



Biostratigraphy of Guadalupian (Middle Permian) ammonoids from the Olinalá Formation, southern Mexico

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Abstract: An ammonoid biostratigraphic analysis was conducted for the Permian Olinalá Formation, Guerrero state, southern Mexico. Bed-by-bed sampling yielded 113 ammonoids belonging to 14 different taxa. The biostratigraphic analysis allowed us to identify two ammonoid Zones: *Paracelmites elegans* and *Coahuiloceras* sp., and one subzone: *Pseudagathiceras spinosum*. According to the GSSP-defined boundaries, these biostratigraphic zones extend from the Roadian-Wordian to the lower Capitanian interval. To support the biostratigraphic analysis, several key taxa were reviewed from a taxonomic perspective. This taxonomic assessment validated the genus *Coahuiloceras*. A quantitative analysis based on morphometric ratios of the species of the genera *Timorites* and *Coahuiloceras* reveals a clear divergence between both groups. In addition, the biostratigraphic framework of the Olinalá succession is compared with previously published biostratigraphic data from Sonora, Coahuila and Texas, highlighting similarities and differences among these areas. The identified fauna in the Olinalá Formation is mainly associated with the American Realm.

Keywords:

- ammonoids;
- Middle Permian;
- Guadalupian;
- Olinalá Formation;
- biostratigraphy

Citation: ALANIS-PAVÓN A., GUERRERO-SUASTEGUI M., JUÁREZ-ARRIAGA E., TORRES-MARTÍNEZ M.A. & MORENO-BEDMAR J.A. (2026).- Biostratigraphy of Guadalupian (Middle Permian) ammonoids from the Olinalá Formation, southern Mexico.- *Carnets Geol.*, Madrid, vol. 26, no. 6, p. 125-150. DOI: [10.2110/carnets.2026.2606](https://doi.org/10.2110/carnets.2026.2606)

Résumé : Biostratigraphie des Ammonoïdés du Guadalupien (Permien moyen) de la Formation Olinalá (Mexique méridional).- Une analyse biostratigraphique fondée sur les Ammonoïdés a été réalisée pour la Formation Olinalá, permienne, dans l'État de Guerrero (Mexique méridional). Un échantillonnage banc par banc a permis de recueillir 113 spécimens appartenant à 14 taxons distincts. L'analyse biostratigraphique a permis d'identifier deux zones à Ammonoïdés, la Zone à *Paracelmites elegans* et celle à *Coahuiloceras* sp., ainsi qu'une sous-zone, celle à *Pseudagathiceras spinosum*. D'après les positions des limites d'étages définies par les GSSP, ces zones biostratigraphiques s'étendent de l'intervalle Roadien-Wordien jusqu'à la base du Capitanien. Afin d'étayer l'analyse biostratigraphique, plusieurs taxons clés ont été réexaminés du point de vue systématique. Cette réévaluation taxinomique a permis de valider le genre *Coahuiloceras*. Une analyse quantitative fondée sur les rapports

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morphométriques des espèces des genres *Timorites* et *Coahuiloceras* révèle une divergence nette entre les deux groupes. Par ailleurs, le cadre biostratigraphique de la succession à Olinalá est comparé aux données biostratigraphiques précédemment publiées pour le Sonora, le Coahuila et le Texas, mettant en évidence des similitudes et des différences entre ces régions. La faune identifiée dans la Formation Olinalá est principalement associée au domaine américain.

Mots-clefs :

- Ammonoidés ;
- Permien moyen ;
- Guadalupien ;
- Formation Olinalá ;
- biostratigraphie

1. Introduction

Through time, ammonoid biostratigraphy has been used as a reliable tool to establish broad and even global correlations among different geographic regions (LEONOVA, 2016). The first Paleozoic standard zonal scheme was based on ammonoids from the Permian Period, developed by BÖSE in 1919; but it was not until 1938 that MILLER proposed an ammonoid biozonation for North America. Since then, several authors have refined these schemes depending on the distinct geographic regions (e.g., RUZHENCEV, 1955; GLENISTER & FURNISH, 1961; JIN *et al.*, 1997; BOGOSLOVSKAYA *et al.*, 1999; LEONOVA, 2011, 2016). This standard zonation has proven to be particularly useful for the Middle Permian in Mexico (MILLER, 1944; FLORES de DIOS & BUITRÓN-SÁNCHEZ, 1982; VILLASEÑOR-MARTÍNEZ *et al.*, 1987; GONZÁLEZ-ARREOLA *et al.*, 1994; ALANIS-PAVÓN *et al.*, 2024). Consequently, the first approach to define a Mexican Permian ammonoid zonation was made by MILLER (1944) for the Paleozoic succession of the Las Delicias Formation, Coahuila, considered one of the most important regions with Permian cephalopods in Mexico. There, MILLER (1944) detected the occurrence of the *Perrinites* Zone (Kungurian-Roadian), followed by the *Waagenoceras* Zone (Wordian), and *Timorites* Zone (Capitanian).

Nevertheless, the Las Delicias Formation is not the only one where ammonoids occur in Mexico. Thus, we highlight the Olinalá Formation exposed in northeastern Guerrero state, southern Mexico (Fig. 1), whose Permian cephalopod fauna is abundant and diverse. Although the ammonoid faunas of this unit have been considered worthy of attention worldwide, studies on them are still scarce. In this context, only two works have focused on these Permian ammonoids. The former was by GONZÁLEZ-ARREOLA *et al.* (1994), who employed the invertebrates, without providing systematic descriptions, to propose the Guadalupian for the unit. Although the authors employed ammonoids to date the formation, the inaccurate identification of the taxa only allowed them to relate the age of the rocks to the Middle Permian. Later, ALANIS-PAVÓN *et al.* (2024) reviewed and updated

the taxonomy of the ammonoids previously reported by GONZÁLEZ-ARREOLA *et al.* (1994), rectifying the stratigraphic position of particular ammonite-bearing rocks. Nonetheless, due to the poor stratigraphic control of these ammonoids, it was not possible to establish more reliable biostratigraphic ranges. It should be noted that GONZÁLEZ-ARREOLA *et al.* (1994) provided an initial framework for understanding the Olinalá Formation; however, due to the limited availability of precise data, other methods were employed to establish the stratigraphic position of the Olinalá Formation. Thus, fusulinid biostratigraphy (VACHARD *et al.*, 1993, 1997) and numerical dating using detrital zircon U-Pb ages (JUÁREZ-ARRIAGA & MURILLO-MUÑETÓN, 2020) were used, but these studies only included some specific strata.

Consequently, despite the effort to establish reliable ranges for the formation using other proxies, previous investigations did not result in precise correlations, only considering it as a Guadalupian unit. Hence, this work aims to study in detail the stratigraphy of the ammonoids recently collected in four different sections of the Olinalá Formation, making an accurate biostratigraphic analysis of the whole unit. This contribution enriches and complements the work started by ALANIS-PAVÓN *et al.* (2024), who resumed the study of Permian ammonoids of the Olinalá Formation, obtaining reliable relative temporal successions based on ammonoid assemblages. The establishment of an accurate stratigraphic position for the Olinalá Formation will enable the creation of reliable regional ammonoid zonation, allowing for the proposal of correlations with Coahuila and Texas assemblages, as well as considering a potential application for other Middle Permian formations where ammonoids from the American Realm are found.



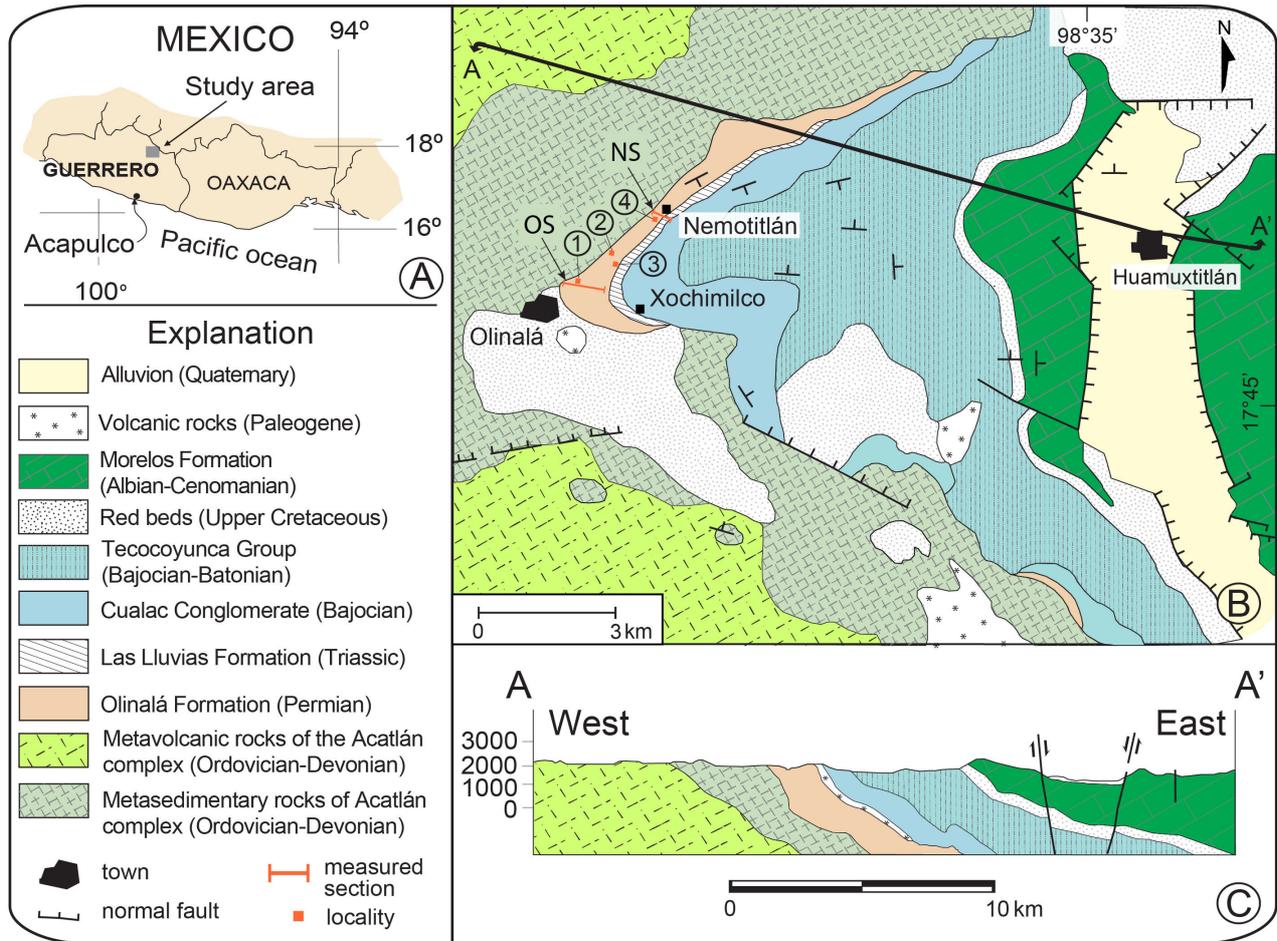


Figure 1: **A)** Geographic location of the study area, Guerrero state. **B)** Geologic map and studied sections. Geology adapted from CAMPA *et al.* (1998); JUARÉZ-ARRIAGA & MURILLO-MUÑETÓN (2020). **C)** Structural cross-section A-A' (modified from CAMPA *et al.*, 1998); location of cross-section A-A' shown in Fig. 1B. Sampling locations: A: Olinalá; B: Terrerillos; C: Barranca Coyomitla; D: Nemotitlán.

2. Geological setting

Study area

In this work, four stratigraphic sections from the Olinalá Formation were studied (Fig. 1.B). The first section, Olinalá, is located at 17°47'14.5"N 98°44'2.3"W, east of the town of Olinalá, and is ~690 m thick. The second section, Terrerillos is located at 17°47'43.7"N 98°43'20.2"W, with a thickness of ~220 m. In both sections, the stratigraphic record of the lower and Middle parts of the formation are observed. The third section, Barranca Coyomitla is located at 17°47'26.2"N 98°43'18.5"W, with a thickness of ~80 m. The fourth section, Nemotitlán is located at 17°48'13.2"N 98°42'43.3"W, 3 km northeast of the town of Olinalá, displaying a thickness of ~860 m. The last two sections represent the best outcrops with strata from the upper part of the formation.

Geology of the Olinalá Formation

Paleozoic outcrops of the Olinalá area were reported for the first time in 1982, when FLORES de DIOS and BUITRÓN-SÁNCHEZ described the marine-origin clastic and carbonate sedimentary rocks in the region, which were related to the Pennsylvanian-Permian. This range was determined based on the fossil content and the stratigraphic position

of the sedimentary succession relative to the Lower Paleozoic metamorphic rocks of the Acatlán complex (ORTEGA-GUTIÉRREZ *et al.*, 1999), which constitutes the basement of the region (Fig. 1.B-C). Given that FLORES de DIOS and BUITRÓN-SÁNCHEZ (1982) recognized the succession as a new unit made up of abundant limonitic concretions in fine-grained marine clastic rocks, they suggested calling these deposits the Olinalá Formation. Subsequently, CORONA-ESQUIVEL (1983, 1985) restricted the formation range to the Upper Permian based on identifying index fossils (*e.g.*, ammonoids and brachiopods). In addition, he suggested that the Olinalá Formation is overlain by the Las Lluvias Formation and the Cualac Conglomerate, both of Jurassic.

CORONA-ESQUIVEL (1983, 1985) subdivided the formation into seven lithologic units: 1) polymictic conglomerate of clasts, which are considered to be derived from the underlying the Acatlán complex; 2) dark shale with intercalation of fine-grained sandstone, containing numerous concretions; 3) basal conglomerate and medium-to coarse-grained sandstone; 4) dark shale with limonitic concretions; 5) limestone; 6) alternating sandstone and shales beds with calcareous concretions; and 7) thick, fine-grained sandstone overlain by shale with concretions. It is worth



mentioning that the Olinalá Formation has been mainly studied with an educational purpose for 30 years, through research projects and academic courses under the guidance of Martín GUERRERO-SUÁSTEGUI from the Universidad Autónoma de Guerrero. These projects have been focused on understanding and interpreting the depositional environments of the formation. After many years of hard work on the unit, the formation has been divided into four informal members: 1) conglomeratic member; 2) sandy member; 3) shaly and sandy shaly member; and 4) carbonate member (e.g., GUTIÉRREZ-QUINTO, 2002; MORÁN-CUEVAS, 2007; VEGA-HERNÁNDEZ, 2011). Facies distribution of the Olinalá Formation indicates a complex sedimentary history that records a gradual transition from a siliciclastic coastal environment to a shallow carbonate platform (JUÁREZ-ARRIAGA & MURILLO-MUÑETÓN, 2020). According to JUÁREZ-ARRIAGA and MURILLO-MUÑETÓN (2020), the transitional change from shallow to deep marine deposits and the absence of reefs, slope deposits, and turbidites indicate that the Olinalá Formation was deposited on a homoclinal ramp developed in warm waters and normal salinity conditions.

Marine fauna and age-calibration

The sedimentary succession comprising the Olinalá Formation contains fossiliferous strata with a high diversity of fauna, which have been reported in several studies and have contributed to establishing the formation's stratigraphic range. FLORES de DIOS and BUITRÓN-SÁNCHEZ (1982) identified the brachiopods, *Wellerella* sp., *Composita* sp., and *Paranorella* sp., as well as the ammonoids, *Agathiceras freschi*, *Stacheoceras rothi*, and *Waagenoceras* sp., allowing a Late Carboniferous to Permian age to be assigned to the fossiliferous strata. Likewise, the biota enabled the establishment of a potential correlation with outcrops from the Mexican states of Sonora, Hidalgo, and Chiapas. Later, CORONA-ESQUIVEL (1983, 1985) made a more precise age-calibration of this formation, assigning a Middle to Late Permian age based on the identification of ammonoids belonging to the genera, *Agathiceras*, *Paraceltites*, *Pseudogastriceras*, and *Stacheoceras*, collected in limonitic concretions. He also reported the presence of bivalves, gastropods, crinoids, and bryozoans. Moreover, he proposed a correlation with coeval formations in Coahuila and Chihuahua in Mexico. Subsequently, VACHARD *et al.* (1993, 2004) identified several microfossils, including algae and small foraminifera, as well as the index fusulinids, *Polydiexodina* (erroneously interpreted as *Parafusulina bosei* DUNBAR & SKINNER, 1937, by VACHARD *et al.*, 1993), *Rauserella erratica* DUNBAR, 1944, and *Codonofusiella extensa* SKINNER & WILDE, 1955. These findings allowed VACHARD *et al.* (1993) to suggest that the base of the formation corresponds to the Wordian Stage, whereas the upper stratigraphic part corresponds to the Capitanian. Based on the proposals of CORONA-ESQUIVEL (1983, 1985) and VACHARD *et al.* (1993), the Olinalá Formation was only considered a Gua-

dalupian unit. One year later, GONZÁLEZ-ARREOLA *et al.* (1994) reported a faunistic assemblage comprising the brachiopods, *Thamnusia depressa*, *Cancrinella rugosa*, *Hustedia* sp., and *Spiriferellina cristata*, the bivalve *Posidoniella* sp., the conulariid *Paraconularia* sp., the nautiloids *Bitaunioce- ras coahuilensis* MILLER, 1944, and the ammonoids *Paraceltites elegans* GIRTY, 1908, *Waagenoceras dieneri* BÖSE, 1919, *Pseudogastriceras roadense* (BÖSE, 1919), and *Stacheoceras toumanskyae* MILLER & FURNISH, 1940. The employment of this assemblage and the identification of typical ammonoid species from the Middle Permian enabled the authors to propose that the Olinalá Formation could be correlated with the Las Delicias Formation in Coahuila, which is mainly Guadalupian. Subsequently, GARIBAY-ROMERO *et al.* (1998) reported for the first time trilobite fragments in the formation, which material consisted of an incomplete pygidium that they assigned to the species *Anisopyge perannulata* (SHUMARD, 1958), which belongs to the Cisuralian-Guadalupian. In 2000, GARIBAY-ROMERO identified three ammonoid genera that had not been previously reported in the formation: *Doryceras* GEMMELLARO, 1887, *Propinacoceras* GEMMELLARO, 1887, and *Coahuiloceras* CANTÚ-CHAPA, 1997, all related to the Guadalupian Series. Likewise, TALAVERA-MENDOZA *et al.* (2005) provided the first zircon dates from the Olinalá Formation, obtained from a quartz-rich calcareous sandstone in the Middle part of the type section; however, their results indicated an Early Permian (Cisuralian) age. Later, GUERRERO-SÁNCHEZ and QUIROZ-BARROSO (2013) described bivalves from the shale facies, Middle part of the formation, confirming the previously proposed Middle Permian (Guadalupian) range. Based on certain bivalve species identified, the depositional environment was interpreted as a shallow, low-energy platform influenced by river sediment. Recently, JUÁREZ-ARRIAGA and MURILLO-MUÑETÓN (2020) determined the maximum depositional age from U-Pb detrital zircon analyses of sandstone samples (Nemo-2 and Nemo-4), obtained near the base of the Olinalá Formation (Fig. 11). The maximum depositional age for the oldest sandstone was established at 268±5 Ma (Roadian-Wordian), coinciding with the stratigraphic range established from ammonoids previously collected near the base of the unit. Finally, ALANIS-PAVÓN *et al.* (2024) conducted a review and update of the material reported by GONZÁLEZ-ARREOLA *et al.* (1994). In that work, the authors suggested that the ammonoid faunal composition from the base to the Middle part of the Olinalá Formation was from the Wordian. Moreover, ammonoid specimens were assigned to the American Realm, but these also indicated an affinity with coeval ammonoid assemblages from the Paleotethys Realm.





3. Material and methods

The ammonoid sampling for this study was carried out in the September 2023 fieldwork campaign. Cephalopods were collected by standard sampling in black shale facies, ensuring meticulous biostratigraphic control. Ammonoids are generally preserved as calcareous molds in siltstone concretions. Due to the wet weather in the Olinalá area, Guerrero, conservation varies between complete and heavily fragmented shells. The generic and supra-generic-level taxonomy follows the proposals by LEONOVA (2002) and FURNISH *et al.* (2009). Shell parameters were quantified using standard morphometric measurements, based on the approaches proposed by KORN (2010) and KLUG *et al.* (2015), with certain modifications adapted for this study. The measured parameters include: Dm (shell diameter), wh (whorl height), ww (whorl width), uw (umbilical width), ww/wh (whorl width index), ww/Dm (shell width index), uw/Dm (umbilical width index), and wh/Dm (whorl height index) (Table 1). All dimensions are given in millimeters. Quantitative data were analyzed through the statistical freeware PAST ver-

Table 1: Data parametrics of specimens of *Timorites striatus*, *T. gemmellaroi*, *T. uddeni* are taken from MILLER and FURNISH (1940) and FURNISH and GLENISTER (1970). Data of *T. schucherti* (IGM 14328) are from ALANIS-PAVÓN *et al.* (2025). Note: Asterisk indicates approximate measurements.

Species	Types	Dm	wh	ww	uw	wh/Dm	ww/Dm	uw/Dm	ww/wh
<i>Timorites striatus</i>	Delft 12754	21	6.93*	10.5	11.5	0.33	0.5	0.55	1.51
<i>Timorites striatus</i>	Iowa 12647	200	86*	90*	56*	0.43	0.45	0.28	1.04
<i>Timorites striatus</i>	Iowa 33572	135	64.8*	64.8*	36.4*	0.48	0.48	0.27	1
<i>Timorites striatus</i>	Iowa 31898	33	11.8	19.1*	14.8*	0.36	0.58	0.45	1.61
<i>Timorites gemmellaroi</i>	No data	162	64.8*	128.5	26	0.4	0.79	0.16	1.98
<i>Timorites schucherti</i>	YPM IP 16692	21.3	8.2	13.3	8.2	0.38	0.62	0.38	1.62
<i>Timorites schucherti</i>	YPM IP 16693	29.5	10.7	16.3	9.7	0.36	0.55	0.32	1.52
<i>Timorites schucherti</i>	YPM IP 16694	86.3	37.1	60.9	25.2	0.42	0.7	0.29	1.64
<i>Timorites schucherti</i>	YPM IP 19133	34.1	10.8	21.5	12.8	0.31	0.63	0.37	1.99
<i>Timorites schucherti</i>	IGM 14328	40.8	16.1	20.4*	12.2	0.39	0.5	0.29	1.26
<i>Timorites uddeni</i>	Iowa 1403	76	35.9*	40	12	0.47	0.53	0.16	1.11
<i>Coahuiloceras</i> sp.	IGM 14459	70.6	26.6	35.8	18.3*	0.37	0.5	0.25	1.34

4. Taxonomic notes

This section focuses on a brief discussion about biostratigraphically significance ammonoids with special attention on the taxa that were not previously taxonomically analyzed by ALANIS-PAVÓN *et al.* (2024). To support the taxonomic analysis, Appendix comprises a list of all studied ammonoids herein, including 120 specimens with the corresponding collection number, fieldwork sample name, and identifications, in addition to measurements of the more complete specimens.

The specimens assigned to *Paracelites elegans* (Fig. 2.I-K) are well preserved, even better than those previously illustrated from the Olinalá Formation (GONZÁLEZ-ARREOLA *et al.*, 1994, Figs. c-e; ALANIS-PAVÓN *et al.*, 2024, Figs. 6.11-13, 10). A very conspicuous characteristic of this genus is the evolute shell. This species exhibits a rather robust, sinuous rib ornamentation on the evolute internal whorls. The ribs have a low density and are strongest in the lower part of the flank. In the

last whorl, ribbing density abruptly increases, and the sinuous ribs become very gracile. These traits allowed us to associate the material studied with typical North American specimens of *P. elegans* (MILLER & FURNISH, 1940; KING *et al.*, 1944; SPINOSA *et al.*, 1975; ALANIS-PAVÓN *et al.*, 2025). *Adrianites* sp. is represented by a single specimen, which is poorly preserved and fragmented (Fig. 3.G), but its main ornamentation is still visible. The umbilicus is wide, evolute (uw/Dm=0.52, Table 2) with rounded shoulders. The phragmocone exhibits a distinct, reticulate pattern, formed by longitudinal lirae and transverse lines, characteristic of the genus *Adrianites* GEMMELLARO, 1887. It is worth mentioning that the recrystallized shell is broken in a part of the phragmocone that exposes the suture line (Fig. 3.G), which consists of a simple line with at least four tongue-shaped lateral lobes and three rounded saddles. This suture line clearly corresponds to the genus *Adrianites* (Fig. 4.A).



Table 2: Dimension (mm) and conch proportions of the most complete specimens. Ratios ww/wh: Whorl width index; ww/Dm: Shell width index; uw/Dm: Umbilical width index.

Species	Types	wh/Dm	ww/Dm	uw/Dm	ww/wh
<i>Paraceltites elegans</i>	IGM 14443	0.25	-	0.52	-
<i>Adrianites</i> sp.	IGM 14401	0.39	-	0.23	-
<i>Pseudagathiceras spinosum</i>	IGM 14402	0.36	0.41	0.15	1.13
<i>Mexioceras</i> sp.	IGM 14541	0.31	0.94	0.27	3.02

Pseudagathiceras spinosum MILLER, 1944 (Fig. 3.C-D), was initially described in the Las Delicias Formation, Coahuila, Mexico (KING *et al.*, 1944; ALANIS-PAVÓN *et al.*, 2025). Our specimens may represent a juvenile form, exhibiting an involute shell with visible internal whorl constrictions (ww/Dm= 0.41; uw/Dm= 0.15, Table 2). The ornamentation is characterized by longitudinal lirae, and the venter bears two rows of spines. The suture is not visible. This report represents the second documented occurrence of the species in a Mexican locality. Besides, it seems that the spine density is a variable character because the specimen from Coahuila (MILLER, 1944, p. 103, Pl. 29, figs. 1-5; ALANIS-PAVÓN *et al.*, 2025, p. 12, Fig. 7.4-7.7) has denser spines.

The material of *Propinacoceras* sp. (Fig. 3.A) comprises a single, very fragmented and small shell. Nonetheless, it is sufficiently well-preserved to reveal the ornamentation. The venter displays a pair of prominent, rounded node rows separated by a poorly developed median furrow. These characteristics allowed us to make a generic assignment, but due to the specimen preservation, obtaining a reliable specific identification was not possible.

A single fragmentary specimen of *Propinacoceras beyrichi* GEMMELLARO, 1887 (Fig. 3.B), shows the flat flanks and part of the venter. The lateral view displays a very involute shell with a venter and a row of rounded nodes. The suture consists of a bifid first-lateral lobe, while the second lateral lobe is more elongated than the first. The lateral lobes are small and bifid, and the saddles are rounded and slightly elongated (Fig. 4.B). This taxon is described and illustrated for the first time from the Guadalupian of Mexico. The traits mentioned correspond with those recorded for the type species of the genus *Propinacoceras*. This taxon was described initially in the Wordian of Sicily, Italy. Later, it was reported in other Wordian localities, including British Columbia (NASSICHUK *et al.*, 1977) and South China (ZHOU, 2017).

The species, *Waagenoceras* cf. *W. girtyi* MILLER & FURNISH, 1940 (Fig. 2.H), is represented by two fragmentary specimens. The inner molds show fine transverse lines. An incomplete suture is also visible, highly arcuate, with at least seven lateral lobes. The lobes are multiply digitated, and the saddles are mushroom-shaped (Fig. 4.E). Unfortunately, no complete specimens were found; however, we were able to compare the suture of our

samples with those illustrated by MILLER (1944, p. 113, Fig. 22C), NASSICHUK (1977, p. 582, Fig. 17) and ALANIS-PAVÓN *et al.*, (2025, p. 21, Fig. 13.5, 17.3, 17.4, 18.1-18.4), concluding that the Mexican specimens are associated with *W. girtyi*. Due to the preservation, it was not possible to make a more precise assignment. This species was previously described in the Wordian-Capitanian of Coahuila state and British Columbia.

Mexioceras sp. (Fig. 2.C-D) has a strongly globular shell with a noticeably wide umbilicus (ww/Dm= 0.94; uw/Dm=0.27, Table 2). The whorl section is depressed, with a broad, rounded venter and low, strongly arched flanks. The ornamentation consists of fine transverse lirae, visible in the preserved areas of the recrystallized shell. Notably, some shell layers can be observed in some of these recrystallized areas of the shell. The origin of these layers is difficult to interpret, but at least three possible explanations can be considered: they may result from taphonomic processes, diagenesis, or perhaps a preservation of the original shell layering. The combination of a globular shell and fine transverse lirae allows identifying the first occurrence of the genus *Mexioceras* RUZHENCEV, 1955, in the Olinalá Formation. This genus has been reported in the Guadalupian of the Delaware Basin (South Wells, Hegler, and Pinery Limestone members) in Texas, USA (MILLER & FURNISH, 1940), as well as in Wordian-Capitanian strata from Coahuila, Mexico (KING *et al.*, 1944; ALANIS-PAVÓN *et al.*, 2025).

Metacrimites sp. is represented by a poorly preserved specimen (Fig. 3.K), in which part of the external suture line is still visible. The shell is involute, with a small, open umbilicus. The whorl section is depressed, and the venter is rounded but slightly flattened ventrolaterally. The lateral lobes are tongue-shaped and consist of at least five lobes that gradually decrease in size toward the umbilicus. All saddles are rounded. Based on its diagnostic features, this specimen could be a representative of the Superfamily Adrianitinae. It should be noted that CANTÚ-CHAPA (1997) established the new genus *Millerites*, with a stratigraphic range that began in the Middle Permian, distinguishing it from the previously used genus, *Adrianites*. Later, FURNISH *et al.* (2009) regarded the genus *Millerites* as a synonym of *Neocrimites*. However, LEONOVA and BOIKO (2015) recognized a lack of revision in RUZHENCEV's (1950) work on the Superfamily Adrianitinae, highlighting that the diagnostic features were more closely related to *Metacrimites*. Therefore, we assign the taxon analyzed herein to the genus *Metacrimites*.

► **Figure 2: A)** *Stacheoceras* sp., lateral view, IGM 14497. **B)** *Stacheoceras* sp., lateral view, IGM 14489. **C-D)** *Mexioceras* sp., lateral and ventral views, IGM 14451. **E-G)** *Waagenoceras* cf. *W. dieneri* (BÖSE, 1919), lateral and ventral views, IGM 14450, IGM 14481, IGM 14449. **H)** *Waagenoceras* cf. *W. girtyi* (BÖSE, 1919), lateral view, IGM 14471. **I-K)** *Paraceltites elegans* GIRTY, 1908, lateral views, IGM 14443, IGM 14409, IGM 14408. Scale bar = 1 cm.



A



B



C



D



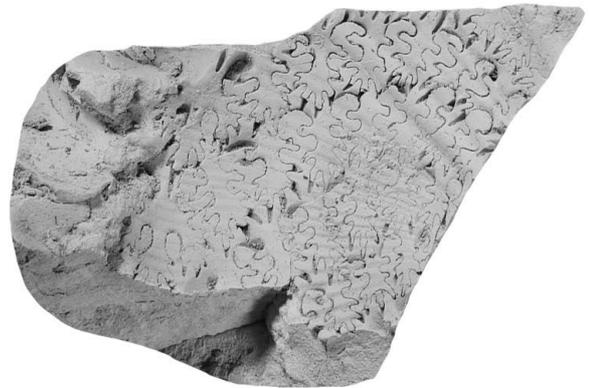
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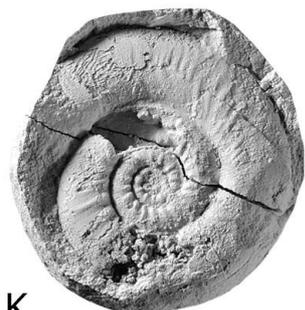
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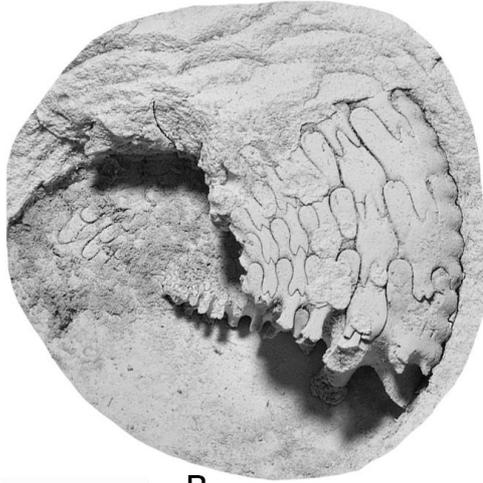
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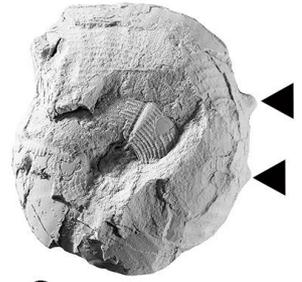
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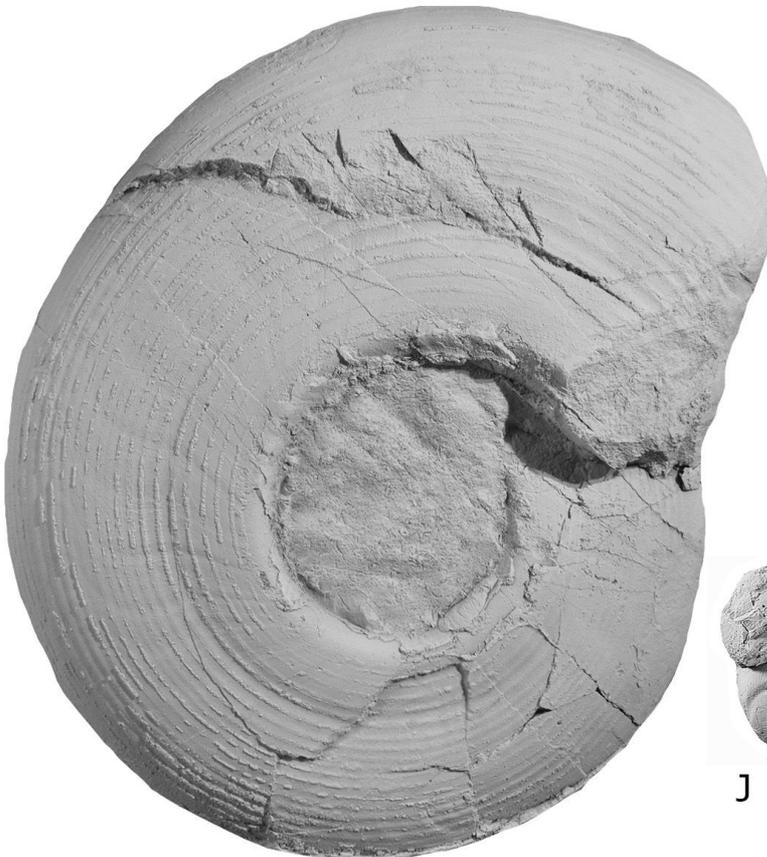
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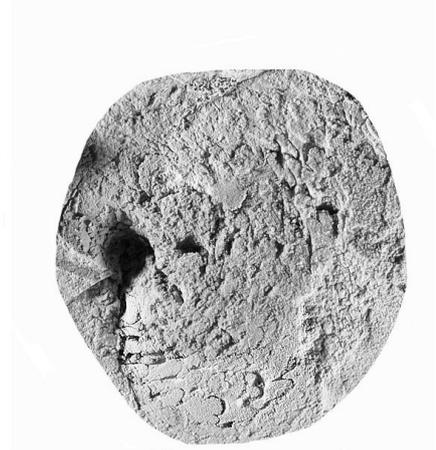
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◀ **Figure 3:** **A)** *Propinacoceras* sp., ventral view, IGM 14439. **B)** *Propinacoceras beyrichi* GEMELLARO, 1887, lateral view, IGM 14468. **C-D)** *Pseudagathiceras spinosum* MILLER, 1944, lateral and ventral views, IGM 14402. **E-F)** *Agathiceras* sp., lateral views, IGM 14426, IGM 14427. **G)** *Adrianites* sp., lateral view, IGM 14401. **H)** *Epithalassoceras* sp., lateral view, IGM 14440. **I-J)** *Roadoceras roadense* (BÖSE, 1919), lateral views, IGM 14404, IGM 14405. **K)** *Metacrimites* sp., lateral view, IGM 14441. Black triangles emphasize two rows of spines at the beginning of the body chamber. Scale bar = 1 cm.

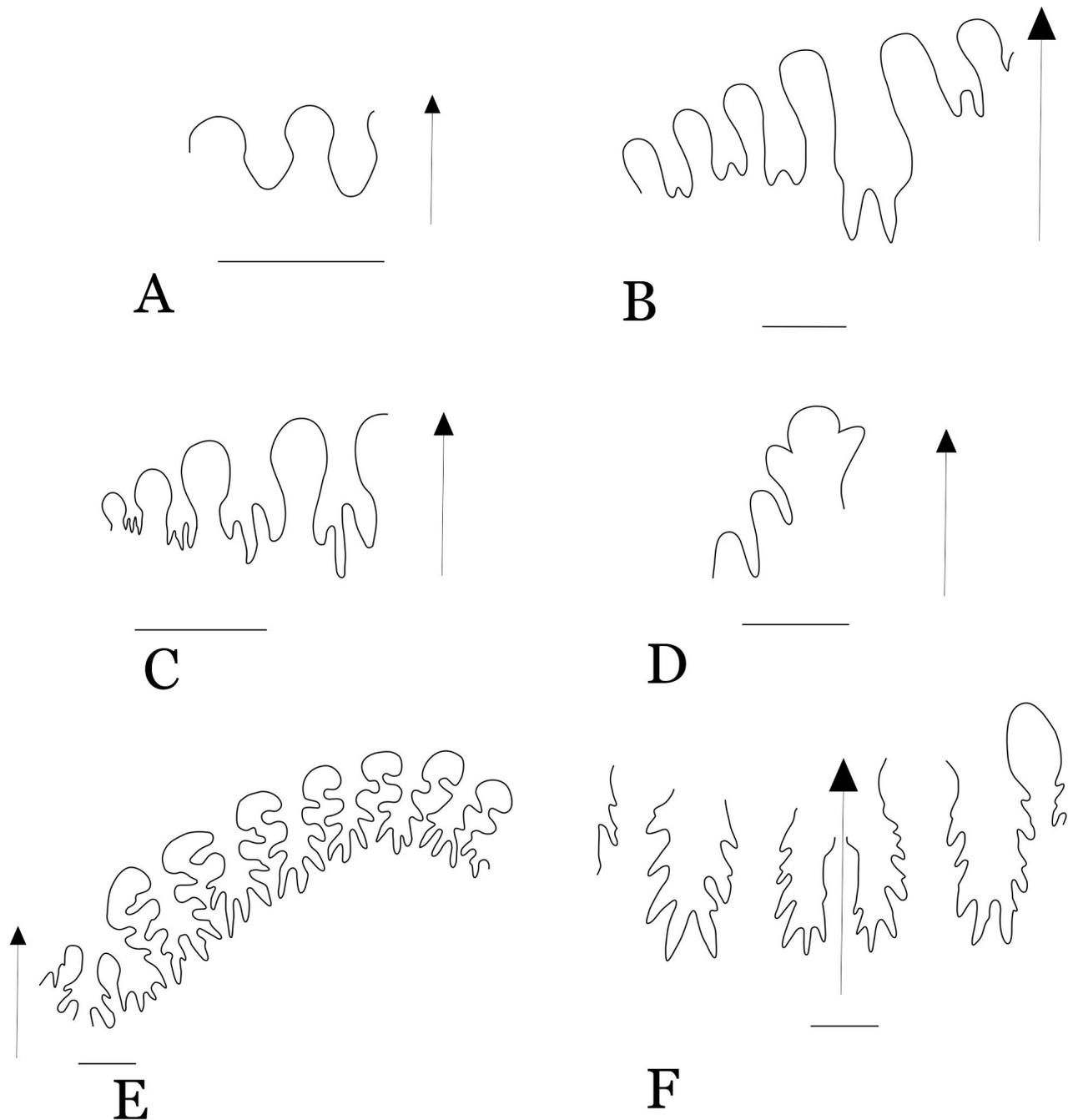


Figure 4: External sutures: **A)** *Adrianites* sp., based on sample IGM 14401. **B)** *Propinacoceras beyrichi*, based on sample IGM 14468. **C)** *Stacheoceras* sp., based on sample IGM 14489. **D)** *Epithalassoceras* sp., based on sample IGM 14440. **E)** *Waagenoceras* cf. *W. girtyi* based on sample IGM 14471. **F)** *Waagenoceras* cf. *W. dieneri*, based on sample IGM 14449. Scale bar = 5 mm.

Coahuiloceras sp. (Fig. 5.E-F) is reported for the first time in the Olinalá Formation. This genus was proposed by CANTÚ-CHAPA (1997, p. 82, Fig. 46.E), who assigned it to the Subfamily Changhsingoceratinae. In our opinion, the three studied specimens, herein, which include one well preserved and complete specimen (Fig. 6; stl file download at https://carnetsgeol.net/cg/26/06/CG2606_

Fig_06.stl), must be only classified in the Family Cyclolobidae. The thick discoidal shell ($wh/Dm=0.37$, $uw/Dm=0.25$), with arcuate transverse striae and prominent sinuous constrictions are diagnostic features of the Family Cyclolobidae. It is worth noting that MILLER (1944) illustrated a similar specimen (Fig. 5.C-D), but it was identified as *Timorites schucherti* (Fig. 5.A-B). In 2019, one of

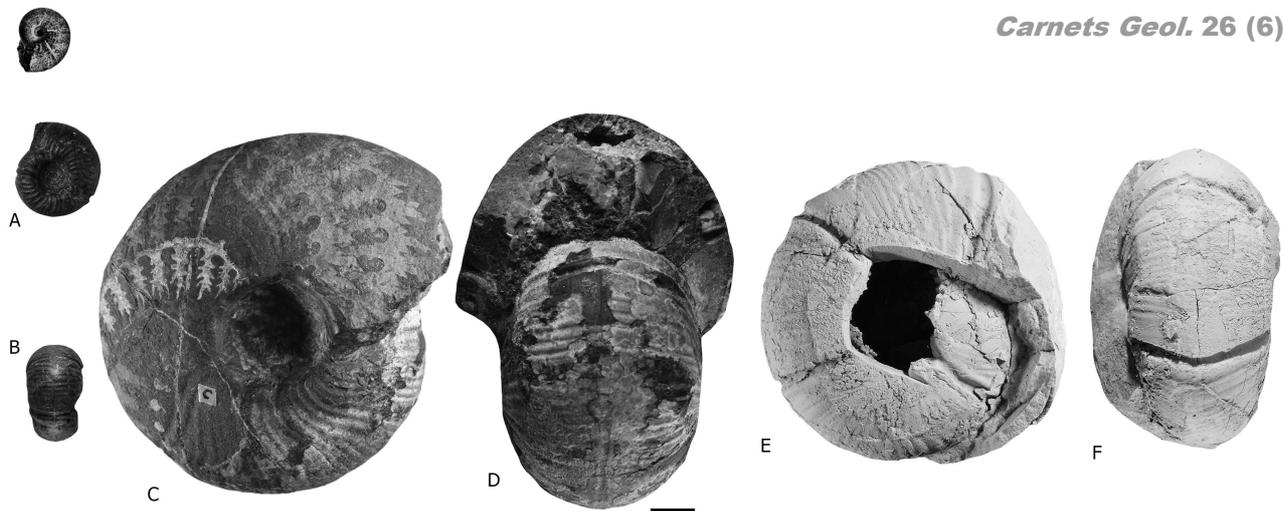


Figure 5: **A-D)** *Timorites schucherti*, lateral, apertural and ventral views, YPM IP 16692 and 16694. **E-F)** *Coahuiloceras* sp., lateral and ventral views, IGM 14459. Scale bar = 1 cm.

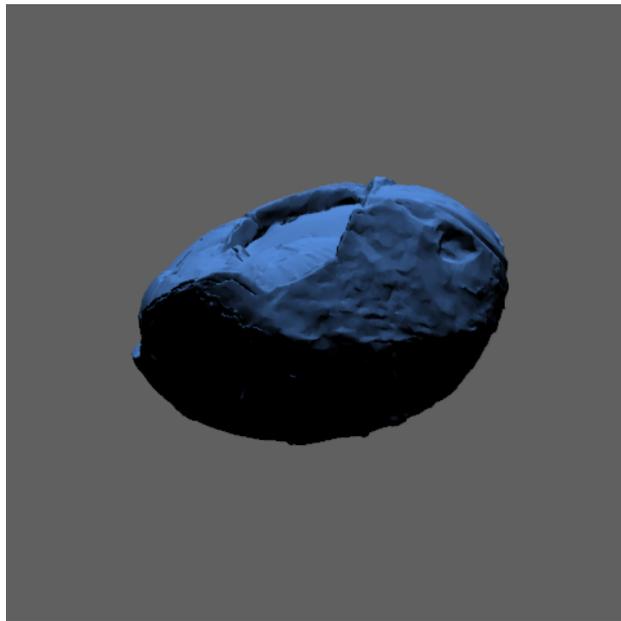


Figure 6: *Coahuiloceras* sp., 3D model, based on sample IGM 14459 (stl file download at https://carnetsgeol.net/cg/26/06/CG2606_Fig_06.stl).

us re-examined and re-photographed (A.A.P.) the ammonoid collection originally sampled by KING (KING *et al.*, 1944) and later described by MILLER (1944). Therefore, we believe that this reconsideration is fully supported due to the direct comparison with MILLER's specimens. As shown in Figure 5.C-F, the specimens illustrated, herein, must be reassigned to the genus *Coahuiloceras*. Regarding species identification, further data are necessary to know the specific content of this genus.

Therefore, to support the qualitative morphological difference between *Timorites schucherti* and *Coahuiloceras* sp., we consider a quantitative morphological analysis based on the following morphometric ratios to be significant: wh/Dm, ww/Dm, uw/Dm, and ww/wh (Table 1). The first two Principal Components Analysis (PCA), based on the whorl ratios width/whorl height (ww/wh) and umbilical width/diameter (uw/Dm), explain 98.72% of the total variance (PC1 = 87.72%; PC2 = 11.00%; Fig. 7). The PCA indicates that the variable with the most significant influence in

distinguishing the morphology of *Coahuiloceras* sp. and *Timorites schucherti* is the ww/wh ratio, which may play a key role in their differentiation. To support previous results, we conducted a Linear Discriminant Analysis (LDA), which revealed a clear morphological difference among the analyzed species, particularly between *Coahuiloceras* sp. and most *Timorites* species (Fig. 8). The first discriminant axis (LD1) explains 91.24% of the total variance among groups. In comparison, LD2 and LD3 account for 4.92% and 3.80%, respectively. This distribution suggests that most morphological differences among species can be effectively summarized along a single dimension, supporting the visual separation observed between groups in the morphospace. *Timorites striatus* forms a well-defined cluster, indicating a distinctive morphology within the group. In contrast, *Timorites schucherti* occupies an intermediate position within the morphospace, suggesting that it shares morphological characteristics with other species of the genus and could represent a transitional form of the genus. *Coahuiloceras* sp. is markedly distinct from the other specimens studied, reinforcing its assignment as a separate genus. This suggests a morphology clearly differentiated from *Timorites* forms. Overall, the results of the discriminant analysis not only support the morphological validity of *Coahuiloceras* as a distinct genus but also reveal considerable heterogeneity within *Timorites*. This pattern may have important taxonomic implications, particularly regarding species delimitation within the group.

5. Biostratigraphic analysis

Ammonoid Zonation of the Olinalá Formation. The Guadalupian ammonoid assemblages of the Olinalá Formation are mainly composed of previously described taxa from the American Realm. Therefore, in this study, we considered the number of samples per species collected bed by bed important, which enhanced the biostratigraphic analysis. The use of interval biozones was preferred because the ammonoid record of the Olinalá Formation allows reliable recognition of the lowest and highest stratigraphic occurrences of key taxa (Fig. 9). This approach, consistent with the definition of MURPHY (1999) and BARRAGÁN *et al.* (2010),

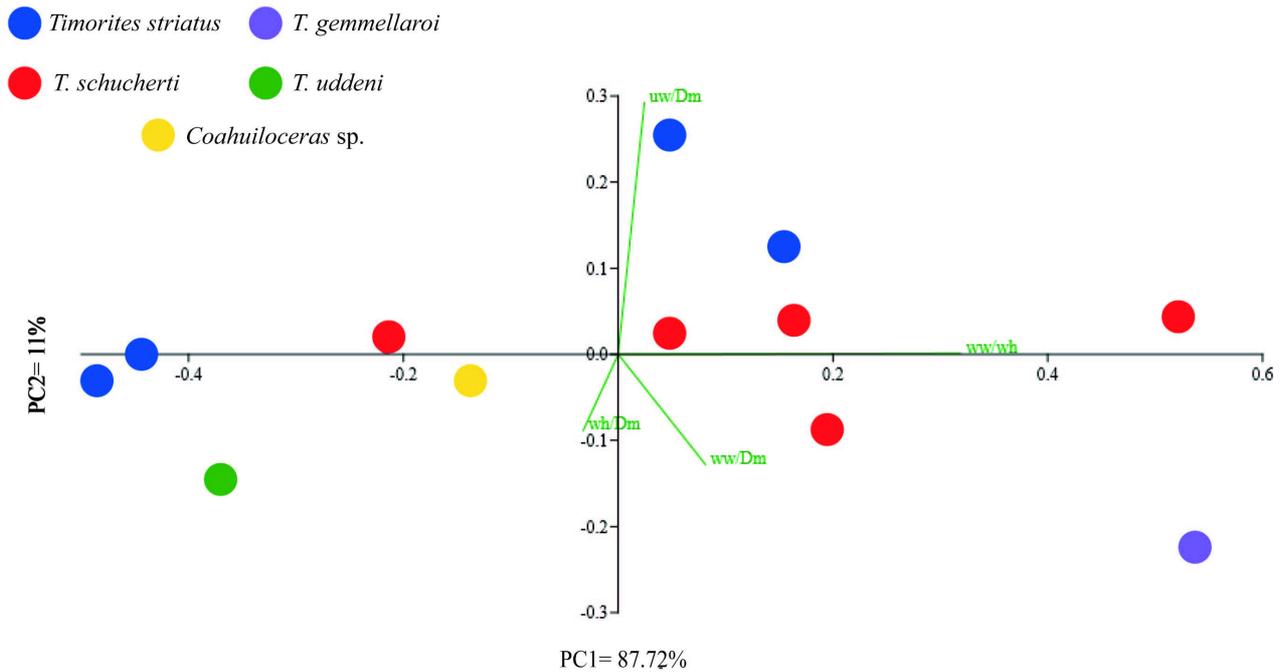


Figure 7: The plot dispersion from the Principal Component Analysis (PCA) illustrates morphological differentiation between *Coahuiloceras* sp. and most *Timorites* species in the analyzed material. Based on the whorl width/whorl height (ww/wh) and umbilical width/diameter (uw/Dm) ratios, the analysis explains 98.72% of the total variance.

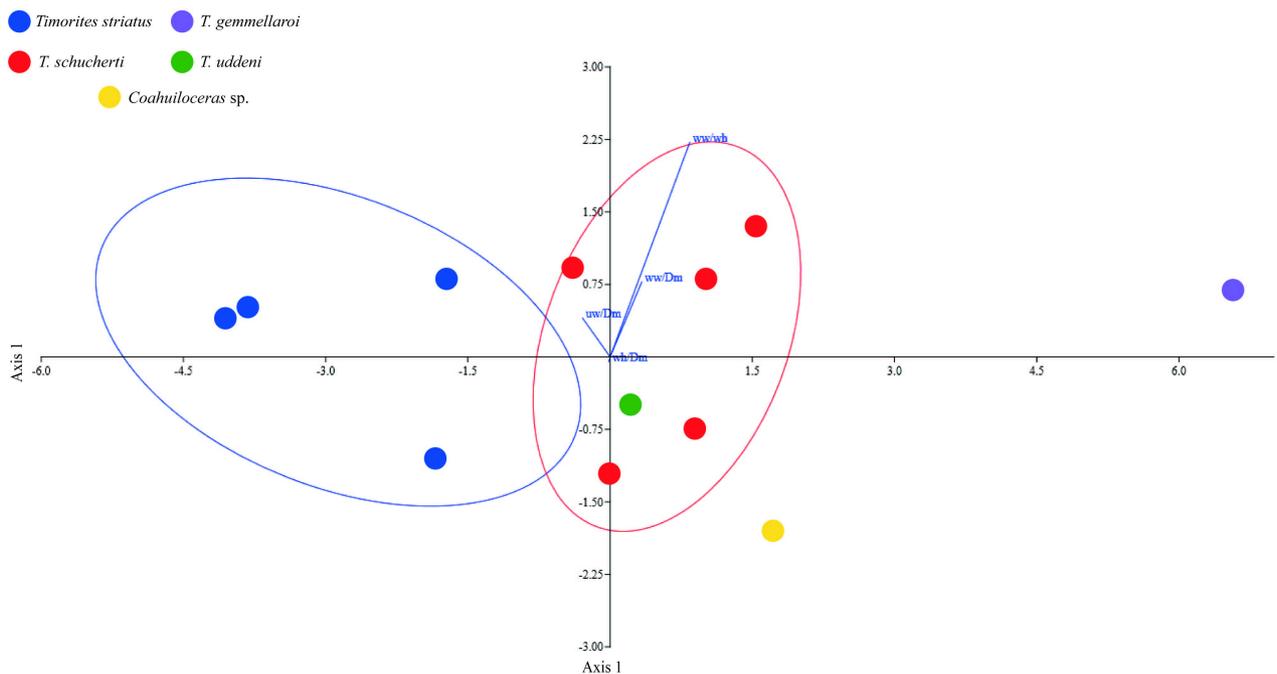


Figure 8: The plot dispersion from the Linear Discriminant Analysis (LDA) illustrates morphological differentiation between *Coahuiloceras* sp. and most *Timorites* species in the analyzed material. The first discriminant axis (LD1) accounts for 91.24% of the total variance among groups, while LD2 and LD3 explain 4.92% and 3.80%, respectively.

provides objective criteria to establish zonal boundaries. According to previous studies and the biostratigraphic data obtained in this work, we propose the following markers for the Olinalá Formation:

- Lithostratigraphic marker 1: JUÁREZ-ARRIAGA and MURILLO-MUÑETÓN (2020), based on U-Pb analyses of detrital zircon grains, providing a maximum depositional age of 268 ± 5 Ma for the base of the sedimentary succession, where-

with the geochronological range may extend from the Roadian to the Capitanian;

- Lithostratigraphic marker 2: Fusulinid biostratigraphy of carbonate facies, because the occurrence of *Polydiexodina*, *Rauserella erratica*, and *Codonofusiella extensa* in rudstone limestone indicates a minimum age of early to middle Capitanian for the fossil-bearing strata (VACHARD *et al.*, 1993, 1997, 2004);



- Lithostratigraphic marker 3: Field observations indicating a transition from carbonate to terrigenous facies (black shale with concretions) (Fig. 9). Accordingly, we propose that the top of the carbonate interval denotes the base of marker 3, further supported by ammonoid assemblages that allow reliable correlation. These assemblages were grouped, in ascending order, into two zones and one sub-zone, as follows.

Ammonoid zones

Paraceltites elegans Zone. The index species is one of the most common ammonoids in the lower and middle parts of the Olinalá Formation (Te2, Nemo2), below the shoal marine platform limestone. The assemblage includes eight taxa: *Paraceltites elegans*, *Propinacoceras* sp., *Pseudagathiceras spinosum*, *Agathiceras* sp. (Fig. 3.E-F), *Epithalassoceras* sp. (Figs. 3.H, 4.D), *Roadoceras roadense* (BÖSE, 1919) (Fig. 3.I-J), *Metacrimites* sp. (Fig. 3.K), and *Adrianites* sp.

Discussion: The specimens of *Paraceltites elegans*, were collected in black shale from the middle part of the Terrerillos and Nemotitlán sections (Fig. 9.2-4). The oldest known representatives of the Order Ceratitida, Family Paraceltitidae are attributable to the genus *Paraceltites*, whose first appearance (FA) occurred during the Roadian (LEONOVA, 2002). *Paraceltites elegans* has been recorded in several Middle Permian units of West Texas, with reported occurrences spanning the Capitanian. It occurs in the Road Canyon Formation and the Williams Ranch Member of the Cutoff Formation (Roadian), as well as in the Getaway Member (Lower Cherry Canyon Formation) and the South Wells Limestone (Middle Cherry Canyon Formation) from the Roadian-Wordian. Likewise, it has been found in the lower three members of the Bell Canyon Formation (Hegler, Pinery, and Rader Limestone members), with a stratigraphic distribution from the Wordian to the Capitanian. Its association with diverse ammonoid faunas highlights its significance for Guadalupian biostratigraphy. Likewise, we think *Paraceltites elegans* to be highly significant for the American Realm. Besides, *Paraceltites elegans* is phylogenetically related to *Cibolites* (Fig. 10.A), another index species used for the Capitanian (SPINOSA *et al.*, 1975; LEONOVA, 2011).

This species has been associated with the following ammonoids: *Agathiceras girtyi* BÖSE, 1919, *Epithalassoceras* sp., *Eumedlicotia burckhardtii* (BÖSE, 1919), *Neocrimites* sp., *Perrinites vidriensis* BÖSE, 1919, *Propinacoceras* sp., *Stacheoceras* sp., *Texoceras texanum* (GIRTY, 1908), *Waagenoceras* sp., *Altudoceras altudense* (BÖSE, 1919), *Roadoceras beedei* (PLUMMER & SCOTT, 1937), *Roadoceras roadense* (BÖSE, 1919), *Mexicoceras guadalupense* (GIRTY, 1908), *Waagenoceras dieneri*, *Newellites richardsoni* (PLUMMER & SCOTT, 1937), *Cibolites uddeni* PLUMMER & SCOTT, 1937, *Timorites?* sp., *Neogeoceras girtyi* (MILLER & FURNISH,

1940), *Timorites* cf. *T. schucherti*. (MILLER & FURNISH, 1940; CLIFTON, 1944; SPINOSA *et al.*, 1975; LAMBERT *et al.*, 2000; SMITH, 2012; BELL *et al.*, 2015). In Mexico, KING *et al.* (1944) recorded *P. elegans* in the *Waagenoceras* Zone and the *Timorites* Zone, corresponding to the Wordian and Capitanian, respectively.

Detrital zircon U-Pb ages reported constrain the maximum depositional age at the base of the formation to 268±5 Ma (Roadian-Capitanian) (JUÁREZ-ARRIAGA & MURILLO-MUÑETÓN, 2020). This age range coincides with the temporal framework proposed by SHEN *et al.* (2019) for the earliest occurrences of *Paraceltites* in the Guadalupe Mountains. Thus, the biostratigraphic framework established here for the Olinalá Formation aligns with previously recognized ages, thereby reinforcing the reliability of the *P. elegans* Zone as a useful proxy for constraining the Roadian-Wordian boundary. The concordance between paleontological and geochronological evidence underscores the potential of *P. elegans* to serve as the basis for a regional zone with broader interregional correlation (Fig. 9).

Coahuiloceras sp. Zone. This ammonoid zone is defined by first occurrence of the index species. *Coahuiloceras* sp. occurs in the Nemotitlán section, a taxon previously considered a synonym of *Timorites schucherti* from Coahuila (see discussion above). This genus was found in the upper part of the section, above the shoal marine platform limestone (Nemo3 level). The ammonoid assemblage includes *Coahuiloceras* sp., *Waagenoceras* cf. *W. dieneri* (Figs. 2.E-G, 4.F), *Waagenoceras* cf. *W. girtyi*, *Mexicoceras* sp. (Fig. 2.C-D), *Propinacoceras beyrichi*, *Roadoceras roadense*, and *Stacheoceras* sp. (Fig. 2.A-B). Although *Coahuiloceras* sp. is only reported from the upper part of the Nemotitlán section (Nemo3), we infer that it may be coeval with the upper part of the Barranca Coyomitla section (Coyo3), based on lithologic correlation and the ammonoid assemblage found in this last section (*e.g.*, *Waagenoceras* cf. *W. dieneri*, *Stacheoceras* sp.). It should be noted that the thickness of strata in the two sections differs: in Nemotitlán, the black shale facies reach approximately 200 m, whereas in Barranca Coyomitla, the black shale facies are less than 100 m thick. Consequently, we suggest that *Coahuiloceras* sp. was not found in the first 100 m of the Coyomitla section either, because its first appearance lies above this interval, as observed in the Nemotitlán section.

Discussion: According to KING *et al.* (1944), the complete faunal assemblage associated with *Timorites schucherti* (= *Coahuiloceras* sp.) from the Las Delicias Formation, Coahuila, included fusulinids (*Polydiexodina capitanensis* and *Rauserella erratica*) and ammonoids (*Propinacoceras* sp., *Roadoceras roadense*, *Stacheoceras toumanskyae*, *Waagenoceras girtyi*, *Paraceltites elegans*, and *Cibolites uddeni*).

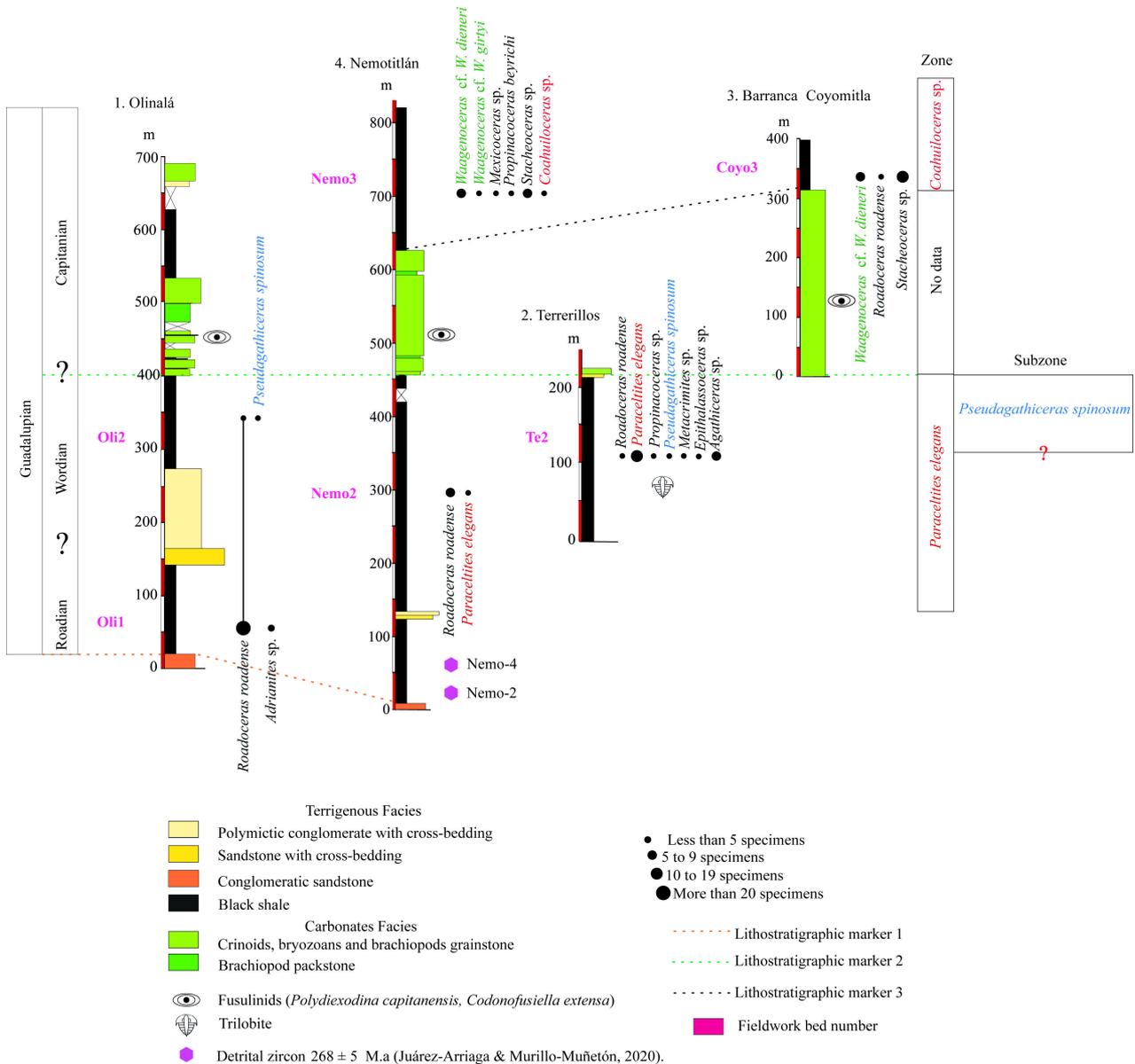


Figure 9: Biostratigraphical scheme of the Guadalupian with ammonoid distribution, abundance and zonation of the Olinalá Formation. Taxa highlighted in red and blue possess the most significant biostratigraphic value. Olinalá and Nemetitlán stratigraphic sections adapted from JUÁREZ-ARRIAGA and MURILLO-MUÑETON (2020).

The occurrence of fusulinids, such as *Rauserella erratica*, *Codonofusiella extensa*, and *Polydiexodina capitanensis*, in the upper part of the Olinalá Formation suggests a lower to middle Capitanian age for the strata (VACHARD *et al.*, 1993, 1997, 2004), as these species are typical late Guadalupian fusulinids of Texas. *Polydiexodina capitanensis* occurs in the Bell Canyon Formation (Pinery and Rader Limestone members), while *C. extensa* is in the McKittrick Canyon Limestone Member (NESTELL *et al.*, 2019). These taxa are included in the *Polydiexodina* Zone, with a stratigraphic range from the Wordian to the Capitanian, and in the *Paraboultonia splendens* Zone, which corresponds to the Capitanian, respectively (Fig. 11) (NESTELL *et al.*, 2019; WAHLMAN & NESTELL, 2024). The ammonoids in these members include *Neogeoceras girtyi*, *Mexioceras guadalupense*, and *Paracelites elegans* (MILLER & FURNISH, 1940),

supporting our record of the genus *Mexioceras* in Capitanian strata.

The occurrence of *Waagenoceras* cf. *W. dieneri* and *Waagenoceras* cf. *W. girtyi* allows extending the stratigraphic range of the genus into the early Capitanian, even though the genus has been considered an index component of the Wordian (FURNISH, 1973; JIN *et al.*, 1997; LEONOVA, 2011, 2018). This is supported by the previous record of *Waagenoceras dieneri* in the Middle part of the Monos Formation in Sonora state, Mexico (COOPER *et al.*, 1953), since at first, this ammonoid's presence suggested a Wordian range for the unit. However, a posterior analysis of the conodont assemblage composed of *Jinogondolella nankingensis*, *J. aserrata*, and *J. postserrata* enabled proposing an early to middle Capitanian range for the interval established as Wordian by COOPER *et al.* (1953; LARA-PEÑA *et al.*, 2021).

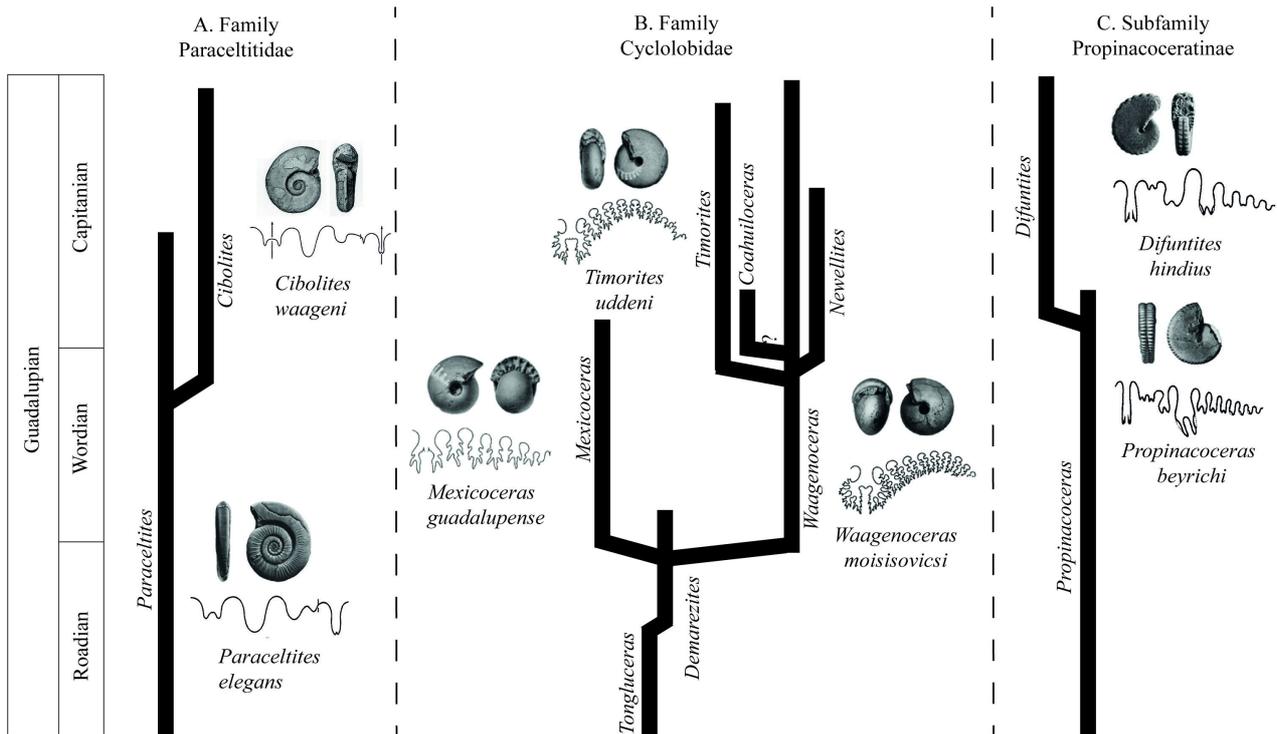


Figure 10: Phylogenetic reconstruction of the **A)** Family Paraceltitidae, **B)** Family Cyclolobidae, and **C)** Subfamily Propinacoceratinae. The arrows indicate that the lineages continue in the stratigraphic record. Modified from SPINOSA *et al.* (1975) and LEONOVA (2010).

Therefore, the presence of this genus would not modify the proposed stratigraphic position, given that, according to LEONOVA (2018), the lower boundary of the first Capitanian zone is defined by the *Timorites schucherti-Cibolites uddeni* assemblage, while the upper boundary is marked by *Eoaraxoceras ruzhencevi-Kingoceras kingi* (Fig. 12). Similarly, ZHOU (2017) established the upper boundary based on the *Eoaraxoceras spinosai-Difuntites furnishi* assemblage (Fig. 12).

In accordance with LEONOVA (2010, 2016), the lineage of the Family Cyclolobidae should be: *Tongluceras* → *Demarezites* → *Waagenoceras* → *Cyclolobus* → *Changhsingoceras*, with the following iterations: *Demarezites* → *Mexioceras* and *Waagenoceras* → *Timorites* and *Newellites* (LEONOVA, 2010, p. 269, Fig. 1). Consequently, we propose an adjustment to LEONOVA's iteration, suggesting *Demarezites* → *Mexioceras* and *Waagenoceras* → *Timorites*, *Coahuiloceras*, and *Newellites*. This proposal is founded on the genera *Timorites* and *Coahuiloceras*, which are two partially coeval offshoots of *Waagenoceras*. Besides, the stratigraphic range of *Coahuiloceras* is clearly shorter of the two (Fig. 10.B), and it could be restricted to Mexico.

A clear ancestor-descendant relationship may exist between *Coahuiloceras* and *Timorites*, as evidenced by the co-occurrence of *Waagenoceras* and *Coahuiloceras*. However, *Waagenoceras* and *Mexioceras* are typically assigned to the Wordian (MILLER & FURNISH, 1940; SMITH, 2012; LEONOVA, 2011, 2016). The proposed ancestor-descendant relationship is based solely on the coexistence of *Waagenoceras* and *Coahuiloceras*. The presence

of species such as *Waagenoceras* cf. *W. dieneri*, *Waagenoceras* cf. *W. girtyi*, and *Mexioceras* sp. in strata of the Olinalá Formation could only represent their last occurrences in North America, rather than evidence of an evolutionary transition (Fig. 10.B).

An ammonoid subzone

***Pseudagathiceras spinosum* Subzone.** The base of this ammonoid subzone is defined by the first occurrence of taxa in the middle part of the Olinalá Formation, Terrerillos section, just below the shoal marine platform limestone beds. This subzone ranges from the middle to the upper part of the *Paraceltitites elegans* Zone, coinciding with the ACME of *P. elegans*.

Discussion: We consider *P. spinosum* an endemic taxon, because previously it was described only from the Las Delicias Formation, Coahuila, within the *Waagenoceras* Zone (KING *et al.*, 1944). Recently, ALANIS-PAVÓN *et al.* (2025) described a juvenile specimen of this taxon corresponding to the *Waagenoceras dieneri-Adrianites elegans* Zone. Thus, the ammonoid assemblage is related to the Wordian Stage. The ammonoid assemblage associated with *P. spinosum* from Coahuila is similar to that found in the present study, including *Roadoceras roadense*, *Epithalassoceras ruzhencevi*, *Eumedlicottia burckhardti*, *Neogeooceras girtyi*, *Agathiceras girtyi*, *Stacheoceras gemmellaroi* MILLER, 1944, *Mexioceras guadalupense*, *M. smithi*, *Waagenoceras dieneri*, *W. girtyi*, and *Paraceltitites elegans* (KING *et al.*, 1944; ALANIS-PAVÓN *et al.*, 2025).



Epoch/Stage		Jin <i>et al.</i> , 1997 Global Zone	Leonova, 2018 Global Zone	Zhou, 2017 South China	Nestell <i>et al.</i> , 2019 North America	This paper	
		Ammonoid Zones				Zone	Subzone
Guadalupian	Capitanian	<i>Timorites</i>	<i>Eoaraxoceras ruzhencevi</i> - <i>Kingoceras kingi</i> <i>Timorites schucherti</i> - <i>Cibolites uddeni</i>	<i>Eoaraxoceras spinosai</i> - <i>Difuntites furnishi</i>			
	Wordian	<i>Waagenoceras</i>	<i>Adrianites elegans</i> - <i>Waagenoceras dieneri</i>	<i>Waagenoceras</i> sp.- <i>Propinacoceras beyrichi</i>		<i>Coahuiloceras</i> sp.	
	Roadian	<i>Demarezzites</i>	<i>Daubichites goochi</i> - <i>Demarezzites oyensi</i>				<i>Paraceltites elegans</i> <i>Pseudagathiceras spinosum</i>

Figure 12: Comparison of the ammonoid standard zones: global zonation (JIN *et al.*, 1997; LEONOVA, 2018), Tethys Realm (ZHOU, 2017), American Realm (NESTELL *et al.*, 2019), and the ammonoid zone of the Olinalá Formation.

al., 1992). It should be noted that the type area of this series is located in Guadalupe Mountains National Park, where the rocks are well-exposed, mainly in West Texas (GRANT *et al.*, 2000). In addition, the definition of the Guadalupian Series was primarily based on the evolutionary sequence of a single conodont genus: *Jinogondolella* (GLENISTER *et al.*, 1999; HENDERSON & SHEN, 2020) (Fig. 13).

The Roadian Stage is the basal stage of the Guadalupian Series and includes the El Centro Member of the Cutoff Formation (GLENISTER *et al.*, 1999; HENDERSON & SHEN, 2020). The marker horizon is the first appearance of the conodont *Jinogondolella nankingensis* (HENDERSON & SHEN, 2020). The age of the base is estimated at 273.01 ± 0.14 Ma based on U-Pb geochronological studies (SHEN *et al.*, 2020). The base of the Wordian Stage is identified in the upper part of the Getaway Limestone Member of the Cherry Canyon Formation (GLENISTER *et al.*, 1999; HENDERSON & SHEN, 2020). The marker horizon corresponds to the first appearance of the conodont *Jinogondolella aserrata* (HENDERSON & SHEN, 2020). The age of the base is estimated at 266.9 ± 0.4 Ma (SHEN *et al.*, 2020). The base of the Capitanian Stage is identified in the Pinery Limestone Member of the Bell Canyon Formation (GLENISTER *et al.*, 1999; HENDERSON & SHEN, 2020). The marker horizon corresponds to the first appearance of the conodont *Jinogondolella postserrata* (HENDERSON & SHEN, 2020). The age of the base is estimated at 264.28 ± 0.16 Ma (SHEN *et al.*, 2020).

7. Previous biostratigraphic studies based on conodont, fusulinacean, and ammonoid zonation of the Guadalupian Series

The Guadalupian Series is divided into three stages: Roadian, Wordian and Capitanian, which are defined by the first appearances of different index conodonts. Nevertheless, other index fossils have been used worldwide to correlate distinct outcrops associated with the Guadalupian Series (LAMBERT *et al.*, 2002; LEONOVA, 2009; WU *et al.*, 2017; CHEN & XU, 2019; SHEN *et al.*, 2019). The use of other fossil groups has presented difficul-

ties for biostratigraphic correlations, mainly due to biogeographic provincialism or the lack of data in the fossil record (NESTELL *et al.*, 2019). For example, although fusulinids are excellent index fossils, these are geographically restricted, making comparisons between North American basins and the Tethys region challenging (HUANG *et al.*, 2017; ZHANG & WANG, 2018; NESTELL *et al.*, 2019; AREFI-FARD & CLAPHAM, 2021; WAHLMAN & NESTELL, 2024). Most Guadalupian North American fusulinid data come from the Permian Basin of West Texas (WAHLMAN & NESTELL, 2024). The reported stratigraphic ranges in early and Middle Guadalupian fusulinids are somewhat inconsistent, likely resulting from the limited amount of available data and from the redefinition of Guadalupian Stage boundaries based on conodont biostratigraphy (NESTELL *et al.*, 2019; WAHLMAN & NESTELL, 2024) (Fig. 11).

Regarding ammonoids, the challenges are different, because Guadalupian ammonoid biostratigraphy has not been as well established globally as that of conodonts or even fusulinids (LEONOVA, 2011; SHEN *et al.*, 2019, 2020). In the early 20th century, a general Permian correlation for West Texas was established based on distinctive ammonoid genera (MILLER, 1938). In this sense, the ammonoid faunas of the Roadian Stage were characterized by the appearance of *Demarezzites*, the ancestral representative of the Cyclolobaceae, which marked the onset of diversification of this group throughout the remainder of the Guadalupian (GLENISTER *et al.*, 1992, 1999). Likewise, *Paraceltites elegans* is present in most faunas, being dominant in West Texas, whereby its occurrence near the base of this stage represents the appearance and initial diversification of the Ceratitida (GLENISTER *et al.*, 1999; SHEN *et al.*, 2019, 2020). Traditionally, the base of the Wordian Stage was recognized in the Pipeline Shale Member at the base of the Brushy Canyon Formation and was defined by the first occurrence of the genus *Waagenoceras* (GLENISTER *et al.*, 1992, 1999; JIN *et al.*, 1997). However, recent studies have shown that the ammonoid *Waagenoceras* also occurs in the upper Roadian Stage, according to the current GSSP definitions (SHEN *et al.*, 2019, 2020; HEN-



DERSON & SHEN, 2020) (Fig. 13). Similarly, the base of the Capitanian Stage was traditionally recognized in the Hegler Limestone Member of the Bell Canyon Formation and was characterized by the occurrence of the genus *Timorites* (GLENISTER *et al.*, 1992, 1999; JIN *et al.*, 1997), although this genus has also been collected in the Middle Guadalupian Manzanita Member of the Cherry Canyon Formation (GLENISTER *et al.*, 1999). Thus, recent studies have proposed that *Timorites* occurs from the upper Wordian, as the currently defined GSSP (NESTELL *et al.*, 2019; SHEN *et al.*, 2019, 2020; HENDERSON & SHEN, 2020) (Fig. 13).

Various authors have employed this ammonoid zonation for global biostratigraphy. However, in recent years, the knowledge about these index fossils has been expanded by the inclusion of new data and review of previous information, including new taxonomic features and recognition of variations in stratigraphic and paleobiogeographic distribution of the faunal assemblages (LEONOVA, 1999, 2002, 2009, 2011, 2016, 2017, 2018; EHIRO & MISAKI, 2005; TAZAWA *et al.*, 2005; EHIRO, 2008, 2022; ZHOU, 2017; ALANIS-PAVÓN *et al.*, 2025). Consequently, EHIRO and ARAKI (1997), EHIRO and MISAKI (2005), and EHIRO (2008, 2022) identified Guadalupian ammonoid faunas in the Paleotethys Realm of northeastern Japan, describing assemblages whose genera, *Waagenoceras* and *Timorites*, allow the correlation of strata with typical regions of the Wordian and Capitanian, respectively. But ZHOU (2017) noticed that ammonoids of the Paleotethys Realm from southern China were commonly endemic, making it difficult to compare the faunas studied with those found in other paleogeographic areas. ZHOU (2017) also explained that endemic ammonoid assemblages were found on the southern China platform, noting that more cosmopolitan faunas were on the slope of the open basin areas. It is worth noting that LEONOVA (2011) recognized the difficulty in developing a Permian ammonoid zonal scale, because ammonoid localities are rare, and the transitions between species and genera that characterize long geological intervals are uncommon. According to LEONOVA (2011), a Permian ammonoid zonal stratigraphy is neither established nor accepted. Nevertheless, LEONOVA proposed a zonal subdivision based on a short stratigraphic interval, in a broad geographic range, and an evolutionary development that allows for comparing species of the same genus (LEONOVA, 2011). This proposal uses two isochronous index species across different biogeographic regions (LEONOVA, 2018). On the contrary, based on the open marine ammonoid assemblages, ZHOU (2017) proposed one zonation for the Guadalupian, which enables comparing different regions worldwide: the *Waagenoceras sp.-Propinacoceras beyrichi* Zone for the Wordian, and the *Eoaraxoceras spinosai-Difuntitesurnishi* Zone for the Capitanian.

All fusulinid biostratigraphic data from Permian Basin formations in Texas, USA (NESTELL *et al.*, 2019), together with the species described by VA-

CHARD *et al.* (1993, 2004) from Olinalá, and the currently accepted conodont-based stages, are used in the preceding discussion. These datasets can be approximately correlated with the stratigraphic ranges of ammonoids shown in Figure 11.

These contrasting biostratigraphic approaches highlight the need for new regional data, such as those presented in this study, which provide additional evidence to refine the Guadalupian ammonoid zonation for North America. The discrepancies between the classic ammonoid zones and the current GSSP framework indicate that the newly recognized stratigraphic ranges of *Waagenoceras* and *Timorites* require a reassessment of previous correlations.

The new Mexican ammonoid biostratigraphic data generated in this study are highly consistent with that of NESTELL *et al.* (2019). The new Mexican data clearly demonstrate that the current Wordian/Capitanian GSSP and its correlation with ammonoid zones can be refined. In particular, the stratigraphic ranges of the genera *Waagenoceras* and *Timorites* appear to be incorrectly represented in the current version of the Geological Time Scale (GTS 2020; updated online by ICS, 2026 version). Here, we combine the Mexican biostratigraphic data from this study with the North American data of NESTELL *et al.* (2019) (Fig. 13). Some inconsistency observed between these datasets concerns the range of *Paraceltites*, which is extended slightly higher in Mexico, with its last occurrence very close to the Wordian/Capitanian GSSP. Based on the coherent data and this minor discrepancy in the range of *Paraceltites*, we propose a new global ammonoid zonation that integrates the Roadian/Wordian and Wordian/Capitanian GSSPs (Fig. 13). This new proposal represents a significant step forward in refining the global biostratigraphic calibration of Middle Permian ammonoids and enhances their potential for accurately dating Middle Permian sedimentary successions.

8. Correlation of Olinalá Formation ammonoid assemblages with global Guadalupian zones

The global Guadalupian ammonoid zonation proposed by LEONOVA (2011, 2018) provides a refined framework that incorporates the zonation of JIN *et al.* (1997), employing index species with broader geographic distributions. A key improvement in this scheme is the subdivision into lower and upper parts of the Capitanian Stage based on ammonoid assemblages, which enhances biostratigraphic resolution. However, inconsistencies remain in the stratigraphic ranges of Guadalupian ammonoid species, mainly due to the conodont-based redefinition of stage boundaries (HENDERSON & SHEN, 2020). Being so, the present work aims to correlate the Guadalupian stages using ammonoid and fusulinid-based chronostratigraphic units in comparison with the currently accepted conodont-based framework (Fig. 11). The Middle Per-



		Conodonts	Ammonoids	Ammonoids			Ammonoids						
		Gradstein <i>et al.</i> (2020)	Gradstein <i>et al.</i> (2020)	Nestell <i>et al.</i> (2019)			This paper						
Permian	Capitanian		<i>Timorites</i>										
	Wordian	<i>Jinogondolella aserrata</i> <i>Jinogondolella postaserrata</i>	<i>Waagenoceras</i>	<i>Waagenoceras</i>	<i>Timorites</i>	<i>Mexioceras</i>	<i>Waagenoceras</i> <i>Coahuiloceras</i> <i>Mexioceras</i>	<i>Paracelites</i>	<i>Roadoceras</i>	<i>Propinacoceras</i>	<i>Stacheoceras</i>	<i>Epithalassoceras</i>	
	Roadian	<i>Jinogondolella nankingensis</i>	<i>Paracelites</i> <i>Demarezites</i>	<i>Demarezites</i>	<i>Paracelites</i>	<i>Epithalassoceras</i>	<i>Roadoceras</i>						

Figure 13: Guadalupian Series time scale showing GSSP conodont markers compared to the ammonoid standard biostratigraphy, modified from NESTELL *et al.* (2019) and GRADSTEIN *et al.* (2020).

mian strata, defined initially and exposed in the Guadalupe Mountains area, can be recognized globally through the succession of conodonts, fusulinids, and ammonoids. Nevertheless, the revised conodont-based Guadalupian boundaries differ from the traditional ammonoid-based scheme, resulting in some correlation inconsistencies within the Permian Basin and its equivalent regions (Fig. 11).

On the other hand, ZHOU's ammonoid zonation from the Nanpanjiang Basin, South China, incorporates Wordian and upper Capitanian data. Zone 5 (*Waagenoceras* sp.-*Propinacoceras beyrichi*) corresponds to the Wordian, while Zone 6 (*Eoaraxoceras spinosai*-*Difuntites furnishi*) is assigned to the upper Capitanian (Fig. 12) (ZHOU, 2017). A key point to consider is that LEONOVA (2002) recognized the lineage *Propinacoceras* - *Difuntites*. According to this data, during the Wordian, *Propinacoceras beyrichi* experienced a radiation event, giving rise to the genus *Difuntites* GLENISTER & FURNISH, 1988, within the Subfamily Propinacoceratinae, marking the last known occurrence of this subfamily (Fig. 10.C). The genus *Difuntites* has

been identified in Capitanian strata (RUZHENCEV, 1976; CANTÚ-CHAPA, 1997). This is particularly significant given that the Mexican species, *P. beyrichi*, has been reported from the lower Capitanian, possibly representing its last occurrences, while in South China, *Difuntites furnishi* (ZHOU, 2017) has been recorded from the upper Capitanian.

Therefore, we propose that the biostratigraphic record of the taxa, *Waagenoceras* cf. *W. dieneri*, *Waagenoceras* cf. *W. girtyi*, *Mexioceras* sp., and *Propinacoceras beyrichi*, should extend at least into the lower Capitanian, possibly representing their last occurrences.

In contrast, the Mexican ammonoid zonation cannot be correlated with LEONOVA's and ZHOU's scheme, because the stratigraphic ranges of several species contradict our data. This discrepancy is particularly evident in the Wordian, since the Mexican species *Waagenoceras* cf. *W. dieneri*, *Waagenoceras* cf. *W. girtyi*, and *Propinacoceras beyrichi* have also been found in lower Capitanian strata. Similarly, ALANIS-PAVÓN *et al.* (2025) reported *Waagenoceras* as ranging throughout the



ammonoid-based Wordian and Capitanian stages. In contrast, NESTELL *et al.* (2019) documented *Waagenoceras* ranging through the Roadian and Wordian stages, and *Timorites* through the Wordian and Capitanian stages, according to the conodont-based framework (Fig. 13).

According to our biostratigraphic data, the Olinalá Formation can be correlated with Guadalupian formations of the American Realm. This statement supports previous studies on the Las Delicias Formation in Coahuila, the Cherry Canyon and Bell Canyon formations in Texas, USA, and the Cache Creek Group in British Columbia. Based on the studied ammonoid assemblages from the Olinalá Formation, the faunal composition and stratigraphic distribution suggest close affinities with the Guadalupian from West Texas.

It is also important to note the affinity between ammonoid assemblages from the American Realm and those from coeval units of South China and Japan. However, differences in taxonomic diversity between these two realms should also be noted. Such disparities may be attributed to paleobiogeographic and paleoecological factors, which warrant further investigation.

9. Conclusions

In the present work, two ammonoid zones and one subzone are recognized in the Olinalá Formation in the Guerrero state: the *Paraceltites elegans* Zone, *Coahuiloceras* sp. Zone and *Pseudagathiceras spinosum* Subzone. Several global ammonoid zonations for the Guadalupian have been proposed by different authors, many using *Waagenoceras* as a key index fossil for the Wordian and *Timorites* for the Capitanian. However, our finding of *Waagenoceras* in the upper levels of the Olinalá Formation (Guerrero, Mexico), which, based on fusulinids and the conodont-based framework, is assigned to the late Wordian-to early Capitanian, suggests that these biostratigraphic schemes may require reconsideration or refinement when applied to this region.

The biostratigraphic age proposed for the base of the formation, based on the *P. elegans* Zone, is consistent with the previously estimated geochronological range, Roadian-Wordian (268±5 Ma). Hence, we propose extending the biostratigraphic range of *Waagenoceras* cf. *W. dieneri*, *Waagenoceras* cf. *W. girtyi*, *Mexioceras* sp., and *Propinacoceras beyrichi* at least into the lower Capitanian in the North American region (American Realm).

The taxon, *Coahuiloceras* sp., is validated, along with its phylogenetic relationship to *Waagenoceras* and *Timorites*. The quantitative analysis reinforces the recognition of *Coahuiloceras* as a morphologically distinct genus, while highlighting substantial morphological variability within *Timorites*. This observed pattern could carry significant taxonomic implications, particularly for defining species boundaries within the genus, because it

can be assigned to the upper Wordian-lower Capitanian.

The ammonoids from the Olinalá Formation are assigned to the American Realm and exhibit faunal affinities with the Guadalupian ammonoid assemblages of the Guadalupe Mountains in West Texas and the Las Delicias Formation in Coahuila state, supporting regional biostratigraphic correlations. The integration of the new Mexican ammonoid data with that of NESTELL *et al.* (2019) allows for a refined correlation of Permian ammonoid genera across the Roadian-Wordian and Wordian-Capitanian boundaries. This new proposal represents a significant step forward in improving the global biostratigraphic calibration of Middle Permian ammonoids and enhances their potential for accurately dating Middle Permian successions.

Acknowledgements

Alberto ALANIS PAVÓN thanks Posgrado de Ciencias del Mar y Limnología of the Universidad Nacional Autónoma de México (UNAM) and the financial support provided by CONAHCYT through the scholarship number 931193 and gratefully acknowledges the members of his Ph.D. committee - M.A. TORRES-MARTÍNEZ, J.A. MORENO-BEDMAR, R.J. ALCÁNTARA-HERNÁNDEZ, P. NAVAS-PAREJO, and J.F. SÁNCHEZ-BERISTAIN - for their guidance and support. This article fulfills a requirement for the Doctorado en Ciencias del Mar y Limnología, UNAM with a specialization in Geología Marina, pursued by ALANIS-PAVÓN. MATM thanks the financial support supplied by the project PAPIIT-DGAPA-UNAM IN114623. We also extend our gratitude to the Division of Invertebrate Paleontology, Yale Peabody Museum because AAP received support from the DUNBAR Grants in Aid Program for Invertebrate Paleontological Research. We also thank M.A. ARGAEZ MARTÍNEZ and D.A. BELTRÁN LÓPEZ for their assistance in preparing and photographing specimens. We would like to express our gratitude to Tatiana LEONOVA and an anonymous referee for their suggestions and comments, which greatly improved the original manuscript. We are particularly grateful to the Editor-in-Chief, Bruno GRANIER, for his support and guidance during the editorial process, and Christina IFRIM, for her time. The Senior Editor, Robert W. SCOTT, for his excellent editorial work. We especially thank him for the final handling of the manuscript and for his careful and thorough reading, which greatly contributed to improving the quality and clarity of the work.

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Appendix

For the fieldwork bed number column, the bold letters indicate the bed number of the section where the ammonoid was collected, while the regular text indicates the specimen number within that bed. For example, Nemo2-4 corresponds to specimen 4 from level Nemo 2 of the Nemititlán section.

Collection number	Fieldwork bed number	Identification	Figured
	Oli1		
14378	Oli1-1	<i>Roadoceras rodense</i>	
14379	Oli1-2	<i>Roadoceras rodense</i>	
14380	Oli1-3	<i>Roadoceras rodense</i>	
14381	Oli1-4	<i>Roadoceras rodense</i>	
14382	Oli1-5	<i>Roadoceras rodense</i>	
14383	Oli1-6	<i>Roadoceras rodense</i>	
14384	Oli1-7	<i>Roadoceras rodense</i>	
14385	Oli1-8	<i>Roadoceras rodense</i>	
14386	Oli1-9	<i>Roadoceras rodense</i>	
14387	Oli1-10	<i>Roadoceras rodense</i>	
14388	Oli1-11	<i>Roadoceras rodense</i>	
14389	Oli1-12	<i>Roadoceras rodense</i>	
14390	Oli1-13	<i>Roadoceras rodense</i>	
14391	Oli1-14	<i>Roadoceras rodense</i>	
14392	Oli1-15	<i>Roadoceras rodense</i>	
14393	Oli1-16	<i>Roadoceras rodense</i>	
14394	Oli1-17	<i>Roadoceras rodense</i>	
14395	Oli1-18	<i>Roadoceras rodense</i>	
14396	Oli1-19	<i>Roadoceras rodense</i>	
14397	Oli1-20	<i>Roadoceras rodense</i>	
14398	Oli1-21	<i>Roadoceras rodense</i>	
14399	Oli1-22	<i>Roadoceras rodense</i>	
14400	Oli1-23	<i>Roadoceras rodense</i>	
14401	Oli1-24	<i>Adrianites</i> sp.	Fig. 3.G
	Oli2		
14402	Oli2-1	<i>Pseudagathiceras spinosum</i>	Fig. 3.C-D
14403	Oli2-2	<i>Roadoceras rodense</i>	
14404	Oli2-3	<i>Roadoceras rodense</i>	Fig. 3.I
14405	Oli2-4	<i>Roadoceras rodense</i>	Fig. 3.J
14406	Oli2-5	<i>Roadoceras rodense</i>	
14407	Oli2-6	Indeterminate	
	Te2		
14408	Te2-1	<i>Paraceltites elegans</i>	Fig. 2.K
14409	Te2-2	<i>Paraceltites elegans</i>	Fig. 2.J
14410	Te2-3	<i>Paraceltites elegans</i>	
14411	Te2-4	<i>Paraceltites elegans</i>	
14412	Te2-5	<i>Paraceltites elegans</i>	
14413	Te2-6	<i>Paraceltites elegans</i>	
14414	Te2-7	<i>Paraceltites elegans</i>	
14415	Te2-8	<i>Paraceltites elegans</i>	
14416	Te2-9	<i>Paraceltites elegans</i>	
14417	Te2-10	<i>Paraceltites elegans</i>	
14418	Te2-11	<i>Paraceltites elegans</i>	
14419	Te2-12	<i>Paraceltites elegans</i>	
14420	Te2-13	<i>Paraceltites elegans</i>	
14421	Te2-14	<i>Paraceltites elegans</i>	
14422	Te2-15	<i>Paraceltites elegans</i>	
14423	Te2-16	<i>Paraceltites elegans</i>	
14424	Te2-17	<i>Paraceltites elegans</i>	
14425	Te2-18	<i>Pseudagathiceras spinosum</i>	
14426	Te2-19	<i>Agathiceras</i> sp.	Fig. 3.E



14427	Te2-20	<i>Agathiceras</i> sp.	Fig. 3.F
14428	Te2-21	<i>Agathiceras</i> sp.	
14429	Te2-22	<i>Metacrimites</i> sp.	
14430	Te2-23	<i>Agathiceras</i> sp.	
14431	Te2-24	<i>Agathiceras</i> sp.	
14432	Te2-25	<i>Agathiceras</i> sp.	
14433	Te2-26	<i>Agathiceras</i> sp.	
14434	Te2-27	Indeterminate	
14435	Te2-28	<i>Metacrimites</i> sp.	
14436	Te2-29	<i>Epithalassoceras</i> sp.	
14437	Te2-30	<i>Roadoceras roadense</i>	
14438	Te2-31	<i>Paraceltites elegans</i>	
14439	Te2-32	<i>Propinacoceras</i> sp.	Fig. 3.A
14440	Te2-33	<i>Epithalassoceras</i> sp.	Fig. 3.H
14441	Te2-34	<i>Metacrimites</i> sp.	Fig. 3.K
Nemo2			
14442	Nemo2-1	Indeterminate	
14443	Nemo2-2	<i>Paraceltites elegans</i>	Fig. 2.I
14444	Nemo2-3	<i>Roadoceras roadense</i>	
14445	Nemo2-4	<i>Roadoceras roadense</i>	
14446	Nemo2-5	<i>Roadoceras roadense</i>	
14447	Nemo2-6	<i>Roadoceras roadense</i>	
14448	Nemo2-7	<i>Roadoceras roadense</i>	
Nemo3			
14449	Nemo3-1	<i>Waagenoceras</i> cf. <i>W. dieneri</i>	Fig. 2.G
14450	Nemo3-2	<i>Waagenoceras</i> cf. <i>W. dieneri</i>	Fig. 2.E
14451	Nemo3-3	<i>Mexioceras</i> sp.	Fig. 2.C-D
14452	Nemo3-4	<i>Waagenoceras</i> cf. <i>W. dieneri</i>	
14453	Nemo3-5	<i>Waagenoceras</i> cf. <i>W. dieneri</i>	
14454	Nemo3-6	Nautiloid	
14455	Nemo3-7	Nautiloid	
14456	Nemo3-8	<i>Waagenoceras</i> cf. <i>W. dieneri</i>	
14457	Nemo3-9	<i>Waagenoceras</i> cf. <i>W. dieneri</i>	
14458	Nemo3-10	<i>Waagenoceras</i> cf. <i>W. dieneri</i>	
14459	Nemo3-11	<i>Coahuiloceras</i> sp.	Fig. 6
14460	Nemo3-12	<i>Stacheoceras</i> sp.	
14461	Nemo3-13	<i>Stacheoceras</i> sp.	
14462	Nemo3-14	<i>Stacheoceras</i> sp.	
14463	Nemo3-15	<i>Stacheoceras</i> sp.	
14464	Nemo3-16	<i>Stacheoceras</i> sp.	
14465	Nemo3-17	<i>Stacheoceras</i> sp.	
14466	Nemo3-18	<i>Stacheoceras</i> sp.	
14467	Nemo3-19	<i>Stacheoceras</i> sp.	
14468	Nemo3-20	<i>Propinacoceras beyrichi</i>	Fig. 3.B
14469	Nemo3-21	<i>Coahuiloceras</i> sp.	
14470	Nemo3-22	<i>Coahuiloceras</i> sp.	
14471	Nemo3-23	<i>Waagenoceras</i> cf. <i>W. girtyi</i>	Fig. 2.H
14472	Nemo3-24	<i>Waagenoceras</i> cf. <i>W. girtyi</i>	
14473	Nemo3-25	Indeterminate	
14474	Nemo3-26	Indeterminate	
Coyo3			
14475	Coyo3-1	<i>Waagenoceras</i> cf. <i>W. dieneri</i>	
14476	Coyo3-2	<i>Waagenoceras</i> cf. <i>W. dieneri</i>	
14477	Coyo3-3	<i>Waagenoceras</i> cf. <i>W. dieneri</i>	
14478	Coyo3-4	<i>Waagenoceras</i> cf. <i>W. dieneri</i>	
14479	Coyo3-5	<i>Waagenoceras</i> cf. <i>W. dieneri</i>	
14480	Coyo3-6	<i>Waagenoceras</i> cf. <i>W. dieneri</i>	
14481	Coyo3-7	<i>Waagenoceras</i> cf. <i>W. dieneri</i>	Fig. 2.F



14482	Coyo3-8	<i>Stacheoceras</i> sp.	
14483	Coyo3-9	<i>Stacheoceras</i> sp.	
14484	Coyo3-10	<i>Stacheoceras</i> sp.	
14485	Coyo3-11	<i>Stacheoceras</i> sp.	
14486	Coyo3-12	<i>Stacheoceras</i> sp.	
14487	Coyo3-13	<i>Stacheoceras</i> sp.	
14488	Coyo3-14	<i>Stacheoceras</i> sp.	
14489	Coyo3-15	<i>Stacheoceras</i> sp.	Fig. 2.B
14490	Coyo3-16	<i>Stacheoceras</i> sp.	
14491	Coyo3-17	<i>Stacheoceras</i> sp.	
14492	Coyo3-18	<i>Stacheoceras</i> sp.	
14493	Coyo3-19	<i>Stacheoceras</i> sp.	
14494	Coyo3-20	<i>Roadoceras roadense</i>	
14495	Coyo3-21	<i>Roadoceras roadense</i>	
14496	Coyo3-22	<i>Stacheoceras</i> sp.	
14497	Coyo3-23	<i>Stacheoceras</i> sp.	Fig. 2.A