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# Dienerian (Early Triassic) ammonoids from the Candelaria Hills (Nevada, USA) and their significance for palaeobiogeography and palaeoceanography

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**Abstract** A well-preserved ammonoid fauna of Early Dienerian age has long been known from the lower portion of the Candelaria Formation in the old Candelaria silver mining district in Mineral and Esmeralda Counties, Nevada, but for a number of reasons, this fauna has never been studied in detail nor illustrated. Previous authors assigned this ammonoid fauna to the Early Dienerian *Proptychites candidus* Zone of Canada. In reality, it more closely resembles the Tethyan faunas than the higher palaeolatitude Canadian faunas, thus indicating the presence of some degree of equatorial faunal exchange between opposite sides of the Panthalassic Ocean during Early Dienerian time. It also indicates the onset of a provincialism, which contrasts with the cosmopolitan Griesbachian faunas. A rigorous taxonomic analysis of the Candelaria fauna allows us to differentiate the following ten species, which include two new species and one new genus (*Mullericeras* nov. gen.) belonging to the new family Mullericeratidae: *Ambites lilangensis* (Krafft, 1909), *Ambites* aff. *radiatus* (Brühwiler, Brayard, Bucher and Guodun, 2008), *Ussuridiscus* sp. indet., "*Koninckites*" aff. *kraffti* Spath, 1934, *Mullericeras spitiense* (Krafft, 1909), *Mullericeras fergusoni* nov. sp., *Mullericeras* sp. indet., *Proptychites haydeni* (Krafft, 1909), *Proptychites pagei* nov. sp., *Vavilovites* sp. indet. and *Parahedenstroemia kiparisovae* Shigeta and Zakharov, 2009. This Early Dienerian fauna correlates with the *Ambites* fauna known from the base of the Ceratite Marls in the Salt Range and from the base of the "*Meekoceras*" beds in Spiti (northern Gondwanian margin). The fauna also permits the precise dating of a shelfal anoxic episode on the equatorial North American margin. This anoxic event correlates in time with similar palaeoceanographic changes in the southern Tethys, which indicates that the Early Triassic biotic recovery was at least partly shaped by such discrete, short events rather than by pervasive and lingering adverse environmental conditions.

**Keywords** Ammonoidea · Ceratitida · Biotic recovery · Anoxia

**Résumé** Une faune d'ammonites bien préservées de la base du Dienérien a depuis longtemps été reconnue à la base de la formation Candelaria dans le district des anciennes mines d'argent de Candelaria, Mineral et Esmeralda County, Nevada, mais pour différentes raisons, celle-ci n'avait jamais été étudiée en détail ni figurée. Les précédents auteurs ont corrélé cette faune avec la Zone à *Proptychites candidus* du Dienérien inférieur du Canada. Elle est en réalité plus proche des faunes téthysiennes que des faunes canadiennes, provenant de plus hautes paléolatitudes, ce qui indique la présence, au niveau de l'équateur, d'échanges de faunes entre les deux côtés de l'Océan Panthalassique au Dienérien inférieur. Cela démontre aussi la mise en place d'un provincialisme qui contraste avec les faunes cosmopolites du Griesbachien.

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Une analyse taxonomique rigoureuse nous a permis de différencier dix espèces, y compris deux nouvelles espèces et un nouveau genre (*Mullericeras* nov. gen.) appartenant à la nouvelle famille Mullericeratidae: *Ambites lilangensis* (Krafft, 1909), *Ambites* aff. *radiatus* (Brühwiler, Brayard, Bucher et Guodun, 2008), *Ussuridiscus* sp. indet., "*Koninckites*" aff. *kraffti* Spath, 1934, *Mullericeras spitiense* (Krafft, 1909), *Mullericeras fergusoni* nov. sp., *Mullericeras* sp. indet., *Proptychites haydeni* (Krafft, 1909), *Proptychites pagei* nov. sp., *Vavilovites* sp. indet. et *Parahedenstroemia kiparisovae* Shigeta et Zakharov, 2009. Cette faune du Dienérien inférieur peut être corrélée avec les faunes à *Ambites* de la base des Ceratite Marls dans les Salt Range et de la base des "*Meekoceras*" beds au Spiti (marge nord Gondwanienne). Elle permet de dater précisément un épisode anoxique sur la marge nord américaine équatoriale. Cet évènement anoxique est contemporain de changements paléoocéanographiques similaires au Sud de la Téthys, ce qui démontre que la récupération biotique du Trias Inférieur était au moins en partie influencée par de tels évènements courts et discrets plutôt que par des conditions environnementales défavorables généralisées et durables.

**Mots clés** Ammonoidea · Ceratitida · Récupération biotique · Anoxie

**Institutional abbreviations**

| | |
|---|---|
| USNM | US Geological Survey Paleontology collections, Washington, D.C., USA |
| PIMUZ | Paläontologisches Institut und Museum collection, University of Zürich, Switzerland |
| NMMNH&S | New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, USA |
| JJ | James F. Jenks' private collection, West Jordan, Utah, USA |

## 1 Introduction

Most of the recent studies regarding Dienerian ammonoids and their biostratigraphy have mainly concerned the boreal realm: for example, Tozer (1961, 1963, 1994) conducted a comprehensive study of faunas from Arctic Canada and British Columbia, while Popov (1961), Ermakova (1981) and Dagys and Ermakova (1996) studied faunas from Siberia. In the lower latitudes, only a few recent studies have focused on the Tethyan realm, but these were in localities where the stratigraphic record is not as refined: e.g., Shigeta and Zakharov (2009) in Primorye (Eastern Russia), and Mu et al. (2007) and Brühwiler et al. (2008) in South China. Faunas from the northern Indian Margin are currently under revision at the University of Zürich. Apart from Guex (1978), who described a few Dienerian species from the Salt Range (Pakistan), there are no recent comprehensive studies of the ammonoids from this area. The most valuable monographs for this region are those by Waagen (1895) for the Salt Range, and Diener (1897) and Krafft and Diener (1909) for the north-western Indian Himalaya.

In this context, Dienerian ammonoids from the western USA provide valuable new insight into Early Triassic palaeobiogeography. Ammonoids from the Candelaria Formation, though previously cited and discussed by several authors (Muller and Ferguson 1936, 1939; Page 1959; Silberling and Tozer 1968), have never been described in detail nor illustrated. They are, however, very important since they come from the only locality in the lower latitudes of the North American continent with well preserved specimens. To their credit, Muller and Ferguson (1939) recognized that the Candelaria fossil assemblage represented two of the earliest Triassic marine faunas then known from North America, namely an older bivalve fauna consisting largely of *Claraia stachei* and a slightly younger *Proptychites* ammonoid fauna. They also documented the close affinity of their Candelaria ammonoids with those described by Waagen (1895) from the Salt Range of Pakistan and Krafft and Diener (1909) from the NW Himalaya. Later, Silberling and Tozer (1968) assigned a late Griesbachian age to the *Claraia* bivalve assemblage and correlated the ammonoid fauna with the Early Dienerian *Proptychites candidus* Zone of Canada.

Intensive field work conducted by the authors during the last 3 years has provided new, well preserved ammonoids as well as the inadvertent discovery of complete, well preserved specimens of marine Dienerian fish (Brinkmann et al. 2010). The purpose of this study is to provide a new, revised taxonomy of the ammonoid fauna and to discuss their palaeobiogeographic and palaeoceanographic implications.

## 2 Palaeogeographical and geological context

During the Early Triassic, two wide oceans, the Tethys and the Panthalassa, were separated by the Pangean supercontinent and several microcontinents. At that time, the Candelaria Hills of western Nevada (Fig. 1) were located on the eastern margin of Panthalassa, just a few degrees north of the equator.

Lower Triassic sedimentary rocks of marine origin are rather common in the western USA, but they are mainly Smithian and Spathian in age. Griesbachian and Dienerian

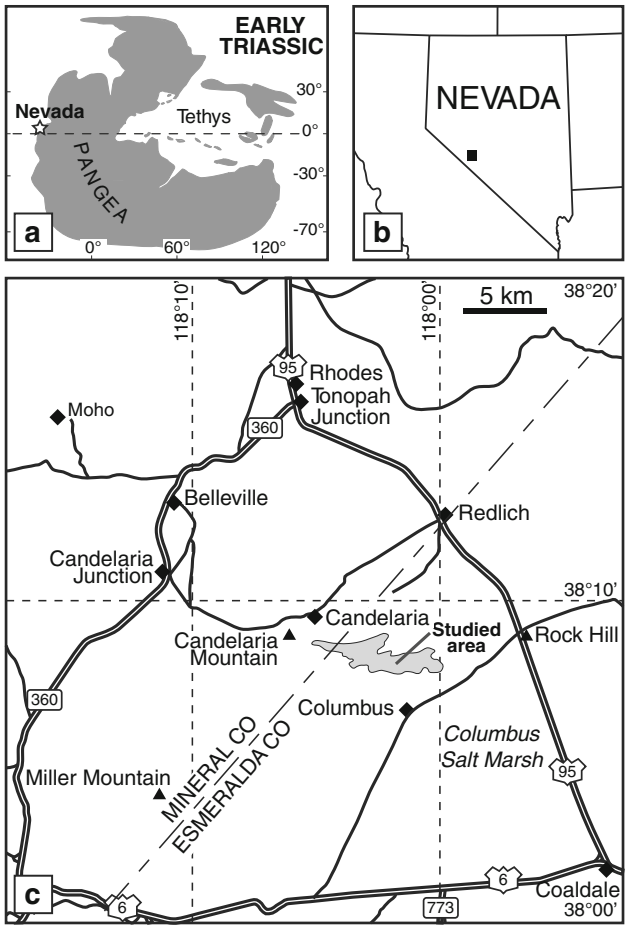


**Fig. 1** **a** Simplified Early Triassic palaeogeography (modified after Brayard et al. 2006) and palaeoposition of Nevada. **b** Location of the Candelaria Hills, Nevada. **c** Location of the studied area showing areal extent of the Candelaria Formation (modified after Silberling 1984)

sediments, while not as common, are usually unfossiliferous, with the exception of the Candelaria Formation.

As discussed by Page (1959), the stratigraphic position of the Permian–Triassic boundary in the Candelaria Hills is not well defined. Muller and Ferguson (1939) regarded it as marked by an angular unconformity. The very base of the Candelaria typically contains a phosphatic nodule rich horizon named "Permian grit" by these authors, which they considered to be part of the Diablo Formation (Middle Permian). Page (1959) disagreed and considered this lower grit to actually be part of the Candelaria Formation and we fully agree with this interpretation. However, the age of the base of the Candelaria Formation remains unknown, as does the amount of time missing between the two formations. The Permian Diablo Formation is interpreted by Speed (1977) as part of the continental borderland. The lower member of the Candelaria Formation consists of ca. 100 m of quartzose and calcareous mudstones and sandstone with minor micritic limestone beds and early diagenetic nodules assigned here to an outer shelf depositional setting. With abundant breccias derived from rocks of the Golconda allochthon, the upper member of the Candelaria Formation as described by Speed (1977) records a major change in the origin of the clastic input and is considered by Saleeby and Busby-Spera (1992) to be syndeformational with the overriding plate of the Golconda. Hence, the palaeogeographic position of the low-paleolatitude Dienerian ammonoid fauna of the Candelaria Formation must be considered as plate-bound and not as belonging to an outboard terrane.

The fossiliferous interval is 20–25 m thick and approximately 45 m above the base of the Candelaria Formation. It is composed of dark bituminous shales, purplish on weathered surfaces, with a few thin beds of impure limestone and early diagenetic concretions. The lower part of this interval consists of pink weathering silty shales with a few thin silty limestone beds containing many bivalves of the genus *Claraia*, while most of the ammonoid fauna described herein is found in concretions and lenses that occur within a 10 m interval beginning about 5 m above the *Claraia* beds. However, three slightly older ammonoids were found in float concretions within the *Claraia* beds. These concretions contained fragments of *Claraia*, but their exact position within this interval will be the subject of ongoing fieldwork.

*Claraia* is represented by *C. stachei* Bittner, 1901 and *C.* cf. *mulleri* Newell and Kummel, 1942 (Fig. 2). The type material of *C. stachei* is from the Early Triassic of Malborgeth/Malborghetto (northern Italy), but Bittner (1901) introduced this species without giving illustrations and stratigraphic context, and he died before completing the envisaged monograph of his material. The current concept of *C. stachei* is based on material from the Griesbachian of east Greenland, which Spath (1930) identified on the basis of Bittner's (1901) short description. *C. stachei* is most abundant in the late Griesbachian (e.g., McRoberts 2010, fig. 3), but the position of the LAD of this species is uncertain. In the Western USA, *C. stachei* characterizes the "*Claraia*" zone of the Dinwoody Fm. in Wyoming and adjacent areas (Newell and Kummel 1942), which might extend into the Dienerian (Carr and Paull 1983). Ciriacks (1963, p. 80) reported an occurrence of *C. stachei* in the Thaynes formation at Hammond Creek (Idaho) in horizons "not dated in terms of ammonite zones but probably younger than the *Meekoceras* fauna, which suggests that the species ranges as high as Owenitan [=Smithian] age". However, specimens from these late occurrences have not been figured and thus their identity appears uncertain. In our samples, *C. stachei* co-occurs with ammonoids Dienerian in age (*Ambites* aff. *radiatus* and *Ussuridiscus* sp. indet.), thus confirming that it straddles the Griesbachian–Dienerian boundary. *C. mulleri* co-occurs with *C. stachei*

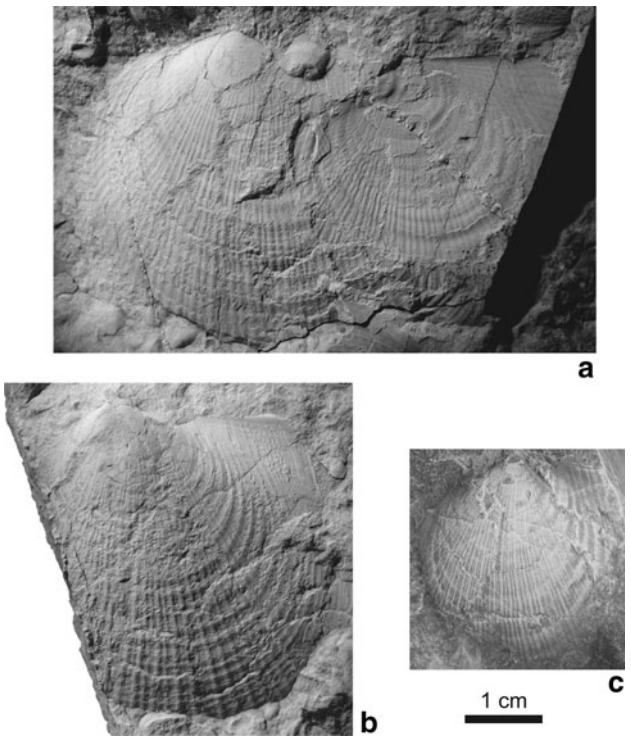


**Fig. 2** *Claraia* from the Candelaria Formation, exact stratigraphic position unknown. **a** *Claraia stachei*, JJ67P, external view or left valve (*left*) and internal view or right valve (*right*). **b** *Claraia stachei*, JJ68P, external view or left valve, showing details of posterior wing. **c** *Claraia* cf. *mulleri*, JJ69P, external view of left valve

in the Dinwoody Fm. of Wyoming and differs from the latter only in having a more extended posterior auricle in the left valve and less pronounced commarginal costae (Newell and Kummel, 1942). Based on these differences, we provisionally assign one of our specimens to that species. However, analysis of larger samples might show that a consistent separation of both species is not possible.

The presence of dark, laminated bituminous shales and limestone yielding complete fishes (basal actinopterygians; Romano et al., unpublished data) is indicative of an anoxic sediment–water interface. The absence of associated benthic molluscs other than *Claraia* is an additional line of evidence diagnostic of oxygen-deficient bottom waters.

Compared to the relatively large areal extent of the Candelaria Formation (Fig. 1c), outcrops of the 25-m thick, recessive dark bituminous shale interval occur only in three areas, each of which is rather limited in size (largest is approx. 15 m × 200 m). The abundance of concretions and lenses is highly variable in these three areas. In the largest area, the slope of the hillside is fairly gentle and therefore, outcrops of concretions and lenses are very limited. Nevertheless, evidence of past collection activity is abundant as indicated by the numerous concretion fragments scattered all over the hillside. We have found only six in situ fossiliferous concretions within this area and since they were found more or less on strike, they likely represent only one concretion horizon. In contrast, the topography at one of the smaller outcrop areas is much steeper and at least three concretion horizons (Fig. 3) have been documented.

Many of our specimens lack accurate stratigraphical positioning because they were found in float concretion fragments scattered on the lower slopes of the largest outcrop area. Similarly, even though the U.S. Geological Survey-Stanford University collection contains many well preserved specimens, it also lacks precise stratigraphical information. Consequently, it is not possible to produce a precise stratigraphical log containing well documented horizons for all of the different ammonoids. Our log (Fig. 3) is based exclusively on those ammonoids occurring in the in situ concretions, with the exception of *Mullericeras spitiense*, which was found in a float concretion fragment a few meters above nodules containing *Ambites lilangensis*. Hence, we assume it co-occurs with *Parahedenstroemia kiparisovae*, but its actual source could be above or below.

## 3 Systematic palaeontology

Systematic descriptions are based on the classification of Waagen (1895), Tozer (1994) and Shigeta and Zakharov (2009). The quantitative morphological range of each species is expressed utilizing the four classic geometrical parameters of the ammonoid shell: diameter (D), whorl height (H), whorl width (W) and umbilical diameter (U). The three parameters (H, W and U) are plotted in absolute values as well as in relation to diameter (H/D, W/D, and U/D) provided measurements were available for at least five specimens. All measurements are given in the online resource.

| | |
|---|---|
| Class | Cephalopoda Cuvier, 1797 |
| Subclass | Ammonoidea Agassiz, 1847 |
| Order | Ceratitida Hyatt, 1884 |
| Superfamily | Meekocerataceae Waagen, 1895 |
| Family | Gyronitidae Waagen, 1895 |
| **Genus** | ***Ambites* Waagen, 1895** |
| *Type species* | *Ambites discus* Waagen, 1895 |

***Ambites lilangensis* (Krafft, 1909)** (Figs. 4, 5, 6)

1909. *Meekoceras lilangense* Krafft, p. 23, pl. 1, figs. 2 (lectotype), 1, 3, 5, 6, 7, pl. 14 figs. 1, 2.
1934. *Prionolobus lilangensis* Spath, p. 101, pl. 4, fig. 4.
?1976. *Prionolobus lilangensis* Wang and He, p. 276, pl. 3, fig. 4, 5, text-fig. 8b.
1996. *Lilangia lilangense* Waterhouse, p. 36

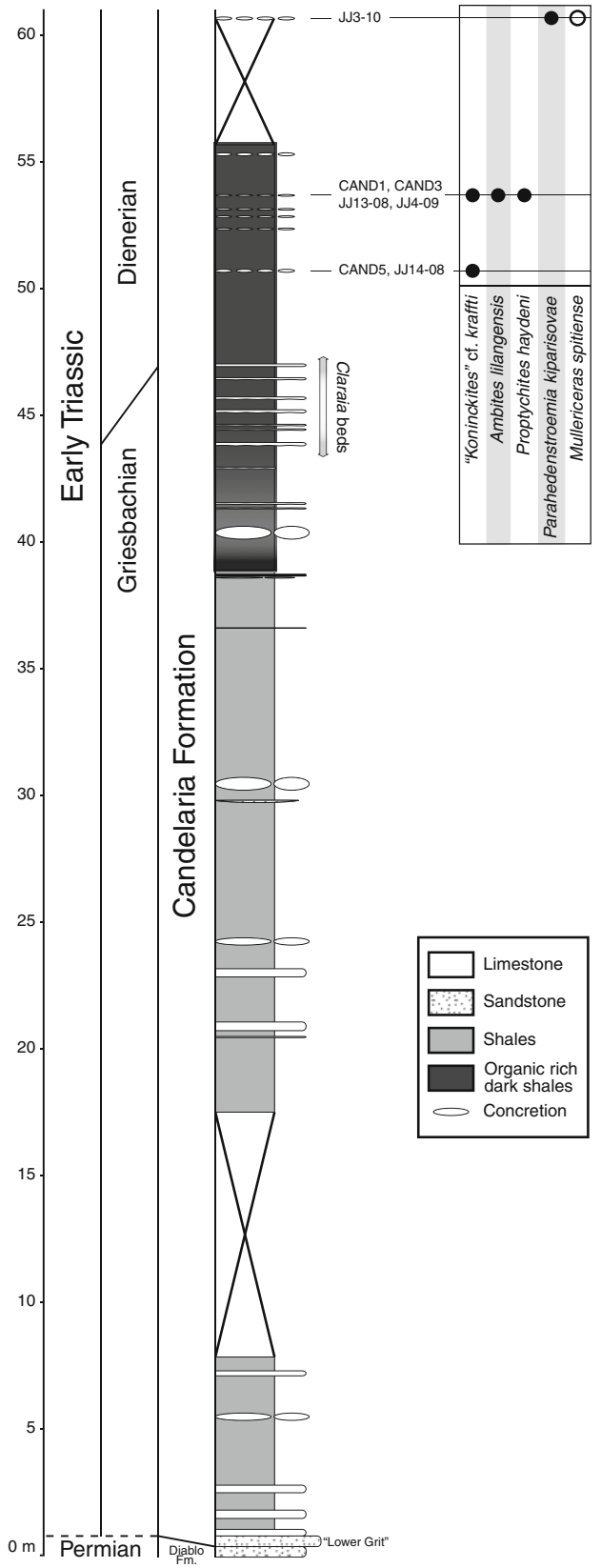


**Fig. 3** Synthetic stratigraphic log with biostratigraphy of the few ammonoids found in situ (*solid circles* actual occurrence; *open circles* probable occurrence; see text for details)

*Material* Two specimens from the PIMUZ, 14 from the USNM, 16 from the Jenks private collection.

*Description* Platyconic shell with tabulate venter and angular, prominent ventrolateral shoulders protruding slightly above the flanks. Inner whorls moderately involute, generally becoming slightly more evolute during ontogeny (U/D changing from 20% to nearly 30%; some specimens, like the one shown in Fig. 4-3a, maintain the same involution during ontogeny, making them appear more involute than other specimens of similar size). Whorl cross section relatively thick (W/H varying from 40 to 60%). Flanks flat and parallel until the external third of the whorl, where they suddenly converge toward the venter. The rapidity of this change in convergence gives one the impression of a spiral line on the flank. Flanks become parallel again just before the ventrolateral shoulders, forming a slight concavity on the part of the whorl just below the ventral shoulder. Maximum whorl width occurs about mid-flank. Umbilical wall vertical and relatively high with subangular shoulder. Growth lines slightly biconcave and projected forward, accentuated on large specimens into indistinct sigmoidal folds. Faint strigation on the venter and below the ventral shoulders, which is visible only on the shell. Suture line ceratitic with three lateral rounded saddles separated by two rounded gently indentated lateral lobes, lateral lobes and saddles having approximately the same width. Auxiliary series not exposed.

*Measurements* See online resource and Fig. 6.

*Remarks* Waterhouse (1996) created a new genus, *Lilangia*, based on this species, and differentiated it from *Ambites* mainly by its denticulated lobes, whereas he considered that the type species of *Ambites* (*A. discus* Waagen, 1895) had a goniatitic suture line. He also considered *Lilangia* to have a higher, more differentiated umbilical wall. A close examination of new specimens from the type locality of *Ambites* (Amb, Salt Range, Pakistan; Ware et al., unpublished data) shows that its suture line actually has finely indentated lobes, just as *A. lilangensis* (Krafft, 1909), which is confirmed by new material collected by the first author from the type locality of this species (Lalung, Spiti Valley, Himachal Pradesh, India). The difference in shape of the umbilical wall is most probably just a consequence of the thicker whorl section of *A. lilangensis* compared to *A. discus*. We therefore consider the genus *Lilangia* to be a junior synonym of *Ambites*.

*Occurrence* Early Dienerian, *Proptychites* beds of Nevada, *Ambites* beds of Spiti valley (India).

### ***Ambites* aff. *radiatus* (Brühwiler, Brayard, Bucher and Guodun, 2008) (Figs. 7, 8b)

2008. *Pleurambites radiatus* – Brühwiler et al., p. 1168, pl. 5, figs. 1 (holotype), 2, 3.

*Material* Two specimens from the Jenks private collection.

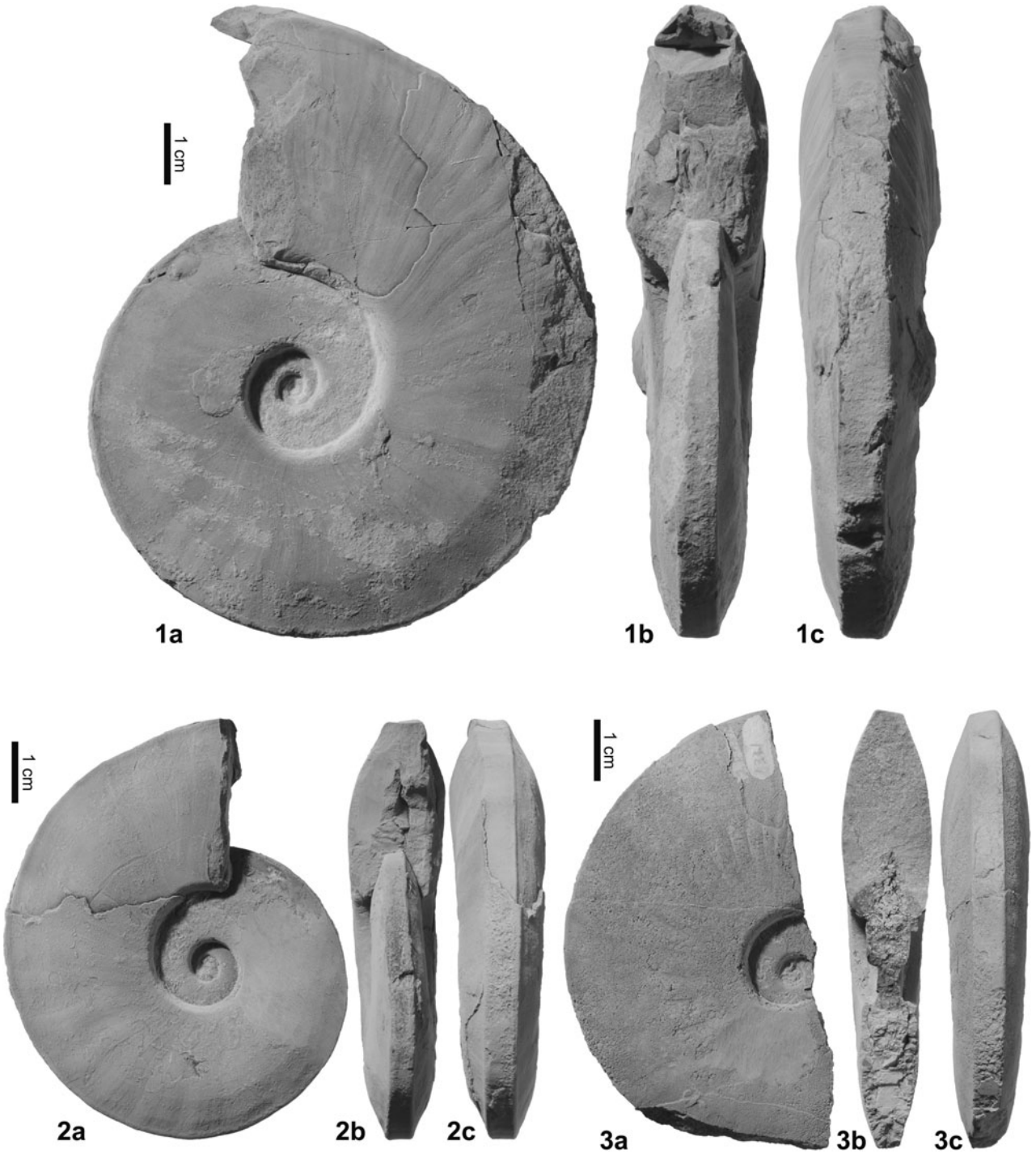


**Fig. 4** *Ambites lilangensis* (KRAFFT, 1909). Three specimens with body chamber, but last septum not visible. **1** PIMUZ28596; **1a** lateral view; **1b** apertural view; **1c** ventral view. **2** USNM542474; **2a** lateral view; **2b** apertural view; **2c** ventral view. **3** USNM542485; **3a** lateral view; **3b** apertural view; **3c** ventral view

*Description* Very evolute platyconic shell with tabulate venter and angular, prominent ventrolateral shoulders protruding slightly above the flanks. Flanks slightly convex until the external quarter of the whorl, where they suddenly converge towards the venter, almost forming a spiral line as in the previously described species *A. lilangensis*. Maximum whorl width occurs about mid-flank. Umbilical wall undifferentiated, the flanks forming a gentle curve just before the umbilical seam. Slightly sigmoid radial folds, following the shape of the growth lines, become more

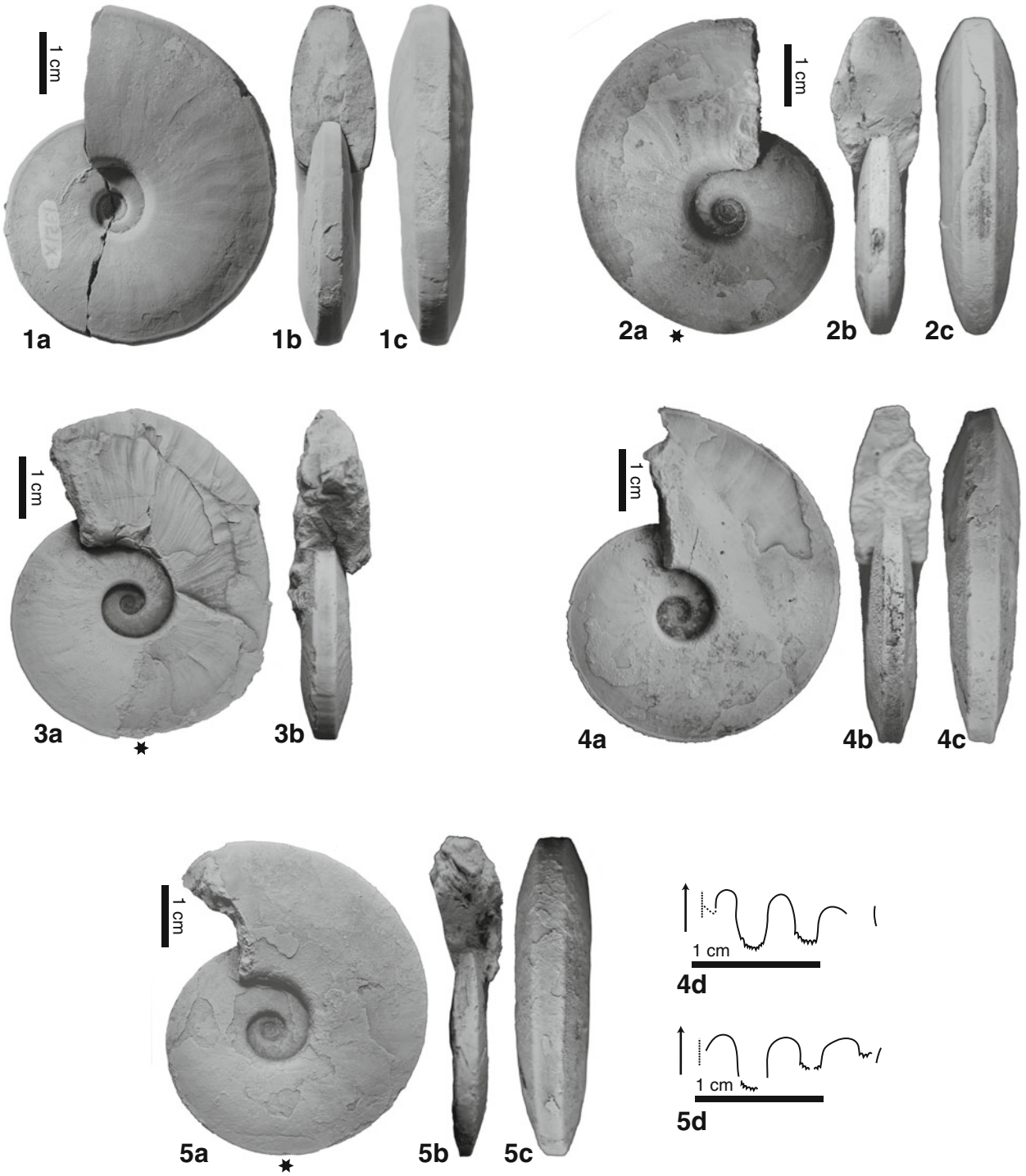


**Fig. 5** *Ambites lilangensis* (Krafft, 1909). **1** USNM542477; **1a** lateral view; **1b** apertural view; **1c** ventral view. **2** JJ2023C; **2a** lateral view; **2b** apertural view; **2c** ventral view. **3** JJ2028C; **3a** lateral view; **3b** apertural view. **4** JJ2157C; **4a** lateral view; **4b** apertural view; **4c** ventral view; **4d** suture line at H = 16 mm. **5** JJ2154C; **5a** lateral view; **5b** apertural view; **5c** ventral view; **5d** suture line at H = 16.5 mm. *Asterisks* indicate last septum where known

abundant but less prominent on the body chamber. Suture line ceratitic with three rounded lateral saddles, the third one being much smaller than the other two. The first lateral lobe is rounded with minor indentation, and is nearly as wide as the two first lateral saddles. The second lateral lobe, also rounded, is much narrower and indentations are not visible probably because of poor preservation. Auxiliary series short.

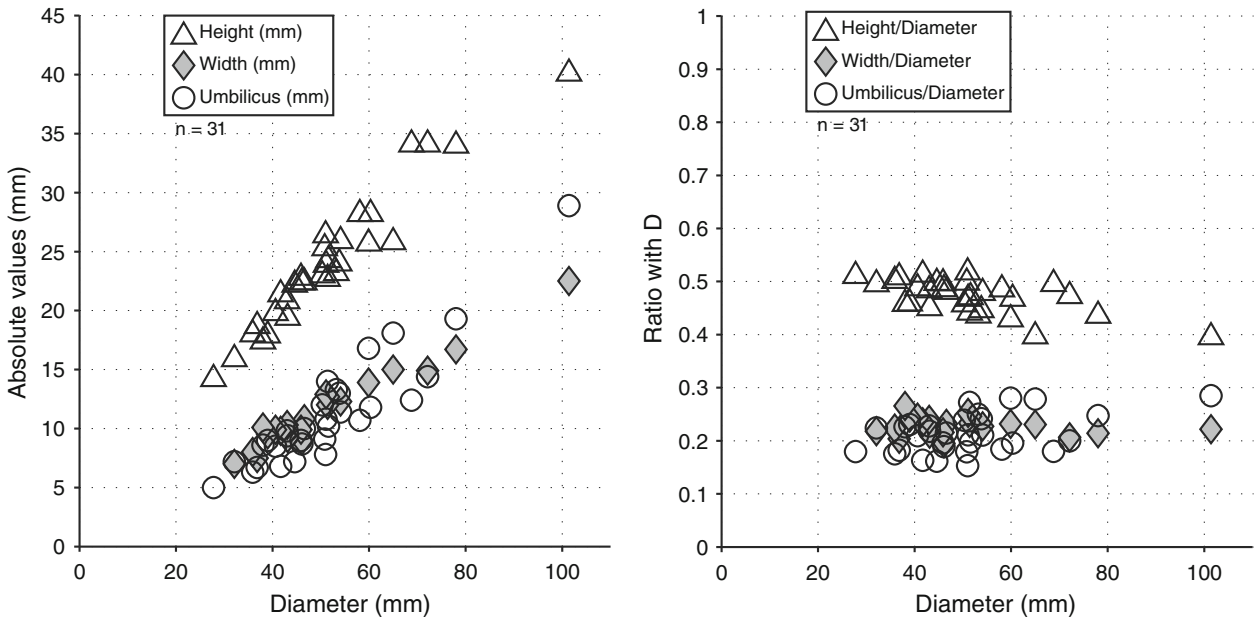


**Fig. 6** Scatter diagrams of H, W, and U (*left*), and of H/D, W/D, and U/D (*right*) for *Ambites lilangensis* (Krafft, 1909). *D* diameter, *H* whorl height, *U* umbilical diameter, *W* whorl width

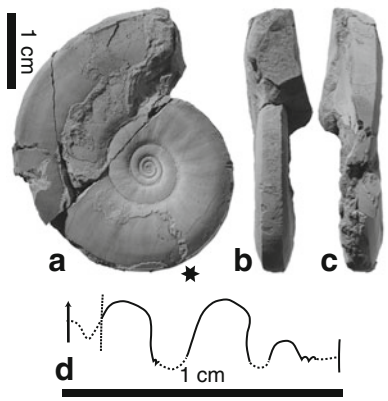


**Fig. 7** *Ambites* aff. *radiatus* (Brühwiler, Brayard, Bucher and Guodun, 2008). JJ2173C, loc. JJ6-10; **a** lateral view; **b** apertural view; **c** ventral view; **d** suture line at H ≈ 8.4 mm, D ≈ 21 mm. *Asterisk* indicates last septum

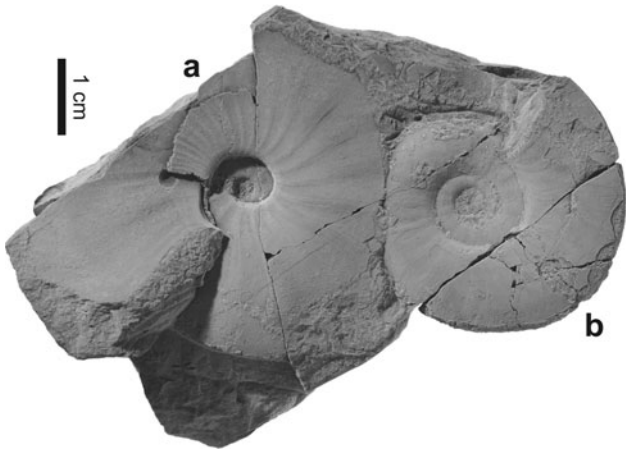


**Fig. 8** JJ2175C, loc. 6-10. **a** *Ussuridiscus* sp. indet. **b** *Ambites* aff. *radiatus* (Brühwiler, Brayard, Bucher and Guodun, 2008). Both specimens retain their body chamber, but last septum is not visible

*Measurements* As the specimens are slightly distorted, no precise measurements were possible. However, the following proportions can be estimated. They are identical for both specimens: D ≈ 35 mm; H/D ≈ 35%; W/D ≈ 20%; U/D ≈ 35%.

*Remarks* These specimens differ from those described by Brühwiler et al. (2008) by their weaker ornamentation and the absence of a clearly differentiated umbilical wall. However, we have insufficient material to determine whether these differences are diagnostic or simply due to intraspecific variability. Brühwiler et al. (2008) attributed their new species to the genus *Pleurambites* Tozer, 1994. Tozer (1994) differentiated this genus from *Ambites* because of its stronger ornamentation. However, his specimens have a thicker whorl section than the type species of *Ambites*, but this difference is probably due to covariation between whorl thickness and ornamentation (first Buckman's law of covariation). Thus, we consider the genus *Pleurambites* to be a junior synonym of the genus *Ambites*. Our specimens, with their very evolute platyconic shape, are very close to the genus *Gyronites*. They, however, exhibit the following characteristics, which are typical of the genus *Ambites*: (1) the first lateral lobe is nearly as wide as the two first lateral saddle (it is much narrower in *Gyronites*), (2) the shell has a faint spiral line on the ventral

half of the flanks, (3) the ventrolateral shoulders protrude slightly above the flanks, and (4) the flank bears sigmoidal folds (some species of *Gyronites* have radial folds).

*Occurrence* Early Dienerian, *Claraia* beds, precise locality and horizon unknown, Candelaria Hills, Nevada, and Luolou Formation of Jinya (northwestern Guangxi, South China).

**Genus *Ussuridiscus* Shigeta and Zakharov, 2009**

*Type species* *Meekoceras* (*Kingites*) *varaha* Diener, 1895

***Ussuridiscus* sp. indet.** (Fig. 8a)

*Material* One specimen from the Jenks private collection.

*Description* Involute platyconic shell with tabulate venter and angular ventrolateral shoulders. Flanks slightly convex with maximum width at inner third of whorl height. Overhanging umbilical wall with angular shoulders. Umbilicus, which is characterized by overhanging wall with angular shoulders, suddenly becomes more open at the beginning of the last whorl. Flank exhibits faint, slightly sigmoidal folds that follow the shape of the growth lines. Suture line not visible.

*Measurements* Measurements not possible, specimen is slightly distorted and incomplete.

*Remarks* This specimen is morphologically close to those described by Shigeta and Zakharov (2009) as *Ussuridiscus varaha*, but it differs by its more convex flanks and its strong egression on the last whorl. As we have only one specimen, it is impossible to determine if these differences are due to intraspecific variability. We attributed this specimen to *Ussuridiscus* based on its overhanging umbilical wall, the main characteristic of the genus. However, this genus occurs in Primorye (where it was originally described by Shigeta and Zakharov 2009) together with the genus *Ambitoides*, which differs only by its sub-vertical umbilical wall and its stronger egression. We question the validity of the genus *Ambitoides*, since some of their very involute specimens are very close to the genus *Ussiridiscus* (differing only by their non-overhanging umbilical wall). However, other specimens become more evolute with growth and are very close to the genus *Ambites*, the genus to which the type species of *Ambitoides* (*Ambites fuliginatus* Tozer 1994) was originally ascribed.

*Occurrence* Early Dienerian, Candelaria Formation, *Claraia* beds, precise locality and horizon unknown, Candelaria Hills, Nevada.

**Genus *Koninckites* Waagen, 1895**

*Type species* *Koninckites vetustus* Waagen, 1895

**"*Koninckites*" aff. *kraffti* Spath, 1934** (Figs. 9, 10)

1897. *Kingites varaha* Diener, p. 143, pl. 6, fig. 2, pl. 7, fig. 6.

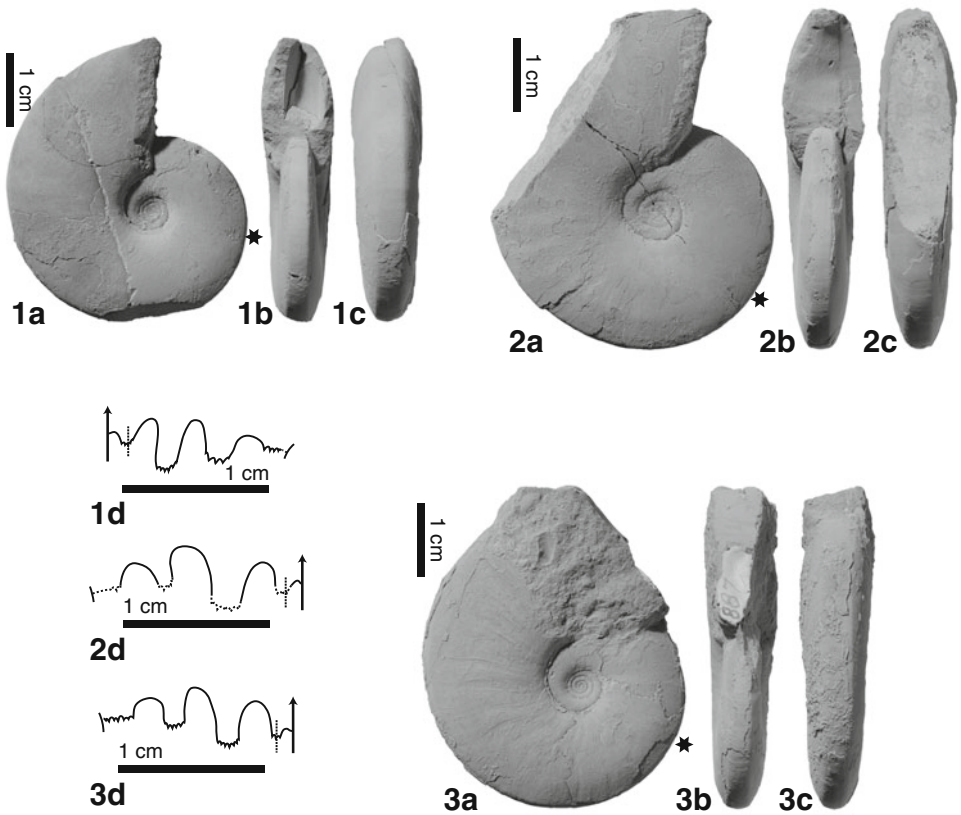


**Fig. 9** "*Koninckites*" aff. *kraffti* Spath, 1934. **1** JJ2031C, loc. JJ14-08; **1a** lateral view; **1b** apertural view; **1c** ventral view; **1d** suture line at H = 10.9 mm, D ≈ 21.3 mm. **2** JJ2032C, loc. JJ14-08; **2a** lateral view; **2b** apertural view; **2c** ventral view; **2d** suture line at H = 13.2 mm, D ≈ 28.4 mm. **3** USNM542467; **3a** lateral view; **3b** apertural view; **3c** ventral view; **3d** suture line at H = 12.1 mm, D ≈ 22.1 mm. *Asterisks* indicate last septum

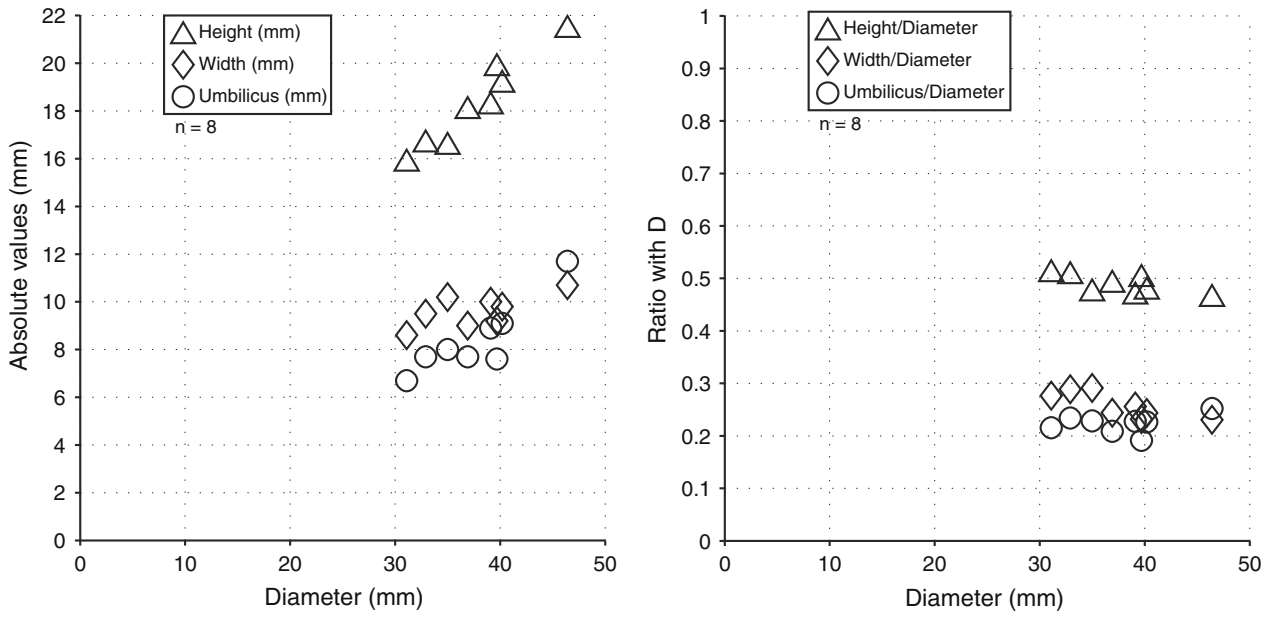


**Fig. 10** Scatter diagrams of H, W, and U (*left*), and of H/D, W/D, and U/D (*right*) for "*Koninckites*" aff. *kraffti* Spath, 1934. *D* diameter, *H* whorl height, *U* umbilical diameter, *W* whorl width

1909. *Meekoceras varaha* Krafft and Diener, p. 17, pl. 2, figs. 4 (lectotype), 2, 3, 5, 6.
1915. *Meekoceras varaha* Diener, p. 195.
1930. *Meekoceras varaha* Spath, p. 28.
1934. *Koninckites kraffti* Spath, p. 155, fig. 43c.

NOT

1895. *Meekoceras* (*Kingites*) *varaha* – Diener, p. 52, pl. 1, fig. 3.

*Material* Two specimens from the PIMUZ, two from the USNM, six from the Jenks private collection.

*Description* Rather involute (U/D ≈ 20%), subplatyconic shell with sub-tabulate venter and indistinct sub-angular ventrolateral shoulders. Flanks convex with maximum whorl width at mid-flank. Umbilical wall varying from quite high vertical wall with rounded indistinct shoulders to low indistinct wall. Shell smooth apart from slightly biconcave growth lines and a very fine strigation on the venter. Some specimens with remains of the external prismatic layer also exhibit strigation on the lower third of the flanks. Suture line ceratitic, quite similar to *Ambites lilangensis* but projected backward, with thinner lateral saddles and less rounded lateral lobes. Auxiliary series short, the largest specimen (USNM542467) showing a slightly differentiated auxiliary lobe.

*Measurements* See online resource and Fig. 10.

*Remarks* These specimens are slightly more evolute than the specimens identified by Krafft and Diener (1909) as *Meekoceras varaha* for which Spath (1934) created the species *K. kraffti*. They are otherwise very similar, and it is possible that the difference in the degree of involution is simply a result of intraspecific variability. Moreover, the genus *Koninckites* is not clearly defined; Waagen (1895) based his definition on the presence of a well-individualized auxiliary lobe, a size-dependent characteristic, which is present on most proptychitids and many other Smithan and Spathian taxa. This genus and its species requires a thorough revision. Our specimens do not exhibit a clearly individualized auxiliary lobe or saddle, but are otherwise very close to the type species of this genus. They are slightly more involute than *Ambites lilangense*, and also differ from this species by their suture line and indistinct ventrolateral shoulders.

*Occurrence* Early Dienerian, *Proptychites* beds of Nevada, *Ambites* beds of Spiti valley (India).

Family Mullericeratidae fam. nov.

*Type genus* ***Mullericeras*** gen. nov.

*Etymology* Named after S. W. Muller.

*Diagnosis* Hedenstroemiidae-like shells without adventitious lobes and saddles.

*Description* Compressed, very involute platyconic shell with a tabulate venter and a simple ceratitic suture line without adventitious lobes and saddles.

*Remarks* Species assigned to this family exhibit a morphology very similar to species belonging to Hedenstroemiidae,

such as *Clypites* or *Pseudosageceras*. They differ only by the absence of adventitious lobes and saddles, the main characteristic of the Sageceratacea, which is why we place it within the Meekoceratacea. The similarity in morphology between Mullericeratidae and Hedenstroemiidae, in addition to the fact that the former occurs in strata older than any from which hedenstroemiids with proper age constraints have thus far been described, suggests that our new family could be the ancestor of the Hedenstroemiidae. However, Waterhouse (1994) assigned a late Griesbachian specimen to the genus *Pseudosageceras*, which would contradict this hypothesis, but this specimen is extremely poorly preserved and its attribution to this genus cannot be confirmed by his illustration. It could also belong to our new family. The genus *Kymatites* Waagen, 1895 may also belong to this family, but a thorough revision of this genus is necessary to confirm it.

*Genera included* The type genus, *Mullericeras* nov. gen.

*Occurrence* Dienerian of the Candelaria Hills (Nevada, USA) and of the Spiti Valley (Himachal Pradesh, India).

**Genus *Mullericeras* gen. nov.**

*Type species* *Aspidites spitiensis* Krafft, 1909

*Etymology* Named after S. W. Muller.

*Diagnosis.* As the family Mullericeratidae fam. nov.

*Description* Compressed, very involute platyconic shell with a tabulate venter of variable width, sharp ventrolateral shoulders and a simple ceratitic suture line without adventitious lobes and saddles.

*Remarks* This genus includes species with morphologies very close to that of early hedenstroemiids such as *Clypites* or *Pseudosageceras*, but which lack adventitious lobes and saddles. Our new genus differs from *Kymatites* by its sharp ventrolateral shoulders, its narrower umbilicus and its ceratitic suture line with a well developed auxiliary series. It differs from *Koninckites* by its sharp ventrolateral shoulders, its more closed umbilicus, and by the absence of any auxiliary lobe or saddle. It differs from *Clypeoceras* (the genus to which they have been ascribed by previous authors) by its clearly tabulate venter.

*Other species* *Aspidites spitiensis* Krafft, 1909; *Meekoceras* (*Koninckites*) *vidharba* Diener, 1897; *Aspidites ensanus* Krafft, 1909.

*Occurrence* Dienerian of the Candelaria Hills (Nevada, USA) and of the Spiti Valley (Himachal Pradesh, India).

***Mullericeras spitiense* (Krafft, 1909)** (Figs. 11, 12)

1909. *Aspidites spitiensis* Krafft, p. 54, pl. 4, figs. 4 (lectotype), 5, pl. 16, figs 3, 4, 5, 6, 7, 8.
1934. *Clypeoceras spitiense* Spath, p. 160.
?1996. *Clypeoceras spitiense* Waterhouse, p. 50, text-fig. 4J, pl. 2, figs 21, 22.
?2009. *Clypeoceras spitiense* Shigeta and Zakharov, p. 125, fig. 113, 114.

*Material* Three specimens from the USNM, two from the Jenks private collection.

*Diagnosis* *Mullericeras* with a relatively thick whorl cross section (W/H ≈ 45%) and occluded umbilicus.

*Description* Involute and moderately compressed (W/D ≈ 25%) platyconic shell with tabulate, slightly sulcate venter of variable width and sharp ventrolateral shoulders. Venter slightly tectiform, making it appear almost tricarinate. Umbilicus occluded. Flanks slightly

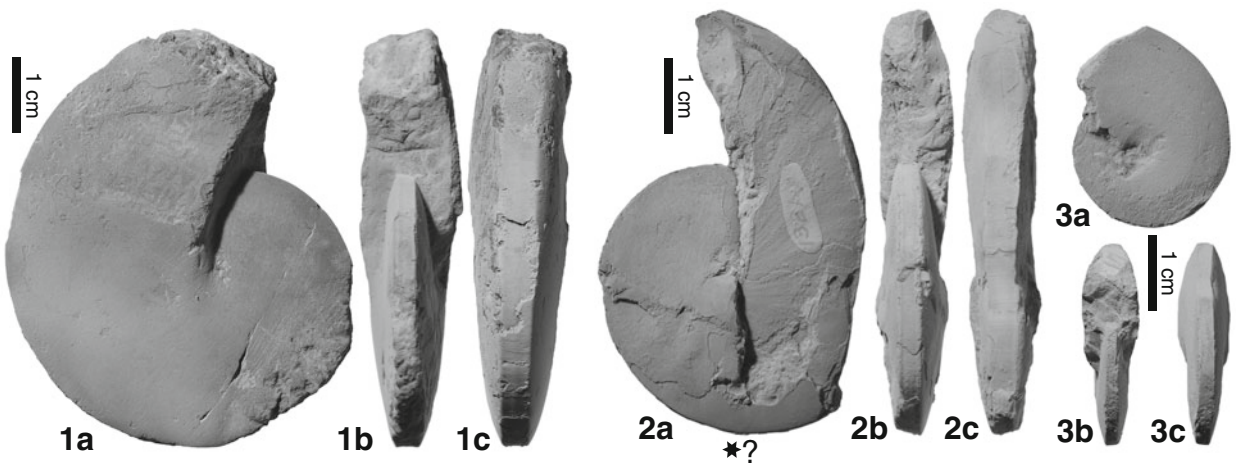


**Fig. 11** *Mullericeras spitiense* (Krafft, 1909). **1** JJ2151C, loc. JJ15-08; **1a** lateral view; **1b** apertural view; **1c** ventral view. **2** USNM542471; **1a** lateral view; **1b** apertural view; **1c** ventral view. **3** USNM542470; **1a** lateral view; **1b** apertural view; **1c** ventral view. *Asterisk* with *question mark* indicates approximate position of last septum where known

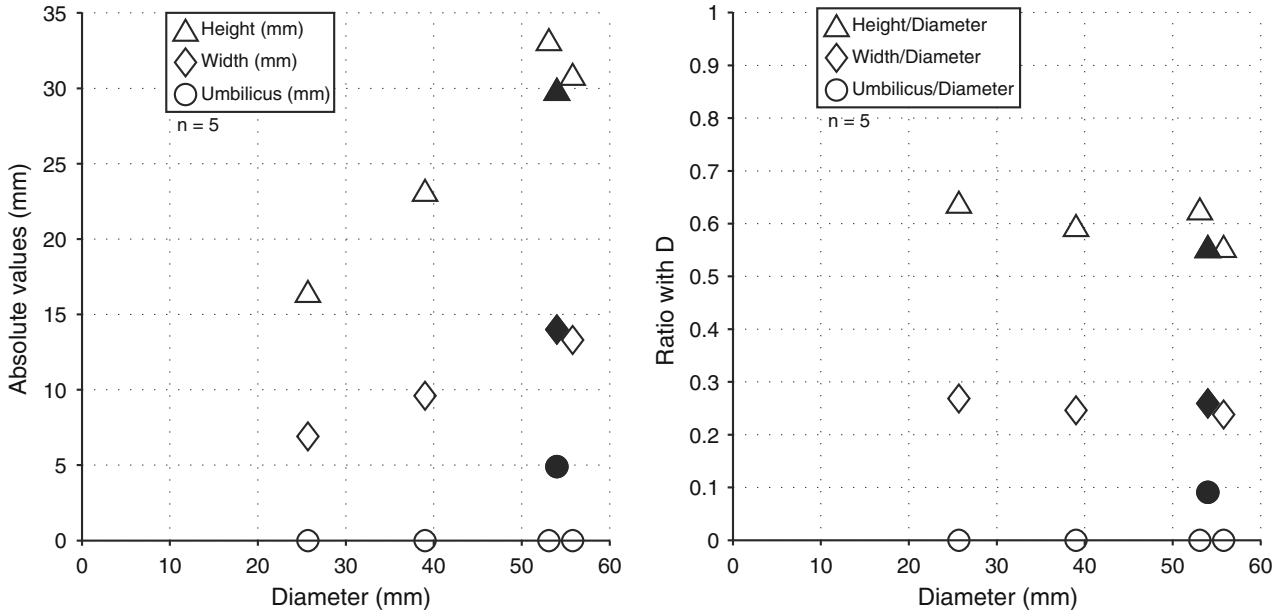


**Fig. 12** Scatter diagrams of H, W, and U (*left*), and of H/D, W/D, and U/D (*right*) for *Mullericeras spitiense* (Krafft, 1909). *Solid symbols* represent the pathologic specimen figured in Fig. 21-3. *D* diameter, *H* whorl height, *U* umbilical diameter, *W* whorl width

convex, with maximum width at inner third of whorl height. Shell smooth apart from very thin, slightly biconcave growth lines. Suture line not well enough preserved to be drawn, but visible parts are coherent with drawings from Krafft and Diener (1909): ceratitic, without adventitious saddle, and with a long auxiliary series.

*Measurements* See online resource and Fig. 12.

*Remarks* Our specimens are morphologically identical to those described by Krafft and Diener (1909). The most striking point is the presence of what they referred to as "a low broad keel […] running along the siphonal area". This feature is unique among Dienerian ammonoids. Note that one of our specimens (2030C, JJ17-08) has an open umbilicus, but this opening is asymmetrical (broader on the right side than on the left side), we therefore interpret this anomaly as pathological (see discussion below). Shigeta and Zakharov (2009), following the lead of Spath (1934) and Waterhouse (1996), placed this species in the genus *Clypeoceras*, in the family Clypeoceratidae. They apparently did so because they considered that since *Clypeoceras superbus* (Waagen, 1895) (the type specimen of the type species of *Clypeoceras*) has a sub-tabulate venter, they then should include in the same genus other species with a clearly tabulate venter. In a recent study, Brühwiler et al. (in press) illustrated additional specimens from the type locality (Ceratite Sandstones of Chiddru, Salt Range, Pakistan), which clearly have a narrowly rounded venter. They actually consider this genus to be monospecific. We herein follow their classification. The specimen figured by Shigeta and Zakharov (2009) differs from the type specimen by its narrower venter, which lacks the "low broad keel […] running along the siphonal area". Moreover, its suture line is closer to that of *Clypites*: it is projected forward and exhibits narrow lateral saddles, with the second lateral saddle bent toward the umbilicus. Therefore, we question its assignment to this species. The specimen figured by Waterhouse (1996) is not well enough preserved to permit a positive identification.

*Occurrence* Dienerian, ?*Proptychites* beds of Nevada, ?Primorye and *Ambites* beds of Spiti valley (India).

***Mullericeras fergusoni* sp. nov**. (Fig. 13)

*Holotype* Specimen NMMNH P-62180, Loc. JJ17-08 (Fig. 13).

*Type horizon and locality* Candelaria Hills (Nevada), Candelaria Formation, precise horizon unknown. Specimen found as float.

*Material* Two specimens from Jenks private collection.

*Etymology* Species named after H. G. Ferguson.

*Diagnosis* Very thin *Mullericeras* with occluded umbilicus.

*Description* Involute and very thin (W/D not possible to measure, estimated at about 15%) oxyconic shell with narrowly sub-tabulate venter and quite indistinct ventrolateral shoulders. Umbilicus occluded. Flanks slightly convex, with maximum width at inner third of whorl

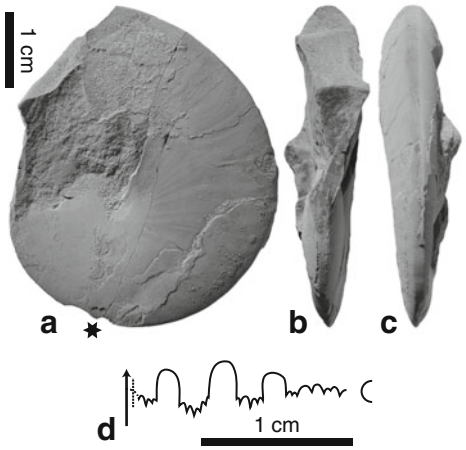


**Fig. 13** *Mullericeras fergusoni* nov. sp. NMMNH P-62180, loc. JJ17-08, holotype; **a** lateral view; **b** apertural view; **c** ventral view; **d** suture line at H = 14.8 mm, D ≈ 25 mm. *Asterisk* indicates last septum

height, converging slowly towards the venter. Shell smooth apart from very thin proverse growth lines. Suture line ceratitic, with three rounded lateral saddles and two flattened lateral lobes of equal width, no adventitious saddles, and a long auxiliary series with a slightly differentiated auxiliary lobe.

*Measurements* See online resource.

*Remarks* *M. fergusoni* differs from *M. spitiensis* only by its thinner whorl section. Since specimens with a whorl width intermediate to *M. spitiense* and *M. fergusoni* have not been found, we decided to erect an additional species. Its thin whorl section makes it appear quite similar to the genus *Pseudosageceras*, but it differs by its very simple ceratitic suture line, which lacks adventitious saddles. It also differs by its whorl section, which exhibits convex flanks rather than the sub-triangular whorl section characteristic of *Pseudosageceras* with maximum width situated just above the umbilicus.

*Occurrence* Dienerian, Candelaria Formation, Candelaria Hills, Nevada.

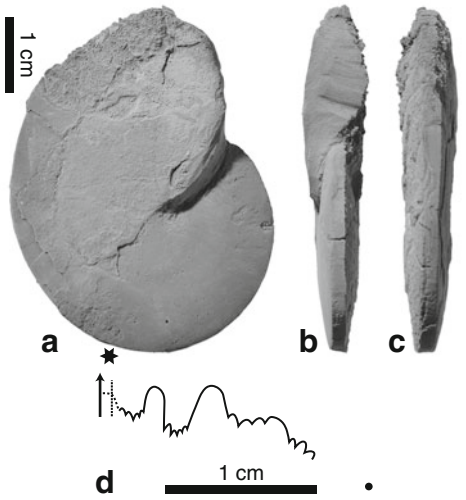


**Fig. 14** *Mullericeras* sp. indet. USNM542468; **a** lateral view; **b** apertural view; **c** ventral view; **d** suture line at H ≈ 16 mm, D ≈ 27 mm. *Asterisk* indicates last septum

***Mullericeras* sp. indet.** (Fig. 14)

*Material* One specimen from the USNM.

*Description* Involute and very thin oxyconic shell with tabulate venter and sharp ventrolateral shoulders. Umbilicus occluded. Flanks sub-parallel, with maximum width just above the umbilicus. Shell smooth, growth lines not visible. Suture line ceratitic, but quite peculiar, very proverse, with narrow, elongated first lateral lobe and saddle, the second lateral saddle being wider. The second lateral lobe is very wide and shallow, the third lateral saddle is also very shallow and is almost not differentiated from the quite long but poorly preserved auxiliary series.

*Measurements* See online resource.

*Remarks* This specimen, with its very peculiar suture line, is clearly different from all of the specimens described above. However, we do not know its precise stratigraphic origin. Its matrix is somewhat different with its reddish iron oxide colour and it is slightly distorted, two points which compel us to consider that it may have come from a different part of the Candelaria Formation. Since it is the only specimen available and considering its uncertainty in age, we prefer to keep it in open nomenclature.

*Occurrence* Dienerian, Candelaria Formation, precise locality and horizon unknown, Candelaria Hills, Nevada.

Family Proptychitidae Waagen, 1895
**Genus *Proptychites* Waagen, 1895**

*Type species* *Ceratites lawrencianus* de Koninck, 1863

***Proptychites haydeni* (Krafft, 1909)** (Figs. 15, 16, 17)

1909. *Koninckites haydeni* – Krafft, p. 68, pl. 17, figs. 1 (lectotype), 2, 3, 4, 5, 6.

*Material* Four specimens from the USNM, one from the PIMUZ, and two from the Jenks private collection.

*Description* Involute (U/D ≈ 10%), relatively thick (W/H ≈ 50%) platyconic shell with rounded venter and indistinct ventrolateral shoulders. Inner whorls very involute (U/D ≤ 10%), becoming slightly more evolute during ontogeny (U/D = 12% for the largest specimen). Narrow, deep umbilicus with high vertical wall and rounded indistinct shoulders. Flanks convex with maximum whorl width at inner third of whorl height. Shell smooth apart from very thin

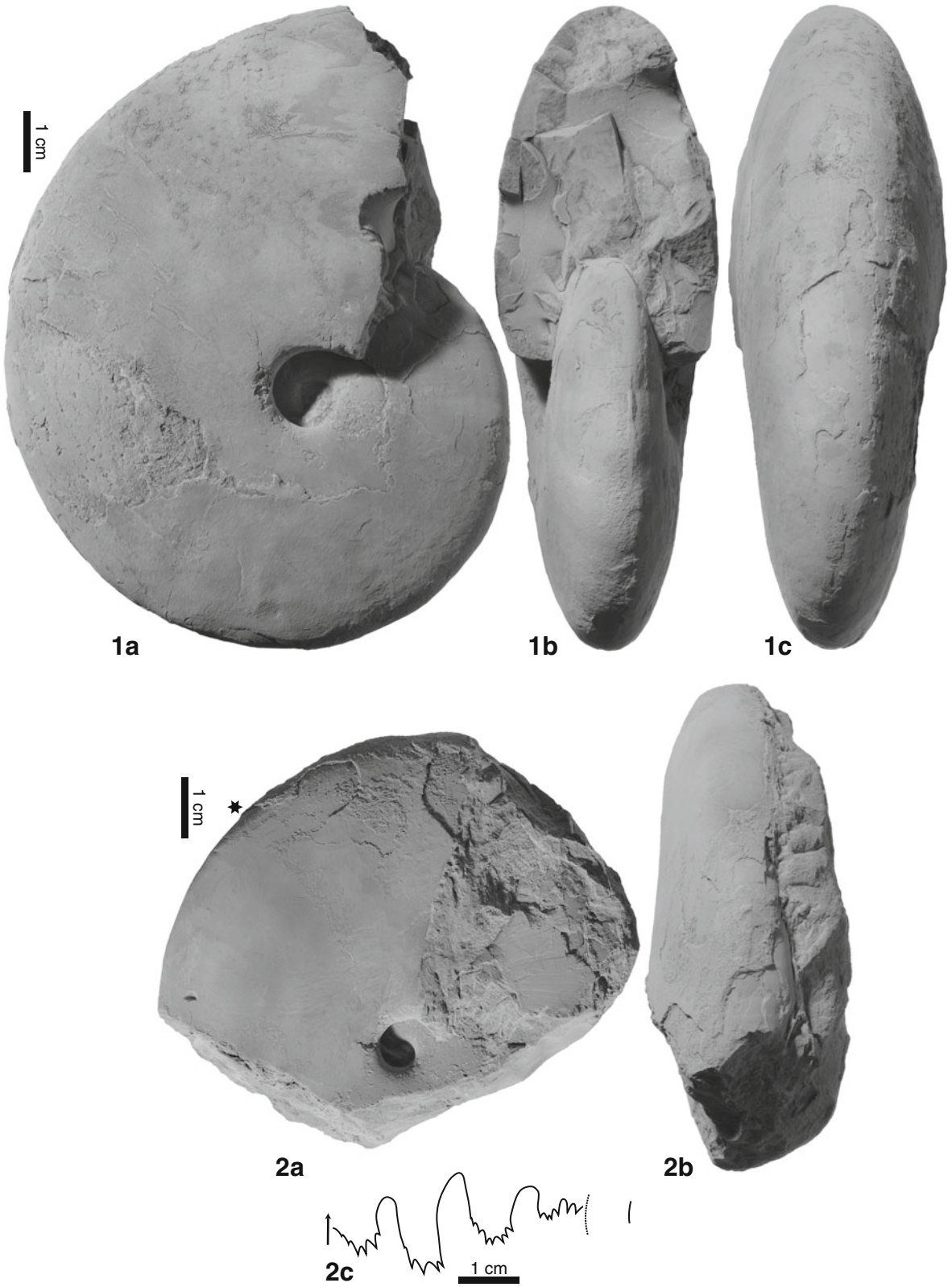


**Fig. 15** *Proptychites haydeni* (KRAFFT, 1909). **1** USNM542461; incomplete phragmocone; **1a** lateral view; **1b** apertural view; **1c** ventral view. **2** USNM542455; **2a** lateral view; **2b** ventral view; **2c** suture line at H = 40.4 mm. *Asterisk* indicates last septum where known

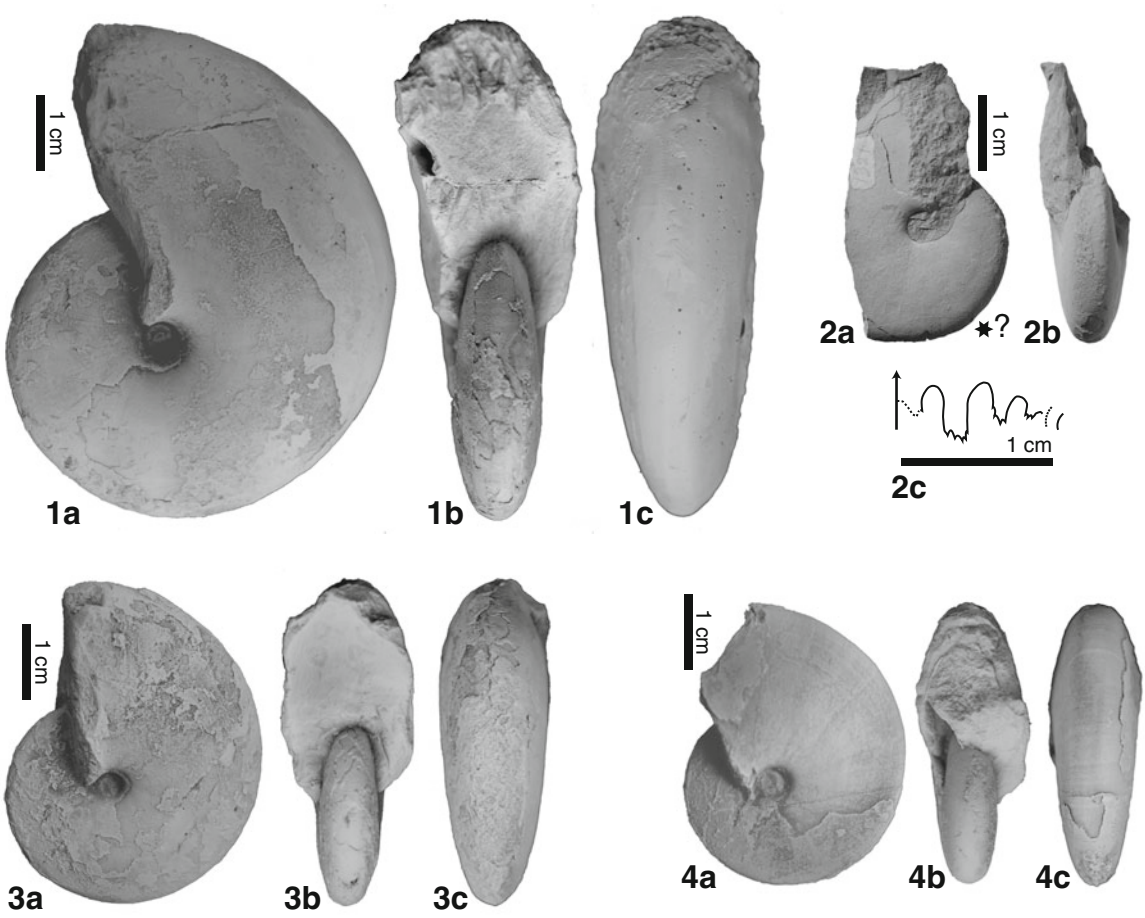


**Fig. 16** *Proptychites haydeni* (Krafft, 1909). **1** JJ2148C. **1a** lateral view; **1b** apertural view; **1c** ventral view. **2** USNM542459; **2a** lateral view; **2b** apertural view; **2c** suture line at H = 9.9 mm, D ≈ 15.5 mm. **3** JJ2149C; **3a** lateral view; **3b** apertural view; **3c** ventral view. **4** JJ2150C; **4a** lateral view; **4b** apertural view; **4c** ventral view. *Asterisk* with *question mark* indicates approximate position of last septum where known

radial growth lines and, on large specimens, weak spiral ribs at the end of the phragmocone. Suture line with elongated thin saddles slightly bent towards the umbilicus, and moderately wide, heavily indentated lobes; auxiliary series with an individualized auxiliary lobe, but not completely exposed.

*Measurements* See online resource and Fig. 17.

*Remarks* This species differs from *P. ammonoides* Waagen, 1895 and *P. alterammonoides* Krafft, 1909 by its thicker whorl section, and from *P. lawrencianus* (de Koninck, 1863) by its thinner whorl section. Originally ascribed to the genus *Koninckites*, this species clearly differs from the type species of this genus (*K. vetustus* Waagen 1895) by its high, vertical umbilical wall, its broadly rounded venter and its suture line with elongated saddles bent towards the umbilicus and heavily indentated lobes. These three characteristics are typical of the genus *Proptychites*.

*Occurrence* Lower Dienerian, *Proptychites* beds of Candelaria Hills (Nevada), *Ambites* beds of the Salt Range (Pakistan) and of Spiti valley (India).

***Proptychites pagei* sp. nov.** (Fig. 18)

*Types* Holotype: specimen USNM542464 (Fig. 18-1). Paratype: specimen USNM 542465 (Fig. 18-2).

*Type horizon and locality* Candelaria Hills (Nevada), Candelaria Formation, precise locality and horizon unknown.

*Material* Two specimens from the USNM.

*Etymology* Species named after Ben M. Page.

*Diagnosis* Compressed proptychitid with occluded umbilicus.

*Description* Relatively thin (W/H ≈ 50%) platyconic shell with rounded venter, indistinct ventrolateral shoulders and occluded umbilicus. Flanks convex with maximum whorl width at inner third of whorl height. Shell nearly smooth with very weak radial folds. Suture line typical of proptychitids with wide, heavily indentated lateral lobes, a well differentiated auxiliary lateral lobe, and thin, elongated lateral saddles, the second one slightly bent towards

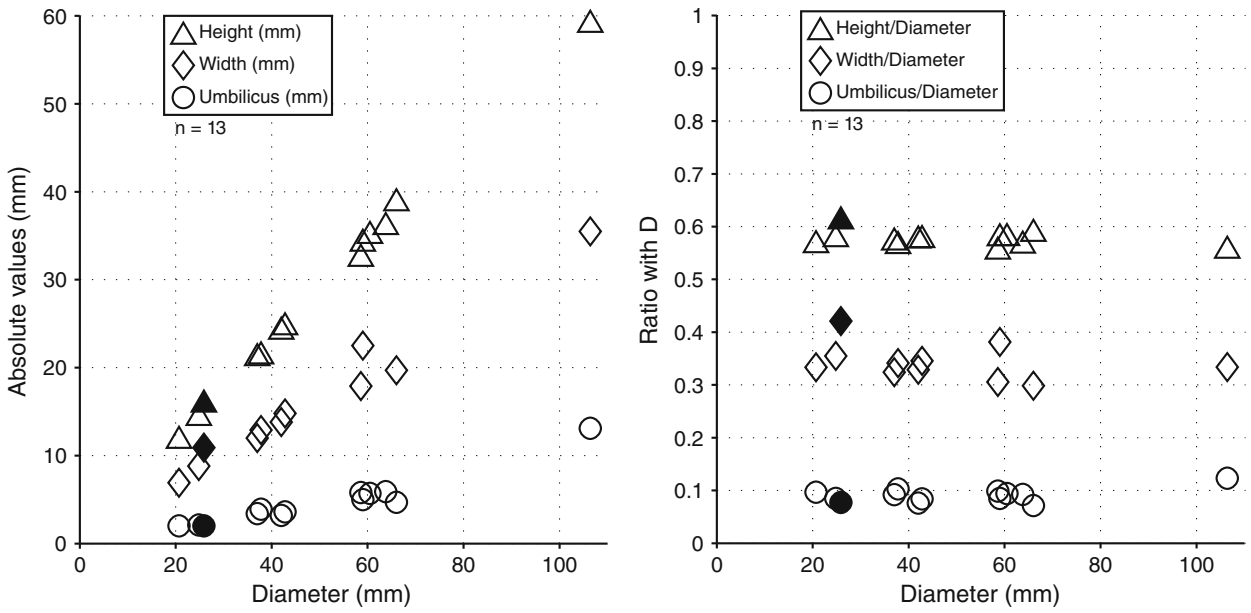


**Fig. 17** Scatter diagrams of H, W, and U (*left*), and of H/D, W/D, and U/D (*right*) for *Proptychites haydeni* (Krafft, 1909). *Solid symbols* represent the pathologic specimen figured in Fig. 21-2. *D* diameter, *H* whorl height, *U* umbilical diameter, *W* whorl width

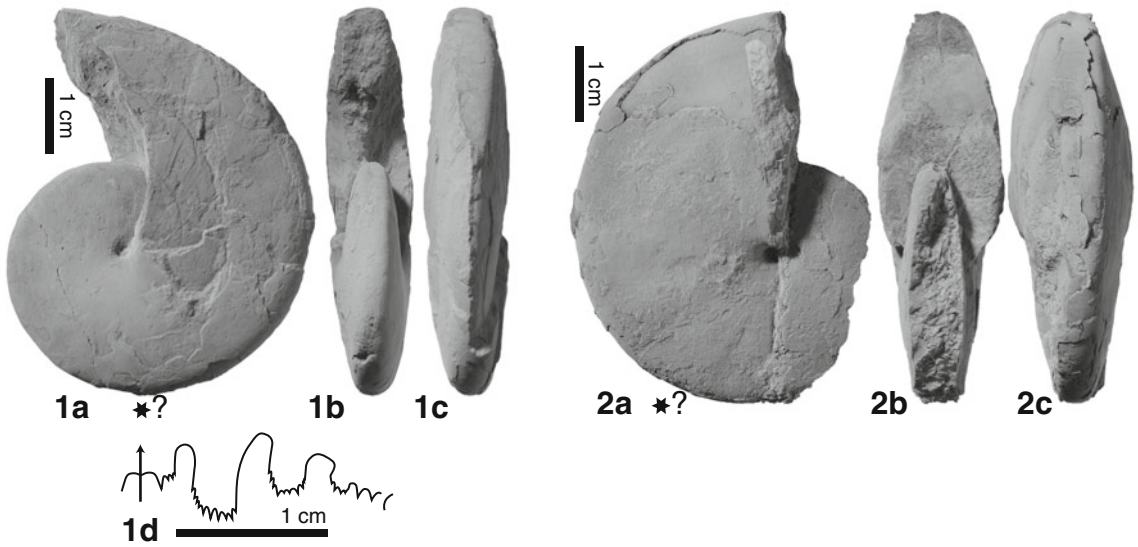


**Fig. 18** *Proptychites pagei* nov. sp. **1** USNM542464, holotype; **1a** lateral view; **1b** apertural view; **1c** ventral view; **1d** suture line at H = 14.6 mm, D ≈ 23.8 mm. **2** USNM542465, paratype; **2a** lateral view; **2b** apertural view; **2c** ventral view. *Asterisks* with *question mark* indicate approximate position of last septum

the umbilicus, the third one flattened. Auxiliary series short apart from the third individualized lateral lobe.

*Measurements* See online resource.

*Remarks* This species clearly differs from any previously described species of *Proptychites* in having a relatively thin whorl section and occluded umbilicus.

*Occurrence* Dienerian, Candelaria Formation, Candelaria Hills, Nevada.

### Genus *Vavilovites* Tozer, 1971

*Type species* *Paranorites sverdrupi* Tozer, 1963

***Vavilovites* sp. indet.** (Fig. 19)

*Material* One specimen from the PIMUZ, one specimen from the USNM.

*Description* Thick (W/H ≈ 65%) platyconic shell with narrow sub-tabulate, slightly arched venter delimited by distinct ventrolateral shoulders, and relatively broad

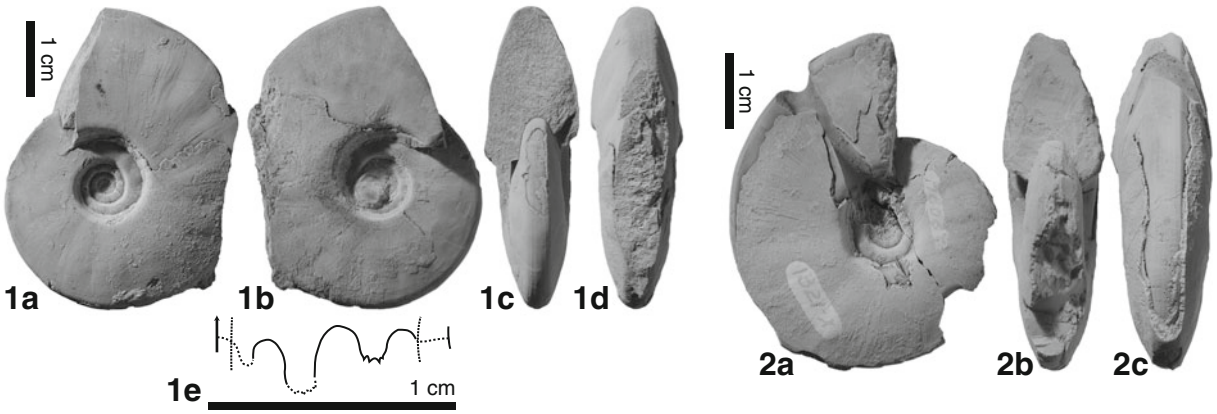


**Fig. 19** *Vavilovites* sp. indet. **1** PIMUZ28850; **1a** lateral view (*right*); **1b** lateral view (*left*, with an encrusting bivalve on the umbilicus); **1c** apertural view; **1d** ventral view **1e** suture line at H = 8.7 mm. **2** USNM542472; **2a** lateral view; **2b** apertural view; **2c** ventral view. Both specimens retain their body chamber, but last septum is not visible

umbilicus (U/D ≈ 25%). Maximum whorl thickness at top of umbilical shoulder, giving the whorl section a sub-triangular shape. High, sub-vertical and slightly concave umbilical wall with distinct, rounded shoulders. Ornamentation consists of weak, but large, sinuous and slightly proverse radial folds that parallel the thin growth lines, and fine strigation on the venter. Suture line ceratitic with three rounded lateral saddles, the second one being larger than the other two and slightly bent towards the umbilicus, and a short auxiliary series starting at the umbilical shoulder.

*Measurements* See online resource.

*Remarks* A Stanford University collection card, dated 1935, that accompanied this specimen identifies it as *Ophiceras* (*Lytophiceras*) *sakuntala*. However, its degree of involution, narrow sub-tabulate venter and the presence of strigation on the venter preclude the attribution of this specimen to Ophiceratidae. Its sub-triangular whorl section and sub-tabulate venter indicate strong affinities with the genus *Vavilovites* Tozer, 1971, especially to juveniles of *V. turgidus* Dagys and Ermakova, 1996, but its suture line differs by its short auxiliary series. However, it was only possible to draw the suture line at a small diameter (at the beginning of the last preserved whorl, corresponding to an estimated diameter of about 2 cm). We have elected to retain the generic assignment of *Vavilovites* for our specimens because the variability of this taxon's juvenile suture lines has never been studied and the suture lines illustrated by Tozer (1963, 1994) represent much larger specimens of the type species of *Vavilovites*. In addition, as these specimens are small compared to other previously described species, we prefer to keep them in open nomenclature. Additional material would be necessary to determine whether they represent a new species. Note that one specimen (USNM542472, Fig. 19-2) is slightly asymmetric, its umbilicus being deeper on the left side than on the right side which could be the consequence of a growth disturbance induced by epizoans, such as in vivo encrusting bivalves on the umbilicus as described below. The other specimen (PIMUZ28850, Fig. 19-1) had bivalves attached to both sides of the umbilicus. The bivalve on the right side was removed during preparation, but that on the left side is visible in Fig. 19-1b. In this case, the bivalves have not induced any obvious growth disturbance.

*Occurrence* Dienerian, Candelaria Formation, precise locality and horizon unknown, Candelaria Hills, Nevada.

Superfamily Sageceratacea Hyatt, 1884
Family Hedenstroemiidae Hyatt, 1884
**Genus *Parahedenstroemia* Spath, 1934**

*Type species* *Hedenstroemia acuta* Krafft, 1909

***Parahedenstroemia kiparisovae* Shigeta and Zakharov, 2009** (Fig. 20)

2009. *Parahedenstroemia kiparisovae* Shigeta and Zakharov, p. 137, fig. 128.

*Material* One specimen from the Jenks private collection.

*Description* Involute, thin (W/D = 27%) oxyconic shell with acute venter and occluded umbilicus. Flanks convex with maximum whorl width at about mid-flank. Shell smooth with fine, sinuous prorsiradiate growth lines. Suture line with a wide ventral lobe and a well individualized adventitious saddle. Lateral lobes relatively thin and deep with strong denticulation at their base. Auxiliary series not preserved.

*Measurements* See online resource.

*Remarks* This specimen appears to be identical in nearly every respect to the specimens considered by Shigeta and Zakharov (2009) to be juveniles. However, our specimen is

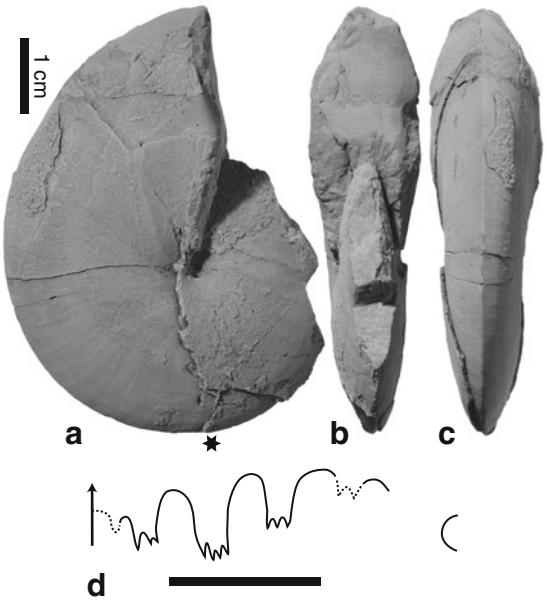


**Fig. 20** *Parahedenstroemia kiparisovae* Shigeta and Zakharov, 2009. JJ2164C, loc. JJ3-10; **a** lateral view; **b** apertural view; **c** ventral view; **d** suture line at H = 20.3 mm, D ≈ 36 mm. *Asterisk* indicates last septum

intermediate in size to their juveniles and their holotype, which is quite different with its thicker whorl section and less-acute venter. Its suture line is also very different, with strongly phylloid saddles and more denticulated lobes. However, we don't have sufficient material to determine if these differences are diagnostic or simply the result of intraspecific variability. Therefore, we prefer to keep our specimen in the same species.

*Occurrence* Dienerian, Candelaria Formation, Candelaria Hills, Nevada, and Zhitkov Formation, South Primorye, Russia.

## 4 Palaeopathology: growth disturbance induced by epizoan bivalves

Many of the ammonoid specimens from the Candelaria Formation exhibit an umbilicus that has been encrusted on both sides by bivalves. On some specimens, these bivalves have induced a distortion of the umbilical wall of the ultimate whorl, thus indicating they encrusted the ammonoids in vivo. Whether or not anoxic bottom waters played a role in this high frequency of epizoans attached to living ammonoids remains to be quantitatively assessed through comparisons with the next older and younger faunas. The resulting modification of the umbilical morphology can be substantial, and it can therefore lead to the mis-identification of some specimens. This feature can best be seen on the complete specimen of "*Koninckites*" cf. *kraffti* (Fig. 21-1). On the right side of this specimen, the body chamber overlaps the completely preserved bivalve, which encrusted the preceding whorl, thus modifying the width of the umbilicus and causing the umbilical wall to overhang. Only a piece of the attached valve is preserved on the specimen's left side, but it did not induce any obvious growth disturbance on that side.

A few ammonoid specimens have bivalves encrusting other parts of the shell, but since no details of the bivalve's shell interior are visible, their taxonomic affinity remains unknown. We cannot exclude the possibility that they may represent more than one species. Some specimens remotely resemble *Placunopsis*, which is well-known for encrusting Middle Triassic ammonoids from the Germanic Basin. However, some individuals exhibit an unusually high doming of the upper valve, a trait which has not been observed in *Placunopsis*.

No remains of bivalves are preserved on the other two illustrated specimens (Fig. 21-2, 21-3), but they both exhibit an umbilicus that has been modified, most likely by the same type of bivalves. Figure 21-2 illustrates a juvenile specimen of *Proptychites haydeni*, whose right side umbilicus is normal, but on its left side, its umbilicus exhibits a very high umbilical wall with a sharp shoulder protruding over the flank. Figure 21-3 shows a fully developed specimen of *Mullericeras spitiense*, which differs from other specimens by having a slightly open umbilicus (a crucial point which could lead to misidentification), but it is asymmetrical, with the umbilicus more open on the right side than on the left side.

## 5 Discussion and conclusions

Although there are no common species between this fauna and the Canadian faunas described by Tozer (1961, 1994), the presence of the genus *Ambites* in each fauna permits the correlation of the Candelaria fauna with the lower Dienerian *Proptychites candidus* Zone of mid-palaeolatitude British Columbia and Arctic Canada, which was already pointed out by Silberling and Tozer (1968). The genus *Ambites* is also very common in the Northern Indian Margin. It is well documented from the base of the Ceratite Marls in the Salt Range, Pakistan (Waagen 1895) and from the base of the "*Meekoceras* beds" in Spiti and Kashmir (Diener 1897; Krafft and Diener 1909). The Candelaria fauna correlates with the base of the "*Prionolobus rotundatus, Paranorites volutus*" Zone of Guex (1978), with the base of the *Proptychites lawrencianus* Zone of Mojsisovics et al. (1895) and with the base of the *Gyronites frequens* Zone of Krystyn et al. (2004, 2007). A general low-paleolatitude correlation scheme based on residual maximal associations (Guex, 1991) translating into a

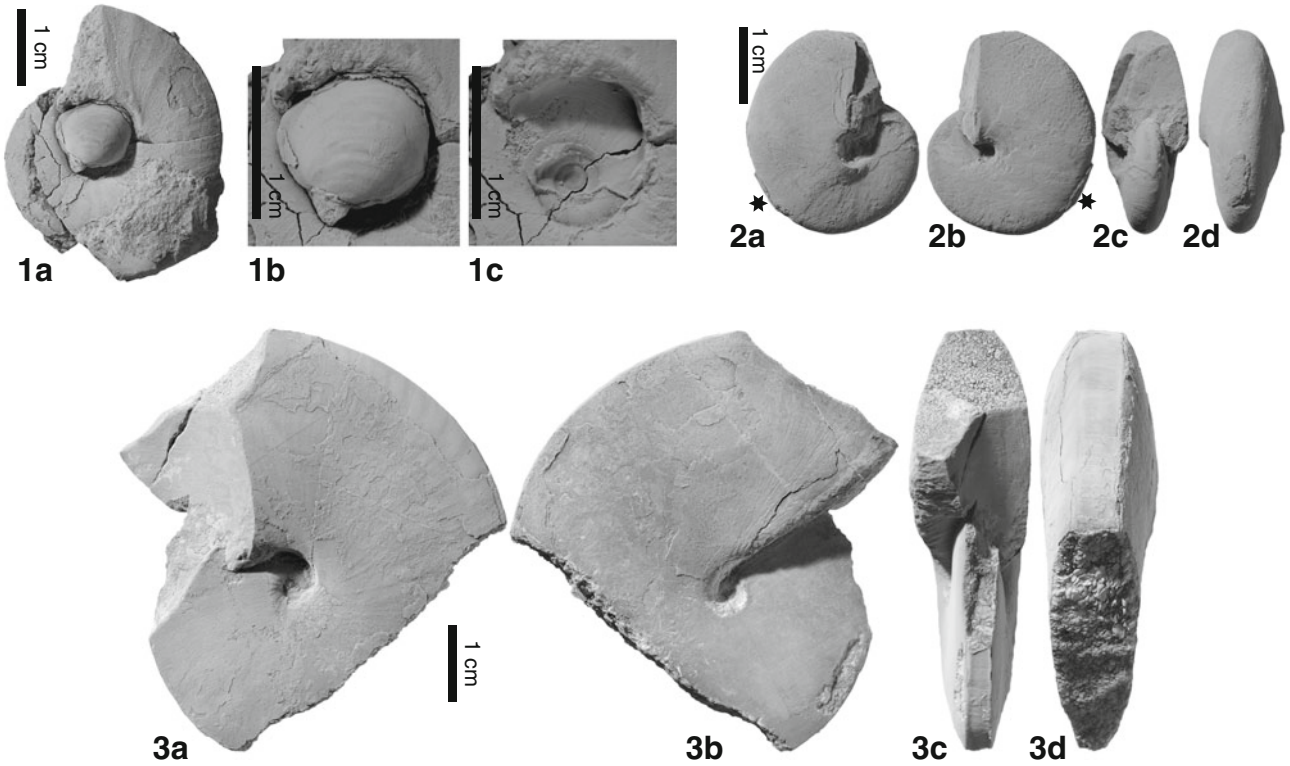


**Fig. 21** Specimens with growth disturbance induced by epizoans: **1** "*Koninckites*" aff. *kraffti* Spath, 1934, PIMUZ28597. Specimen with preserved bivalve attached to the umbilicus. **1a** Lateral view; **1b** close-up view of the umbilicus with the bivalve and **1c** without the bivalve. **2** *Proptychites haydeni* (Krafft, 1909), USNM542458; **2a** lateral view (*left*); **2b** lateral view (*right*); **2c** apertural view; **2d** ventral view. **3** *Mullericeras spitiense* (Krafft, 1909), JJ2030C, loc. JJ17-08; **3a** lateral view (*right*); **3b** lateral view (*left*); **3c** apertural view; **3d** ventral view. *Asterisks* indicate last septum where know

homogenous biochronological nomenclature must await the completion of the high-resolution analyses of the Dienerian faunal successions from Spiti and from the Salt Range (Ware et al., unpublished data).

Not surprisingly, the low-palaeolatitude Candelaria ammonoid fauna tends to more closely resemble the Tethyan faunas than the higher palaeolatitude Canadian faunas. This observation is supported by the presence of *Proptychites haydeni*, *Ambites lilangensis* and *Mullericeras spitiense*, which occur in the southern Tethys but not in the boreal realm. These similarities at least demonstrate that equatorial faunal exchanges occurred across the Panthalassa during Early Dienerian times. The differences between the low palaeolatitude faunas and those from the boreal realm document the onset of provincialism, which contrasts with the cosmopolitan Griesbachian ammonoid faunas. This Dienerian provincialism likely induced a weak latitudinal diversity gradient (Brayard et al. 2006).

The Early Dienerian fauna typically occurs within a 20–25 m thick anoxic episode in the Candelaria Formation. The fauna described here allows the precise dating of this discrete anoxic episode, which occurred in the equatorial region of the North American continental margin. Coeval anoxic or dysoxic events have also been reported from several localities in the Tethys: in the Salt Range (Pakistan; Hermann et al. 2011), in Spiti (NW India; Galfetti et al. 2007) and in Guangxi (South China, Galfetti et al. 2008), as well. This discrete anoxic episode clearly recorded in the north Gondwanian shelves can now be safely extended to the equatorial North American margin. If it apparently reflects a large scale oceanographic change within the low paleolatitude shelves, the bathymetric extension of this Early Dienerian anoxic event must be assessed in order to test the commonly invoked scenario of a rise of the oxygen minimum zone coupled with transgressions. How this Dienerian event is manifested into the higher palaeolatitude records also remains to be investigated. It nevertheless already appears that the "complex" image of a pervasive anoxia popping up here and there at many different times during most of the Early Triassic (e.g., Wignall and Twitchett 2002) does not withstand the accumulation of new evidence. The new general trend that is globally emerging is that of a discrete time distribution of a few events of oxygen deficiency.

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