni* n. sp. **I-N**, NMMNH P-81692, paratype, in **I**, lateral (right), **J**, apertural, **K**, lateral (left), **L**, ventral, **M**, unwhitened left lateral, and **N**, unwhitened ventral views. **O-S**, NMMNH P-81691, paratype, in **O**, lateral (right), **P**, apertural, **Q**, lateral (left), and **R**, ventral views. **S**, close-up view of venter (Fig. 11P) showing V-shaped hyponomic sinus. **T-W**, NMMNH P-81693, holotype, in **T**, lateral (right), **U**, apertural, **V**, lateral (left), and **W**, ventral views. **X-Y, D'**, NMMNH P-81694, paratype, in **X**, lateral (right), **Y**, ventral and **D'**, lateral (left). **Z-C'**, NMMNH P-81695, paratype, in **Z**, lateral (right), **A'**, apertural, **B'** lateral (left), and **C'** ventral views. All scale bars = 1 cm.
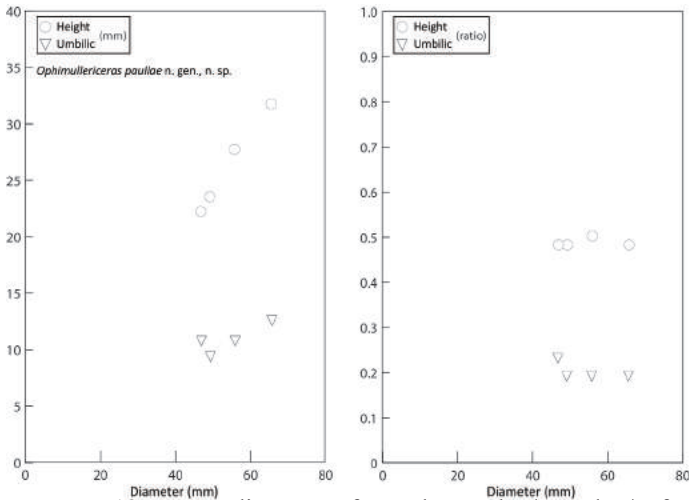
FIGURE 12. Scatter diagrams of H and U, and H/D and U/D for *Ophimullericeras paullae* n. gen., n. sp.
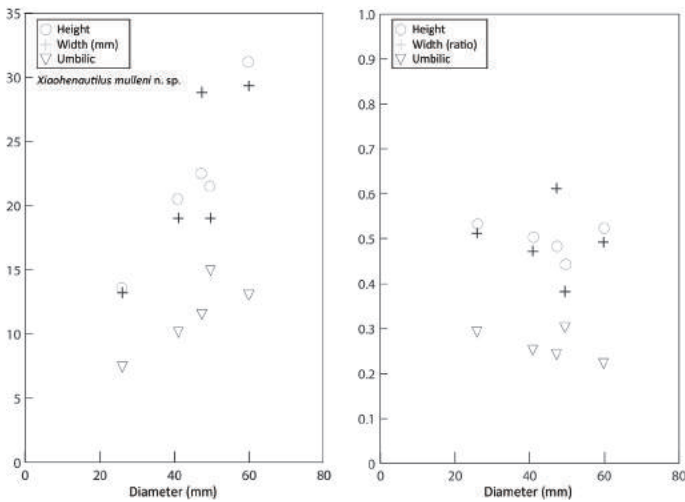

FIGURE 13. Scatter diagrams of H, W and U, and H/D, W/D and U/D for *Xiaohenautilus mulleni* n. sp.

consider *Ophiceras (Lytophiceras) dubium* as a *nomen dubium* until a proper revision of this species becomes available.

Occurrence: Found in a 2-3 cm thick siltstone bed represented by locality number NMMNH L-12682, ~75 m below the top of the Dinwoody Formation.

Order NAUTILIDA Agassiz, 1847
Superfamily TRIGONOCERATOIDEA Hyatt, 1884
Family GRYPOCERATIDAE Hyatt, 1900
Genus *Xiaohenautilus* Xu, 1988
Type species: *Xiaohenautilus sinensis* Xu, 1988
***Xiaohenautilus mulleni* n. sp.**
Figure 11I-D'

Type series: Five specimens: Holotype, specimen NMMNH P-81693 (Fig. 11T-W); paratypes, four specimens: NMMNH P-81691 (Fig. 11O-S), NMMNH P-81692 (Fig. 11I-N), NMMNH P-81694 (Fig. 11X-Y, D'), NMMNH P-81695 (Fig. 11Z-C').

Etymology: Named in honor of Chris E. Mullen of Denver, Colorado.

Diagnosis: Moderately evolute *Xiaohenautilus* with subquadratic (early growth stages) to quadratic (later growth stages) whorl section.

Description: Moderately evolute, fairly compressed shell with subquadratic whorl section, broadly rounded venter, rounded ventral shoulder and slightly convex flanks with maximum whorl width just above umbilical shoulder on early growth stages. As shell increases in size, whorl section becomes quadratic with broadly tabulate venter, abruptly rounded ventral shoulders and nearly parallel flanks. Umbilicus fairly narrow with moderately high, vertical wall and rounded shoulders. Umbilical perforation fairly small (2-4 mm). Embryonic shell and body chamber lengths unknown. Ornamentation consists of fine, sinuous growth lines with deep, V-shaped hyponomic sinus on venter. Siphuncle located near venter at one fifth of whorl height. Suture simple with shallow, wide ventral lobe (Fig. 11M, N)

Measurements: See Table 1.

Discussion: *Xiaohenautilus mulleni* n. sp. is easily distinguished from *X. sinensis* Xu (1988, p. 439) by its more evolute coiling, and *X. huananensis* Xu (1988, p. 439) and *X. abrekensis* Shigeta and Zakharov (2009, p. 53) by its quadratic whorl section at later growth stages. However, the shells of *X. mulleni* n. sp. and *X. abrekensis* are very similar at early growth
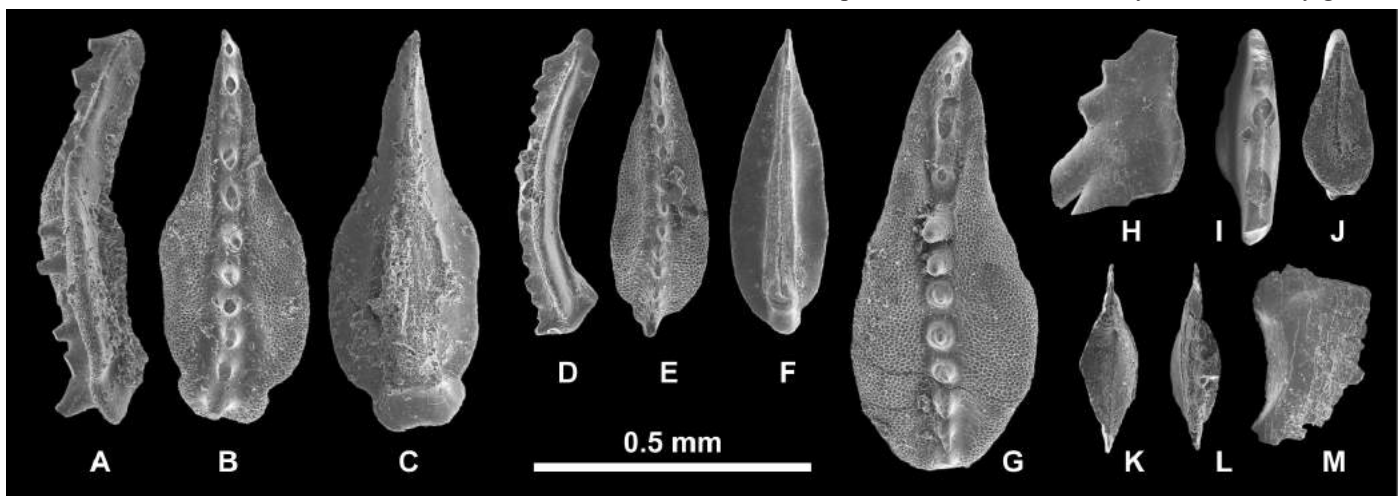

FIGURE 14. **A-C**, *Clarkina carinata* (Clark), NMMNH P-81697, from Loc. ②, in **A**, lateral, **B**, upper and **C**, lower views. **D-F**, *Clarkina griesbachiensis* (Orchard), NMMNH P-81698, from Loc. ⑤+2, in **D**, lateral, **E**, upper and **F**, lower views. **G**, *Clarkina tulongensis* (Tian), NMMNH P-81699, from Loc. ②, upper view. **H-J**, *Merrillina* sp., NMMNH P-81700, from Loc. ⑤+2, in **H**, lateral, **I**, upper and **J**, lower views. **K-M**, *Hindeodus* sp., NMMNH P-81701, from Loc. 201507b, in **K**, lower, **L**, upper and **M**, lateral views. See Fig. 5 for conodont sample points.

stages, which suggests they may be closely related.

Occurrence: Five specimens found as float, within a ~2.5 m interval (locality NMMNH L-12683) located ~11 m stratigraphically above the ammonoid bed, about 15 m west of the ammonoid site, on a gentle, east-facing slope, just across the small gulley at the foot of the ammonoid-containing hillside (Fig. 4).

CONCLUSIONS

1. Newly discovered cephalopod assemblage from the Dinwoody Formation at Crittenden Springs represents the first significant report of late Griesbachian ammonoids and nautiloids in the low-paleolatitudes of eastern Panthalassa.

2. This discovery greatly expands our knowledge of the earliest part of the ammonoid recovery record in eastern Panthalassa following the P-T extinction event.

3. This discovery also signifies the first report of *Wordieoceras wordiei* and two co-occurring taxa, i.e., *W. mullenae* n.sp. and *Ophimullericeras paullae* n. gen., n. sp., outside of the Boreal Realm.

4. The similarity in low-paleolatitude and Boreal ammonoid faunas corroborates the concept of weak latitudinal diversity gradients following the end-Permian extinction.

5. The Boreal affinity of the late Griesbachian ammonoid fauna contrasts with the western Panthalassa affinity of the nautiloids, i.e., *Xiaohenautilus mulleni* n. sp., a genus reported only from South China and South Primorye.

ACKNOWLEDGMENTS

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