

## **Ammonoids and their biozonation across the Santonian-Campanian boundary in north-eastern Coahuila, Mexico**

**Christina Ifrim and Wolfgang Stinnesbeck**

### **ABSTRACT**

Fossil-rich shelf carbonates of Santonian-Campanian age are superbly exposed at Tepeyac near Jiménez, northern Coahuila, north-eastern Mexico. In this paper we describe 24 species of ammonoids assigned to 12 genera from this section. The 330 specimens were mostly recorded in situ and allow for a detailed biozonation of the section. We propose the first formal biozonation across the Santonian-Campanian boundary in the Gulf Coast region. The section yields abundant *Parapuzosia* assigned to *P. (P.) seppenradensis* and may thus correspond to one of the historical sites from which Böse and Cavins documented this giant ammonite ca. 90 years ago. The faunal assemblage provides evidence for repeated and increasing faunal exchange with Europe and southern latitudes, but also includes intervals of faunal cut-off and endemic evolution. The abundance of fossils, the excellent outcrop conditions, and biozonal completeness favor the use of the Tepeyac section as a potential reference section for the Santonian-Campanian boundary in the Americas.

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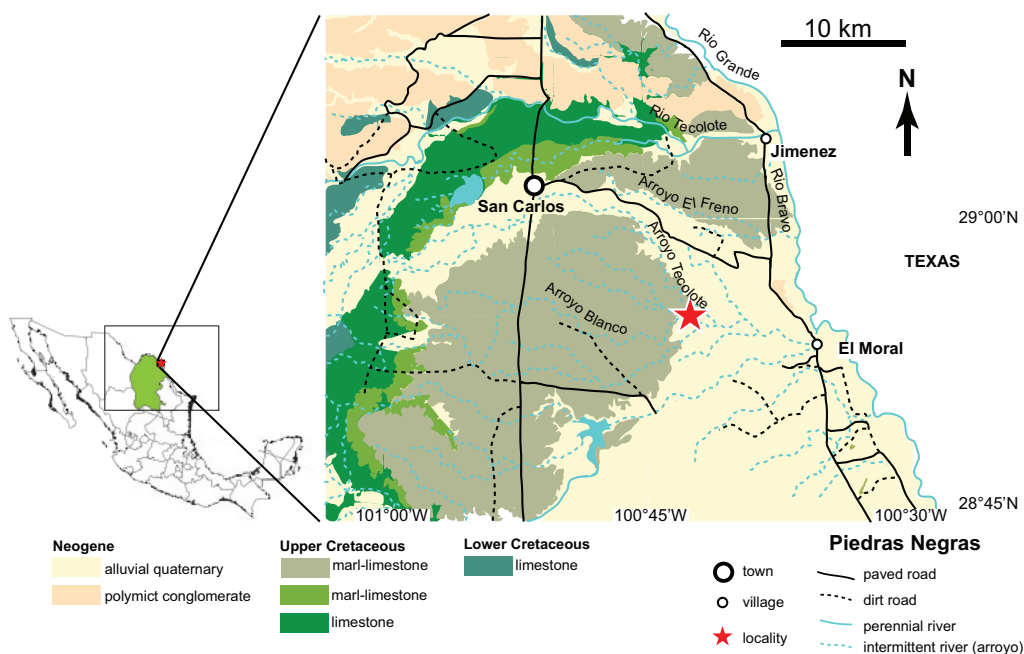
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## INTRODUCTION

To date, the only description of a Mexican locality with *Parapuzosia* is by Böse (1927). According to these authors, the horizon providing evidence for this giant Upper Cretaceous (Santonian-lower Campanian) ammonite “is very well developed in the Rio de San Rodrigo near Piedras Negras, and still better in the Arroyo (= creek) del Tecolote and Arroyo Blanco near Jimenez, Coahuila, where it contains an enormous number of fossils, especially ammonites. Some of the *Pachydiscus* there measure over 1.5 meters in diameter and ammonites of a diameter of between one-half meter and 1 meter are quite common.” Böse and Cavins (1927) further stated that the “lower Santonian consists of a white to gray chalky limestone with beds of hard gray limestone and light gray marls. A suitable place to measure the thickness has not been found, but it is probably not over one hundred meters and possibly even less. The horizon is very fossiliferous; the most common fossils are: *Mortoniceras texanum* Roemer and related members of the group, *Pachydiscus flaccidicosta* Roemer, *Baculites* sp., large undescribed *Inoceramus* related to *I. regularis* d’Orbigny; locally it contains great numbers of echinoderms, small *Exogyra*, *Gryphaea* sp., etc. The frequency of *Mortoniceras texanum* shows that the horizon rep-

resents the lower Santonian. We have never found a single *Placenticerias* in these beds although several species of this genus have been cited from Texas”.

In this paper we describe ammonoid specimens from one of the historical sites originally documented by Böse (1927), Renz (1936), and Böse and Cavins (1927) as Arroyo Blanco. This site was relocated by us near the village of Tepeyac, about 40 km north of the Piedras Negras and 15 km SSW of Jiménez, Coahuila, in the bed of the intermittent Arroyo Blanco river, a tributary to the Rio Grande, and close to the mouth of the Arroyo Tecolote (Figure 1). We logged a section of 28.9 m of rhythmically bedded bright grey to light yellow-coloured layers of chalk and limestone, and intercalated units of marl and marly clay (Figure 2). Both litho- and biofacies indicate that these sediments were deposited on the shelf of the ancient Gulf of Mexico. The ammonite assemblage documented here consists of about 220 specimens mostly found in situ, i.e., in their bed of origin. Additionally, ca. 100 determinable moulds were documented in the field. This study thus comprises ca. 320 stratified specimens, providing a solid base for biozonation across the Santonian-Campanian boundary (Figure 2).



**FIGURE 1.** A: Map of Mexico with the state of Coahuila marked. B: Geological map of the Jimenez area (redrawn from Servicio Geológico de México, 2008). The Tepeyac locality is marked by an asterisk.



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## SYSTEMATIC PALEONTOLOGY

### Higher Systematics, Taxonomy, and Nomenclature

The systematics of ammonites majorly follows the Treatise of Invertebrate Paleontology (Wright et al., 1996). Exceptions refer to Texanitinae, for which the generic definition of Klinger and Kennedy (1980) was used, to Puzosiinae, which are here used in the sense of Kennedy (2019), and to *Amanpondella* Klinger and Kennedy, 1997. Synonymy lists are abbreviated to the most important citations and references used for determination. More complete synonymies are indicated where available.

Ornament is described in the sense of Ifrim et al. (2018).

### Abbreviations

**Dimensions.** All dimensions are given in mm; dimensions in brackets are % of diameter. D: diameter; WH: whorl height; U: umbilical diameter. L: undeformed length in heteromorphs taken dorsally. Asterisks mark estimated values or those from deformed or weathered individuals.

**Collections.** Specimens described here are inventoried in the CPC: Colección de Paleontología de Coahuila, housed at the Museo del Desierto, Saltillo, Coahuila, Mexico and in the IGM: Instituto de Geología de México of the Universidad Autónoma de México (UNAM), housed in the Museo María del Carmen Perrilliat M., Colección Nacional de Paleontología, UNAM, Mexico City. Other collections mentioned are: BEG: collections of the Bureau of Economic Geology, University of Texas, Austin, Texas; GPIB: Geologisch-Paläontologisches Institut der Universität Bonn, Germany; NMBE: Naturhistorisches Museum Bern, Switzerland; SAM: South African Museum, Cape Town, South Africa; TMM: Texas Memorial Museum, Austin, Texas, USA; USNM: United States Museum of Natural History, Washington, D.C., USA; UT: Department of Geology, University of Texas, Austin, Texas; WSA: W. S. Adkins collection of the University of Texas at Austin, Texas.

Phylum MOLLUSCA

Class CEPHALOPODA Cuvier, 1797

Order AMMONOIDEA Zittel, 1884

Suborder AMMONITINA Hyatt, 1889

Superfamily ACANTHOCERATOIDEA de  
Grossouvre, 1894

Family COLLIGNONICERATIDAE Wright and  
Wright, 1951

Subfamily TEXANITINAE Collignon, 1948

This subfamily is discussed in detail by Klinger and Kennedy (1980). We follow these authors and consider *Texanites* and *Plesiotexanites* as separate genera instead of subgenera.

Genus PLESIOTEXANITES Matsumoto, 1970

The genus is discussed in detail by Klinger and Kennedy (1980).

*Plesiotexanites shiloensis* Young, 1963

Figure 3A–G, Table 1

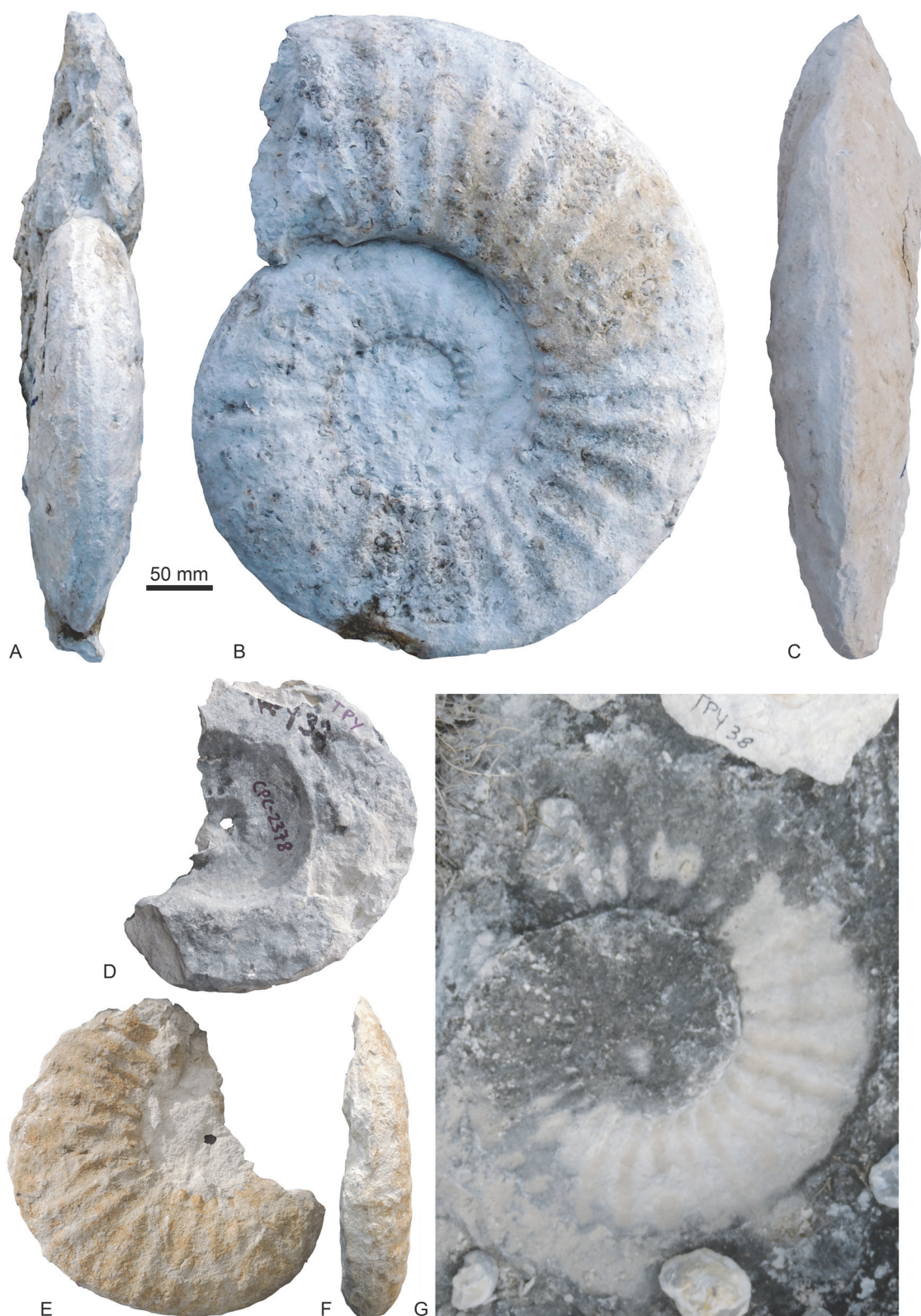
- 1952 *Texanites internodosus* Young and Marks, p. 477 ff [non plate 1, figure 4 = *Texanites internodosus* Renz]
- 1963 *Texanites shiloensis* n. sp.; Young, p. 89, plate 46, figures 1–4; plate 54, figures 4–7; plate 70, figures 5, 6, 8; text-figure 24d
- 1970 *Texanites* sp. cf. *Texanites* (*Plesiotexanites*) *shiloensis* Young; Matsumoto, p. 296, plate 47[51], figure 1; text-figure 26 [100]
- 1980 *Plesiotexanites shiloensis* (Young); Klinger and Kennedy, p. 65
- 1991 *Texanites* (*Plesiotexanites*) *shiloensis* Young, 1963; Kennedy and Cobban, p. 179, figure 8.30
- 1997 *Texanites* (*Plesiotexanites*) *shiloensis* Young, 1963; Kennedy and Cobban, p. 18, figure 13

**Type.** The holotype is TMM 1986 by original designation by Young (1963, p. 89, plate 46, figures 1–4, plate 70, figure 5; text-figure 24d). It is from the Dessau Chalk on Brushy Creek, 23.2 km south of Hutto, Williamson County, Texas.

**Material.** CPC–2363, –2371, –2376, –2378, –2384, –2385, –2543, IGM 12795, and uncollected specimens in beds TPY 23 to TPY 46.

**Description.** Evolute, with U ranging from 0.31 to 0.44. Whorl section moderately compressed, with WB/WH of between 0.55 and 0.75, increasing with D. The umbilical wall is undercut and bends in a narrow arch into flattened flanks. Rib index is 27 to 32 at D > 200 mm. Ribs strengthen across the umbilical wall into sharp, closely spaced umbilical bullae that project into the umbilicus. Blunt, straight, slightly prorsiradiate ribs arise from these bullae. A row of weak, rounded tubercles is located at midflank, while a submarginal row of weaker tubercles is close to a marginal row of somewhat stronger clavate tubercles, each of which is linked by a low, broad rib to a strong, external clavus. A broad, smooth zone separates the external clavi from a strong siphonal keel.

**Dimensions.** Table 1.



**FIGURE 3.** *Plesiotechanites shiloensis* Young, 1963 from the Tepeyac section. A–C: IGM 12795, bed TPY 14; D–F: CPC–2378, bed TPY 33; G: bed TPY 38, not collected. Scale: 50 mm.

**TABLE 1.** Dimensions of *Plesiotexanites shiloensis*.

	bed of origin	D	WB	WB/D	WH	WH/D	WB/WH	U	U/D
CPC-2371	TPY25	-	77	-	135	-	0.57	-	-
CPC-2363	TPY	185	10	0.05	-	-	-	-	-
CPC-2384	TPY37	-	28	-	51	-	0.55	-	-
CPC-2543	TPY36	145	34	0.23	59	0.41	0.58	45	0.31
CPC-2543	TPY36	175	42	0.24	69	0.39	0.61	57	0.33
CPC-2378	TPY33	230	48	0.21	85	0.37	0.56	73	0.32
CPC-2385	TPY37	280	50	0.18	90	0.32	0.56	116	0.41
CPC-2376	TPY33	-	73	-	118	-	0.62	-	-
CPC-2585	TPY53	245	60	0.24	85	0.35	0.71	103	0.42
CPC-2585	TPY53	362	84	0.23	112	0.31	0.75	158	0.44

**Remarks.** The species was included into *Plesiotexanites* by Matsumoto (1970), a view accepted by Kennedy et al. (1997a) and here, based on tuberculation, i.e., the presence of umbilical, lateral, submarginal, marginal, and external tubercles. The compressed, dense, and finely ribbed juvenile stage of the species (e.g., Figure 3B) distinguish *P. shiloensis* from all other North American *Plesiotexanites*. *Texanites* s.s. is distinguished by tuberculation and details in ribbing.

**Occurrence.** Upper Santonian to lower Campanian of the Jiménez area of Coahuila, Mexico, the central Texas and Big Bend areas of Texas as well as the state of Mississippi in the US, and Hokkaido, Japan.

Genus TEXANITES Spath, 1932

*Texanites lonsdalei* Young, 1963

Figure 4A–G, Table 2

1963 *Texanites lonsdalei* n. sp.; Young, 1963, p. 90, plate 34, figure 1; plate 51, figures 3–7; plate 58, figures 5, 6; text-figures 22a, d

1967 *Texanites lonsdalei* Young, 1963; Wolleben, p. 1152, pl. 147, figures 4, 5; text-figures 8c, d

1997 *Texanites (Texanites) lonsdalei* Young, 1963; Kennedy and Cobban, p. 17, figures 9–12

**Type.** The holotype is TMM-UT 30474 by original designation by Young (1963: 90, plate 34, figure 1; plate 51, figures 3–7; plate 58, figures 5, 6; text-figures 22a, d). It is from the Dessau Chalk of Kitchens Ranch, Travis County, Texas.

**Material.** CPC-2375, -2377, -2584, IGM 12796, and 12797, and uncollected specimens from beds TPY 21 to TPY 53.

**Description.** Evolute shell with U/D of about 0.4. 28 to 33 sharp ribs rise on the umbilical wall and

strengthen into pointed bullae that project into the umbilicus. These bullae give rise to sharp, straight, moderately prorsiradiate ribs, which are occasionally intercalated by secondary ribs. A row of strong, lateral tubercles is located dorsal of midflank and separated from the umbilical row of bullae. A third slightly weaker row of tubercles is present ventrolaterally; they are rounded to feebly clavate. A fourth row of larger tubercles, respectively coarse clavi, is seen on the venter, next to a siphonal keel from which they are separated by a smooth zone. The secondary ribs also show these outer rows of tubercles, resulting in 36 ventral clavi per whorl. The keel and lateral clavi disappear at largest diameters, and ribs in these large-sized specimens cross the venter in a moderately narrow arch.

**Dimensions.** Table 2.

**Remarks.** Klinger and Kennedy (1980) casted doubt on the validity of *Texanites lonsdalei*, but subsequently, Kennedy et al. (1997a) discussed the species in detail and presented characters for distinction from similar taxa. According to these latter authors, *T. lonsdalei* is distinguished by sharper, straighter ribs than coeval species of *Plesiotexanites* or *Menabites (Delawarella)*.

**Occurrence.** Uppermost Santonian and lowermost Campanian *Menabites (Delawarella) tequesquitense* Zone of Texas. At Tepeyac, the species occurs in the uppermost *Plesiotexanites shiloensis* zone of the Santonian and in the top of the lower Campanian *M. (D.) delawarensis* Zone.

Genus BEVAHITES Collignon, 1939

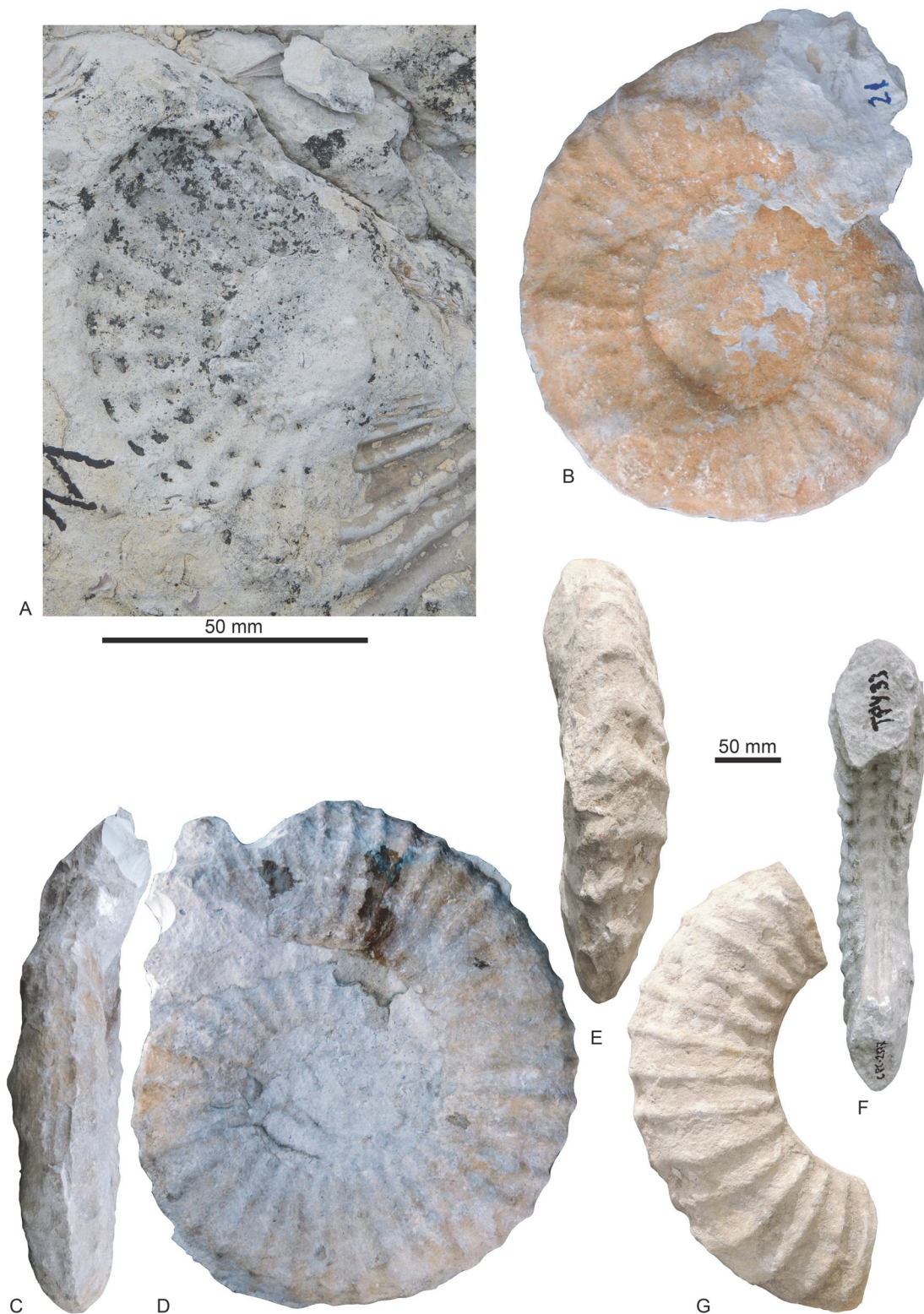
The genus is discussed in detail by Klinger and Kennedy (1980).

*Bevahites bevahensis* Collignon, 1948

Figure 5A–B, G–J, Table 3

1928 *Mortoniceras* sp.; Adkins, plate 34, figure 1





**FIGURE 4.** *Texanites lonsdalei* Young, 1963 from the Tepeyac section. A: in bed TPY11; B: IGM 12796, bed TPY 21 C–D: IGM 12797, bed TPY 14; E–G: CPC–2377, bed TPY33. Scale: 50 mm.

**TABLE 2.** Dimensions of *Texanites lonsdalei*.

	bed of origin	D	WB	WB/D	WH	WH/D	WB/WH	U	U/D
CPC-2377	TPY33	265	51	0.19	95	0.36	0.54	-	-
CPC-2375	TPY33	285	67	0.24	108	0.38	0.62	93	0.33
CPC-2377	TPY33	365	72	0.20	108	0.30	0.67	160	0.44
CPC-2375	TPY33	400	70	0.18	143	0.36	0.49	155	0.39
CPC2584	TPY33								

1948 *Behavites* [sic] *bevahensis* nov. sp.; Collignon, p. 84, plate 11 (5), figures 3, 3a, 3b

p. 1952 *Texanites densinodosus*; Young and Marks, p. 480, 482-483 [not plate 1, figure 1]

1963 *Bevahites bevahensis* Collignon, 1948; Young, p. 94, plate 53, figures 1-7; text-figures 15c, 21d, 27b

1967 *Bevahites bevahensis* Collignon, 1948; Wolleben, p. 1153, plate 148, figure 4; text-figures 8a, b

**Type.** The holotype is the original of Collignon (plate 11, figures 3, 3a, b) by monotypy. It is from the upper Santonian of Bevah, Madagascar, and stored in the Collections de l'École Nationale Supérieure des Mines, Paris, currently housed in the Villeurbanne campus, Université Lyon.

**Material.** Two specimens, CPC-2374 and -2547, from bed TPY26.

**Description.** Moderately involute, with U/D between 0.30 and 0.39. Whorl section suboval; WB/WH = 0.56, with WB largest at mid-flank. Ribs moderately sinuous. One or two ribs arise from prominent, strong umbilical tubercles, although ribbing is moderately inequidistant. Ribs are moderately prorsiradiate and flex back in a wide arch to become straight and rursiradiate ventrolaterally. Bullae are located on the ribs at mid-flank, while broad, faint ventrolateral tubercles are connected to weak clavi next to the venter.

**Dimensions.** Table 3.

**Remarks.** Ribbing and whorl section readily distinguish *Bevahites bevahensis* from other Texanitinae. The adult stage of this species is discussed in detail by Wolleben (1967).

**Occurrence.** Uppermost Santonian of westernmost to central Texas, Chihuahua, Tepeyac in Coahuila, Madagascar.

*Bevahites costatus* Collignon, 1948 *coahuilaensis* Young, 1963  
Figure 5D-F, Table 4

1963 *Bevahites costatus* Collignon, 1948, subsp. *coahuilaensis*, n. subsp.; Young,

p. 96, plate 47, figures 1-4, plate 71, figure 5; text-figures 34b

1967 *Bevahites costatus coahuilaensis* Young, 1963; Wolleben, p. 1156, plate 150, figure 8

**Type.** The holotype is BEG-20288 through original designation by Young (1963, p. 96, plate 47, figures 1-4, plate 71, figure 5, text-figure 34b), from Arroyo Tecolote near Jiménez, Coahuila.

**Material.** Three specimens, CPC-2372, -2546, and -2548 from beds TPY27 to TPY44.

**Description.** Moderately involute, with subrectangular whorl section and a maximum WB at mid-flank. Blunt ribs arise from umbilical tubercles and reach to mid-flank where they bifurcate at a rounded tubercle. From here, secondaries reach to the venter and wear two rows of shallow, ventrolateral tubercles, as well as a third ventrolateral row of clavi. The venter is keeled, with a smooth area between the ventrolateral clavi and the keel.

**Dimensions.** Table 4.

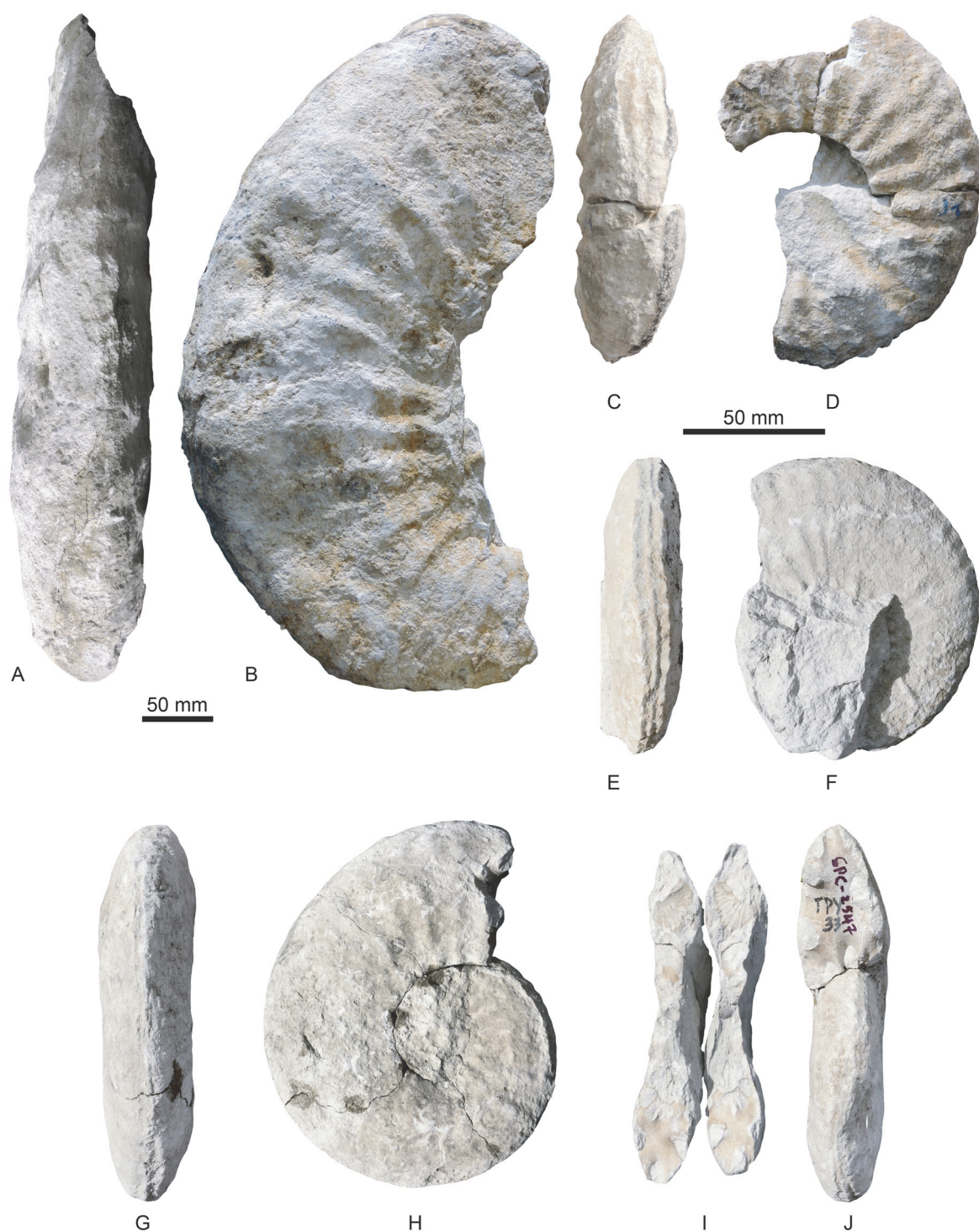
**Remarks.** Young's (1963) type specimens are from the Arroyo Tecolote, located at about 5 km north of Tepeyac. Wolleben (1967) noted that this subspecies of *Bevahites costatus* is rare in the area, but that it occurs in several stratigraphic levels. It differs from *Bevahites bevahensis* in a stout whorl section and ribs bifurcating at D of about 130 mm.

**Occurrence.** *Bevahites costatus coahuilaensis* occurs at about the Santonian-Campanian boundary in the Ojinaga Formation of eastern Chihuahua and in the Jiménez area of Coahuila, Mexico, as well as in western Texas. At Tepeyac, it was identified in beds 27, 36, and 44-46, i.e., in the interval across the Santonian-Campanian boundary. The species was also reported from the lower Campanian of Madagascar (Collignon, 1969).

Genus MENABITES Collignon, 1948  
Subgenus DELAWARELLA Collignon, 1948

Many species described below were earlier included into *Submortonicer* based on quinquetuberculation seen in lower Campanian Texanitinae from Texas, at least during part of their ontogeny, while other species were based on juveniles. How-





**FIGURE 5.** *Bevahites* from the Tepeyac section. A–B, G–J: *Bevahites bevahensis*, A–B: CPC–2374; G–J: CPC–2547, both bed TPY26; C–F: *Bevahites costatus coahuilaensis*, C–D: CPC–2372, bed TPY27; E–F: CPC–2548, beds TPY40–46. Scale: 50 mm.

**TABLE 3.** Dimensions of *Bevahites bevahensiis*.

	bed of origin	D	WB	WB/D	WH	WH/D	WB/WH	U	U/D	number of ribs
CPC-2547	TPY 33	80	26	0.33	-	-	-	-	-	38
CPC-2547	TPY 33	115	44	0.38	50	0.43	0.88	34	0.30	30
CPC-2547	TPY 33	199	44*	0.22*	80	0.40	0.55*	64	0.32	29
CPC-2374	TPY 33	315	70	0.22	125	0.40	0.56	123	0.39	-

**TABLE 4.** Dimensions of *Bevahites costatus coahuilensis*.

	bed of origin	D	WB	WB/D	WH	WH/D	WB/WH	U	U/D	rib index
CPC-2546	TPY36	70	9	0.13	23	0.33	0.39	42	0.60	-
CPC-2546	TPY36	104	21	0.20	39	0.38	0.54	44	0.42	-
CPC-2546	TPY36	154	36	0.23	57	0.37	0.63	54	0.35	-
CPC-2546	TPY36	245	55	0.22	79	0.32	0.70	86	0.35	-
CPC-2548	TPY44-46	123	34	0.28	50	0.41	0.68	33	0.27	64

ever, *Submorticeras* is based on the South African *Morticeras woodsi* Spath, 1921. This taxon defined by Spath (1926) was interpreted to have evolved from *Texanites soutoni soutoni* in South Africa at about the Santonian-Campanian boundary, there producing a large number of endemic species (Klinger and Kennedy, 1980). *Menabites* (*Delawarella*) *tequesquitense* (Morton, 1830), on the other hand, was interpreted to have evolved during the late Santonian from *Plesioexanites shiloensis* (Young, 1963), or alternatively, from the South African *soutoni* lineage (Klinger and Kennedy, 1980); it cannot be assigned to the younger South African genus *Submorticeras*. In the North American *Menabites* (*Delawarella*) group two lineages are distinguished: *M. (D.) tequesquitense* gave rise to the *tequesquitense* – *delawarensis* – *danei* lineage. The proximity between early Campanian Texanitinae from Texas and South Africa suggests a close relationship. The other lineage departs from *M. (D.) vanuxemi* giving rise to *M. (D.) mariscalense* and *M. (D.) uddeni* (Young, 1963) and some more compressed species of this genus endemic to Texas. They are here all included into *Menabites* (*Delawarella*).

*Menabites* (*Delawarella*) *tequesquitense*  
(Young, 1963)

Figure 6A–B, Figure 7A–C, Figure 8, Figure 9,  
Figure 10A–C, Table 5

- 1963 *Submorticeras tequesquitense*, n. sp.;  
Young, p. 97, plate 28, figure 1; plate 42,  
figures 1, 2; plate 44, figures 4, 5; plate  
51, figures 1, 2; plate 52, figures 1-4;  
plate 57, figure 4; plate 70, figure 1; text-  
figures 12b, 28b

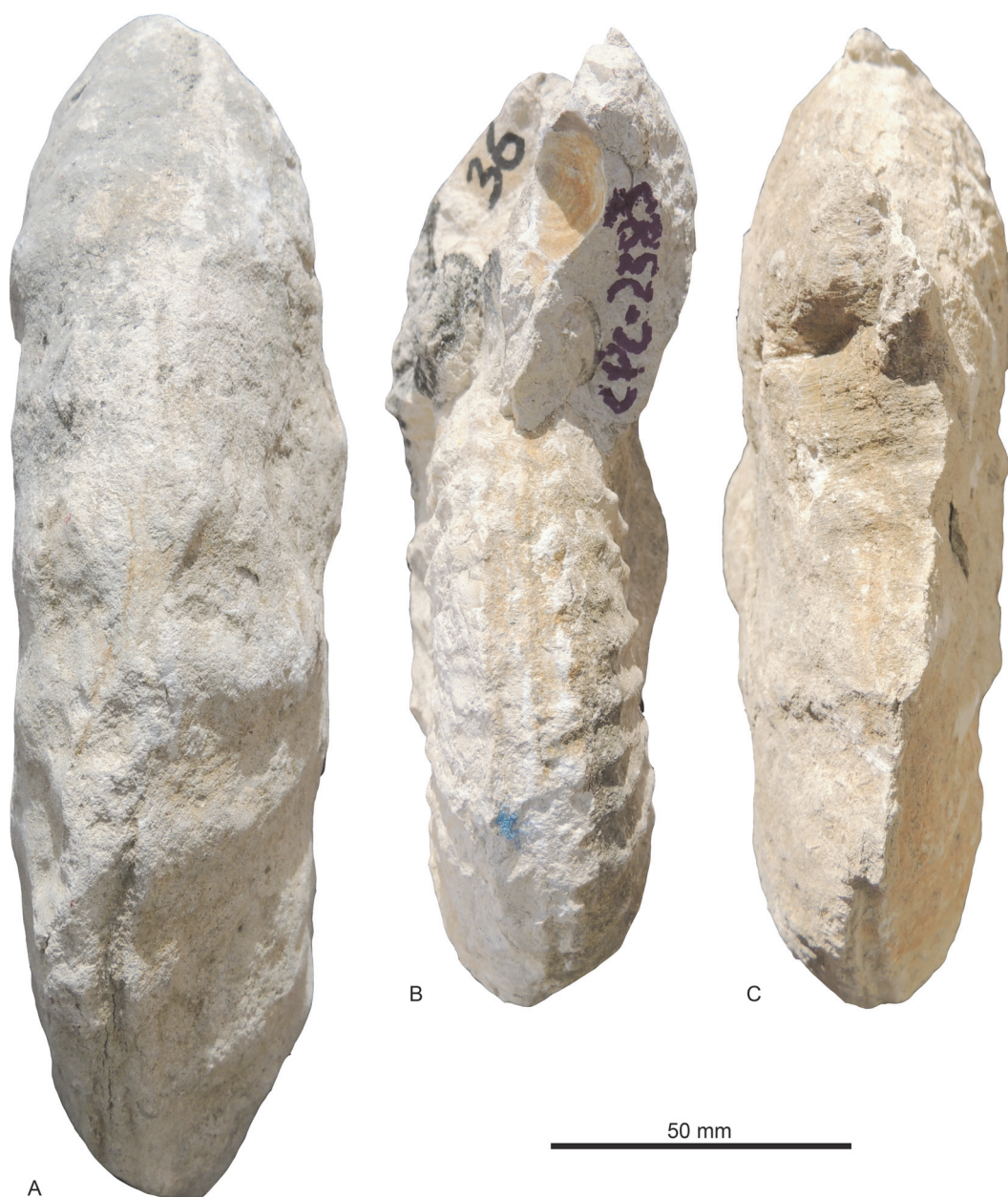


**FIGURE 6.** *Menabites* (*Delawarella*) *tequesquitense* (Young, 1963) from bed TPY33 of the Tepeyac section. A–B: CPC–2381. Scale: 50 mm.

- 1991 *Submorticeras tequesquitense* Young,  
1963; Cobban and Kennedy, p. B3, plate  
1, figures 1, 2  
1997 *Submorticeras tequesquitense* Young,  
1963; Kennedy et al., p.23, figures 14, 15

**Type.** The holotype is TMM 34742 by original designation of Young (1963, p. 97, plate 42, figures 1-2; plate 52, figures 1-2, 4, text-figure 28b). It is from





**FIGURE 7.** *Menabites (Delawarella) tequesquicense* (Young, 1963) from the middle Tepeyac section. A: CPC-2381, TPY33, B–C: CPC-2383, TPY36. Scale: 50 mm.

the upper part of the Dessau Chalk, "downstream from the concrete spillway of the new (1932) Del Rio-Eagle Pass highway crossing on Tequesquite Creek, Kinney County, Texas" (Young, 1963, p. 97).

**Material.** Eight specimens, CPC-2381,–2383, –2387, –2422, –2550,–2551, –2564,–2567, in addition to uncollected specimens, from beds TPY 25 to TPY 50.

**Description.** Evolute shell with a moderately high expansion rate and a relatively wide U (U/D of

0.29–0.41). The umbilical wall seems to be undercut. 24 sharp umbilical bullae are present per whorl and project into the umbilicus. Sharp single or paired ribs arise from these bullae. They are broad and low, straight to slightly prorsiradiate, and efface markedly on the flanks. A row of sharp lateral tubercles is situated near mid-flank and separated by a row of weaker, ventrolateral tubercles. Each of these tubercles is connected by a low and broad rib to stronger elongate clavi; the latter are separated from the strong siphonal keel by a



**FIGURE 8.** *Menabites (Delawarella) tequesquitense* (Young, 1963) from bed TPY36 of the Tepeyac section. CPC-2383, left lateral view. Scale: 50 mm.

smooth sulcate-shaped zone. The external clavi thus flank the bisulcate-carinate venter. In adult specimens the clavi and keel are replaced by weaker, broad rounded tubercles, and the ribs cross a moderately wide rounded venter.

**Dimensions.** Table 5.

**Remarks.** The well-developed ribs on the inner whorls readily distinguish this species from all other Gulf Coast representatives of the genus described by Young (1963) as *Submortonicerases*, including *S. sancarlosense*, *S. mariscalense*, *S. uddeni*, and *S. vandaliaense*.

Klinger and Kennedy (1980) suggested *Menabites (Delawarella) tequesquitense* to be closely allied if not conspecific with *Submortonicerases woodsi*, because dimensions of the two species overlap. Apart from a slightly narrower whorl section, denser and more forwardly curved costation, there seems to be little difference between *M. (D.) tequesquitense* and *S. woodsi*. However, this difference is here considered to be sufficient for specific differentiation. Young (1963, p. 98) suggested that *M. (D.) tequesquitense* could be derived from *Plesiotelexanites shiloensis*. However, affinities of *Menabites (Delawarella) tequesquitense* with the





**FIGURE 9.** *Menabites (Delawarella) tequesquitense* (Young, 1963) from bed TPY36 of the Tepeyac section. CPC-2383, right lateral view. Scale: 50 mm.

South African *T. soutoni* seem closer than with *P. shiloensis*. In this view *M. (D.) tequesquitense* would also be derived from *T. soutoni* and then give rise to the North American succession of species. It nevertheless appears that both lineages are closely connected and that a repeated interchange of these species occurred between the South African – Madagascar Southern Ocean and the Ancient Gulf of Mexico.

**Occurrence.** *Menabites (Delawarella) tequesquitense* is the index fossil of the identical uppermost Santonian-lowermost Campanian ammonite

zone, introduced for the Gulf Coast region by Young (1963). The zone has been recorded in Mississippi, Alabama, and Texas (Young, 1963; Kennedy et al., 1997a). A single specimen documented by Kennedy et al. (1997a) from New Mexico, has been collected from the *Scaphites (Scaphites) hippocrepis* I zone.

*Menabites (Delawarella) delawarensis*  
(Morton, 1830)

Figure 11, Figure 12, Figure 13, Table 6

1830 *Ammonites delawarensis* Morton, p. 244,  
plate 2, figure 4.



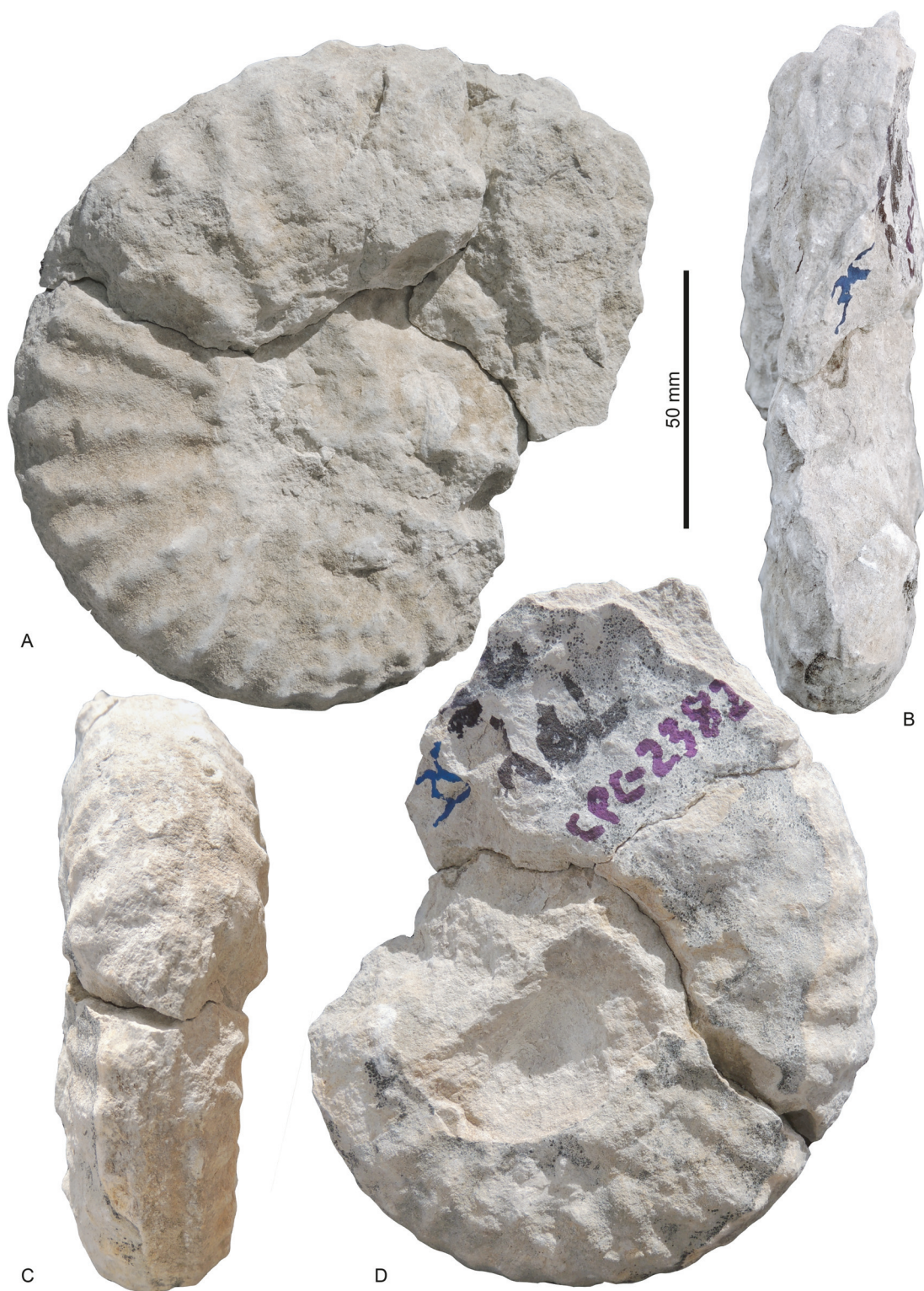
**FIGURE 10.** *Menabites (Delawarella) tequesquitense* (Young, 1963) from the Tepeyac section. CPC-2422, bed of origin unknown. Scale: 50 mm.

1948	<i>Menabites (Delawarella) delawarensis</i> (Morton; Collignon, p. 29 (86) (with synonymy))	445, figures 4.6-4.9, 5.1, 5.2, 5.6, 5.7, 5.11-5.13
1986	<i>Menabites (Delawarella) delawarensis</i> (Morton, 1830); Kennedy, p. 81, plate 3, figures 3, 4 (with synonymy)	1993a <i>Menabites (Delawarella) delawarensis</i> (Morton, 1830); Kennedy and Cobban, p. 836, figures 5.10, 5.11, 9.5-9.13, 10.3, 11.1, 11.2, 11.4-11.6, 11.8, 11.9, 11.11
1992a	<i>Menabites (Delawarella) delawarensis</i> (Morton, 1830); Cobban and Kennedy, p. 73, plate 6, figure 9	1996 <i>Menabites (Delawarella) delawarensis</i> (Morton); Wiese, plate 1, figure 1a-b
1992b	<i>Menabites (Delawarella) delawarensis</i> (Morton, 1830); Cobban and Kennedy, p.	1997 <i>Menabites (Delawarella) delawarensis</i> (Morton, 1830); Kennedy et al., p. 23, figures 16, 17, 18d-e

**TABLE 5.** Dimensions of *Menabites (Delawarella) tequesquitense*.

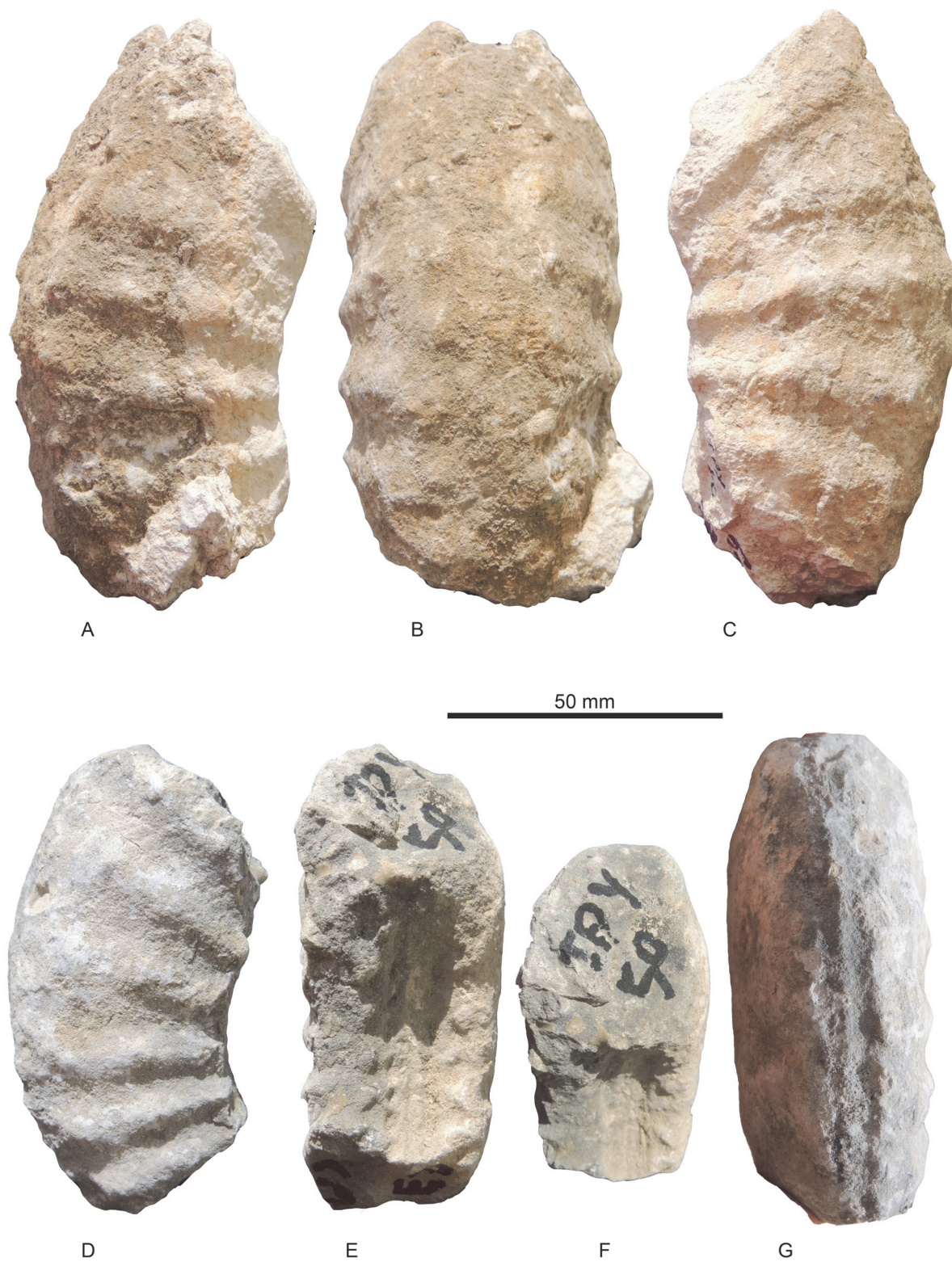
	bed of origin	D	WB	WB/D	WH	WH/D	WB/WH	U	U/D	rib index
CPC-2422	TPY	83	28	0.34	26	0.31	1.08	25	0.30	-
CPC-2422	TPY	115	35	0.30	42	0.37	0.83	43	0.37	-
CPC-2567	TPY33	104	28	0.27	43	0.41	0.65	24	0.23	42
CPC-2564	TPY23-25	117	42	0.36	39	0.33	1.08	45	0.38	30
CPC-2383	TPY36	121	32	0.26	46	0.38	0.70	50	0.41	-
CPC-2383	TPY36	162	45	0.28	63	0.39	0.71	65	0.40	-
CPC-2381	TPY33	-	45	-	68	-	0.66	0	-	-
CPC-2551	TPY35	172	45	0.26	62	0.36	0.73	66	0.38	30
CPC-2387	TPY50	-	50	-	78	-	0.64	-	-	-
CPC-2550	TPY35	215	56	0.26	71	0.33	0.79	68	0.32	30



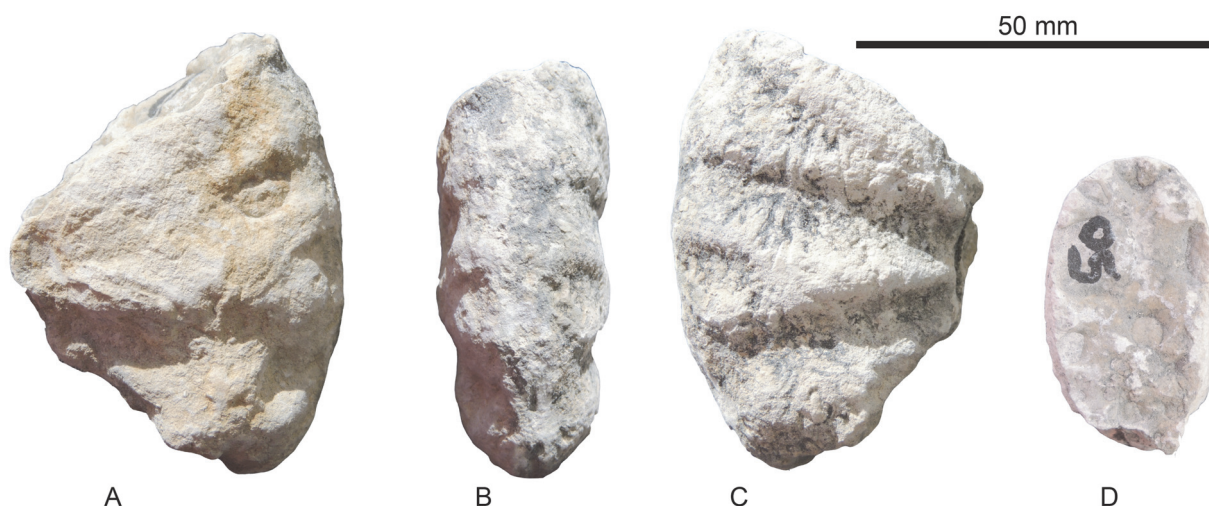


**FIGURE 11.** *Menabites (Delawarella) delawarensis* (Morton, 1830) from bed TPY35 of the Tepeyac section. A–D: CPC-2382. Scale: 50 mm.





**FIGURE 12.** *Menabites (Delawarella) delawarensis* (Morton, 1830) from the middle Tepeyac section. A–C: CPC–2386, TPY40. D–G: CPC–2388, TPY50. Scale: 50 mm.



**FIGURE 13.** *Menabites (Delawarella) delawarensis* (Morton, 1830) from bed TPY50. A–D: CPC–2388. Scale: 50 mm.

**Types.** The types are lost (see Reeside, 1962 p. 132, and Kennedy, 1986 p. 81).

**Material.** Fourteen specimens, CPC-2382,–2386, –2388, –2389, –2550, –2551, –2552, –2564, –2568,–2569, –2573,–2584, –2585, and –2586 from beds TPY33 to above TPY 60, in addition to uncollected specimens.

**Description.** Evolute coiling, with U/D between 0.32 and 0.51 and a depressed whorl section. Greatest WB occurs below mid-flank intercostally

and at the lateral tubercles costally. The umbilicus is deep, with a flat, vertical wall and narrowly rounded umbilical shoulder. The inner flanks are flattened and subparallel, the outer flanks broadly rounded and convex, and the venter is broadly arched. Sharp umbilical bullae on the umbilical shoulder give rise to 27 to 36 broad, slightly rursiradial single or paired ribs, their number increasing with diameter. These bullae give rise to strong, straight prosiradial ribs. Each submarginal tuber-

**TABLE 6.** Dimensions of *Menabites (Delawarella) delawarensis*.

	bed of origin	D	WB	WB/D	WH	WH/D	WB/WH	U	U/D	number of ribs
CPC-2389	TPY50	-	22	-	38	-	0.58	-	-	-
CPC-2382	TPY35	74	25	0.34	34	0.46	0.74	-	-	-
CPC-2569	TPY35	95	34	0.36	35	0.37	0.97	33	0.35	-
CPC-2388	TPY50	-	35	-	38	-	0.92	-	-	-
CPC-2569	TPY35	110	39	0.35	41	0.37	0.95	36	0.33	27
CPC-2382	TPY35	114	32	0.28	43	0.38	0.74	36	0.32	-
CPC-2568	TPY60+	127	31	0.24	46	0.36	0.67	53	0.42	-
CPC-2573	TPY46	138	30	0.22	60	0.43	0.50	28	0.20	?
CPC-2552	TPY60	150	45	0.30	47	0.31	0.96	62	0.41	26
CPC-2568	TPY60+	159	53	0.33	58	0.36	0.91	62	0.39	22
CPC-2551	TPY35	172	45	0.26	62	0.36	0.73	66	0.38	30
CPC-2586	TPY42-44	175	55	0.31	66	0.38	0.83	65	0.37	20
CPC-2552	TPY60	203	73	0.36	45	0.22	1.62	75	0.37	25
CPC-2550	TPY35	215	56	0.26	71	0.33	0.79	68	0.32	30
CPC-2585	TPY53	245	60	0.24	85	0.35	0.71	103	0.42	28
CPC-2585	TPY53	362	84	0.23	112	0.31	0.75	158	0.44	33
CPC-2584	TPY33	475	100	0.21	165	0.35	0.61	190	0.40	36

cle splits into a marginal clavus and conical submarginal tubercle, while a lateral tubercle is situated near mid-flank. A broad, smooth sulcate zone separates the external clavi from the siphonal keel, which is only preserved in smaller specimens.

**Dimensions.** Table 6.

**Discussion.** *Menabites (Delawareella) delawarensis* is similar to *M. (D.) tequesquitense* from which it differs by coarser ribbing. *M. (D.) danei* Young, 1963 is characterized by even coarser ribbing, stronger umbilical, submarginal, and external tubercles only. *M. (D.) vanuxemi* (Morton, 1834), also described below, is more compressed and involute, and tubercles are subordinate to ribs.

Our specimens present a slightly lower WB/WH ratio than specimens published by other authors. This may partially be due to diagenetic compression but majorly reflects wide intraspecific variation, as known for *Schloenbachia varians* (Wilmsen and Mosavinia, 2011) and *Pseudoschloenbachia mexicana* (see Ifrim et al., 2013).

**Occurrence.** Middle lower Campanian *Menabites (Delawareella) delawarensis* zone in Delaware and New Jersey, Texas, and Oklahoma (Young, 1963; Cobban and Kennedy, 1992b; Kennedy and Cobban, 1993a; Kennedy et al., 1997a; Kennedy et al., 1997b). Isolated specimens are also reported from the lower Campanian of Aquitaine, France, from Spain, the lower Campanian of Zululand (South Africa) and, possibly, Madagascar (Besaire, 1930; Klinger and Kennedy, 1980; Kennedy, 1986), but not in western Coahuila (Ifrim et al., 2013).

*Menabites (Delawareella) danei* (Young, 1963)  
Figure 14A–B

- 1929 *Mortonicerias delawarensis* (Morton), Dane, 1929, pl. 10, figures 1, 2
- 1963 *Delawareella danei*, n. sp.; Young, 1963, p. 114, plate 57, figure 6, plate 62, figures 1, 2; p. 64, figures 1, 5; p. 65, figures 1, 2; plate 66, figures 3, 4; text-figures 24e, 33b
- 1992a *Menabites (Delawareella) danei* (Young, 1963); Cobban and Kennedy, p. 74, plate 2, figures 5–8; plate 3, figures 1–3; plate 4, figures 1, 12
- 1992b *Menabites (Delawareella) danei* (Young, 1963); Cobban and Kennedy, p. 448, figures 3.2–3.4, 5.5, 5.10
- 1997 *Menabites (Delawareella) danei* (Young, 1963); Kennedy et al., p. 29, figures 19, 20

**Type.** The holotype is UT–30646 by original designation by Young (1963, p. 114, plate 57, figure 6;

plate 62, figures 1, 2; plate 65, figure 1; plate 66, figure 4; text-figure 33b). It is from “a formation equivalent in age to the Gober chalk,” in McCurtain County, Oklahoma, 1 mile west of the Oklahoma–Arkansas state boundary on Route 3 from Foreman, Arkansas, to Tom, Oklahoma.

**Material.** Three specimens, CPC–2409 and –2421 from beds TPY 75 and TPY 77, CPC–2590 from bed TPY83, in addition to an uncollected specimen from bed 50.

**Description.** Evolute coiling, with an U/D ratio of 0.43. The WB/WH ratio is 0.67, with greatest breadth at about mid-flank. Seventeen strong umbilical bullae per whorl give rise to coarse, blunt, prorsiradiate ribs, which efface at mid-flank and again strengthen on the outer flank, where they develop coarse, submarginal tubercles. Broad, coarse ribs link to a row of clavi, with about the same number of additional clavi intercalated. A deep ventral groove separates the row of clavi from the siphonal keel. Faint tubercles at mid-rib are present on the last half whorl, and a second row of ventrolateral tubercles is seen on the last three ribs.

**Dimensions.** CPC-2421, D: 117, WB: 29 (0.25), WH: 43 (0.37), WB/WH: 0.67, U: 50 (0.43). CPC-2590, WB: 16, WH: 24, WB/WH: 0.67.

**Remarks.** Specimens of this species show a prolonged *Australiella* stage and a transition to a typically penta-tuberculate *Delawareella* ornamentation at large diameters. *Menabites (Delawareella) danei* is distinguished from all other American *Delawareella* by the unique coarseness of tuberculation and ribbing. The species is closely related to *M. (D.) sabinalensis* (Young, 1963), which has no tubercles and intercalated secondaries, instead of the bifurcating ribs and strong tuberculation of *M. (D.) danei*.

Traces of septate spines as described by Kennedy et al. (1997a) cannot be identified in the Tepeyac specimens, although the tubercles seem to be extended.

**Occurrence.** Upper lower Campanian of Oklahoma, Texas, Colorado (zone of *Baculites obtusus*), and now north-eastern Mexico.

*Menabites (Delawareella) sp.*  
Figure 15A–C

**Material.** Two specimens, CPC–2588 from bed TPY77 and –2590 from bed TPY80.

**Dimensions.** CPC-2588, D: 140, WB: 40(0.29), WH: 62 (0.44), WB/WH: 0.65, U: 43 (0.31), ribs per whorl: 34.

**Remarks.** This morphotype has no tubercles and strong, simple ribs, contrasting with all other spe-





**FIGURE 14.** *Menabites (Delawarella) danei* (Young, 1963) from bed TPY77. A–B: CPC– 2421. Scale: 50 mm.

cies in this genus. The two specimens may or may not belong to the same species. CPC–2590 has a polygonal whorl section comparable to *M. (D.) danei* but has more convergent flanks, and ribbing is finer. *Menabites (Delawarella) sabinaiensis* (Young, 1963, p. 112, Pl. 54, figure 2, Pl. 63, figures 1, 3, 4, text-figures 20c, 21e, 26c) is a boldly and distantly ribbed species, with weakly developed tubercles and quadri-tuberculate ornamentation in adults. However, tubercles are absent in our specimens.

**Occurrence.** Only known from the upper Tepeyac section close to the early-middle Campanian boundary.

*Menabites (Delawarella) vanuxemi* (Morton, 1830)  
Figure 16A–F, Table 7

- 1830 *Ammonites vanuxemi* Morton, p. 244, plate 3, figures 2–4.
- 1962 *Submortonicerias vanuxemi* (Morton); Reeside, p. 133, plate 72, figures 4, 5 (with synonymy)
- 1963 *Submortonicerias vanuxemi* (Morton); Young, p. 98, plate 54, figure 3; plate 56, figure 2; plate 57, figure 7; plate 58, figure 3; plate 67, figure 3; plate 69, figure 1, 2, 6; text-figures 12c, 12e, 26d– 26e (with synonymy)
- 1967 *Submortonicerias vanuxemi* (Morton); Wolleben, p. 1156, plate 17, figure 1, plate 148, figure 3

- 1992b *Menabites (Delawarella) vanuxemi* (Morton); Cobban and Kennedy, p. 76, plate 2, figures 2–4 (with additional synonymy)
- 1993a *Menabites (Delawarella) vanuxemi* (Morton, 1830); Kennedy and Cobban, p. 838, figures 11.3, 11.7, 11.10, 11.11, 11.12, 12.5, 12.6, 12.17–12.19, 13.1
- 1997a *Menabites (Delawarella) vanuxemi* (Morton, 1830); Kennedy et al., p. 27, figure 18a
- 2013 *Menabites (Delawarella) vanuxemi* (Morton, 1830); Ifrim et al., p. 889, figures 3.8, 3.9, 4.5, 4.6

**Types.** The holotype, by monotypy, is No. 19492 in the collection of the Academy of Natural Sciences in Philadelphia (Morton, 1830, plate 3, figures 2–4; refigured by Reeside, 1962, plate 72, figures 4, 5). It is from the Chesapeake and Delaware Canal in Delaware, USA.

**Material.** Eight specimens, CPC-2379, –2390, –2391, –2575, –2578, –2579, –2587, and –2591, and numerous uncollected specimens from bed TPY33 to TPY77.

**Description.** Moderately involute shell with compressed whorls; the WB/WH ratio is between 0.43 and 0.67 and decreases upsection; U/D is between 0.16 and 0.27. The umbilical wall bends narrowly into parallel, then convergent flanks; greatest whorl width is below mid-flank. The ventrolateral shoulders are narrowly rounded. Eight to nine umbilical bullae per half whorl give rise to pairs of straight, moderately prorsiradiate ribs. Secondaries are intercalated. Weak but pointed tubercles are present on the ventrolateral shoulder. Ribs terminate at small external clavi; there is a smooth zone between these and the siphonal ridge.

**Dimensions.** Table 7.

**Remarks.** Among the finely ornamented species of this subgenus, this is the least compressed form. *Menabites (Delawarella) mariscalense* is almost smooth at similar diameters, *M. (D.) uddeni* and the other compressed species differ in their type of ribbing at similar diameters.

**Occurrence.** Records are from the upper lower Campanian of the Atlantic Coast, northern and western Gulf Coastal Plain, and the Western Interior of North America (Reeside, 1962; Young, 1963; Wolleben, 1967, 1977; Cobban and Kennedy, 1992a, 1992b; Larson et al., 1997; Ifrim et al., 2013). The species was described to be restricted to the upper lower Campanian, but at Tepeyac it was identified near the base of the Campanian.



**FIGURE 15.** *Menabites (Delawarella)* n. sp. from the upper Tepeyac section. A–C: CPC– 2393, TPY73. D–F: CPC– 2560, TPY74. Scale: 50 mm.

*Menabites (Delawarella) mariscalense*  
(Young, 1963)

Figure 17A–K, Table 8

1963 *Submortonicerias mariscalense*, n. sp.;  
Young, p. 104, plate 59, figure 3; plate  
60, figures 1, 4–6; text-figure 14b, f

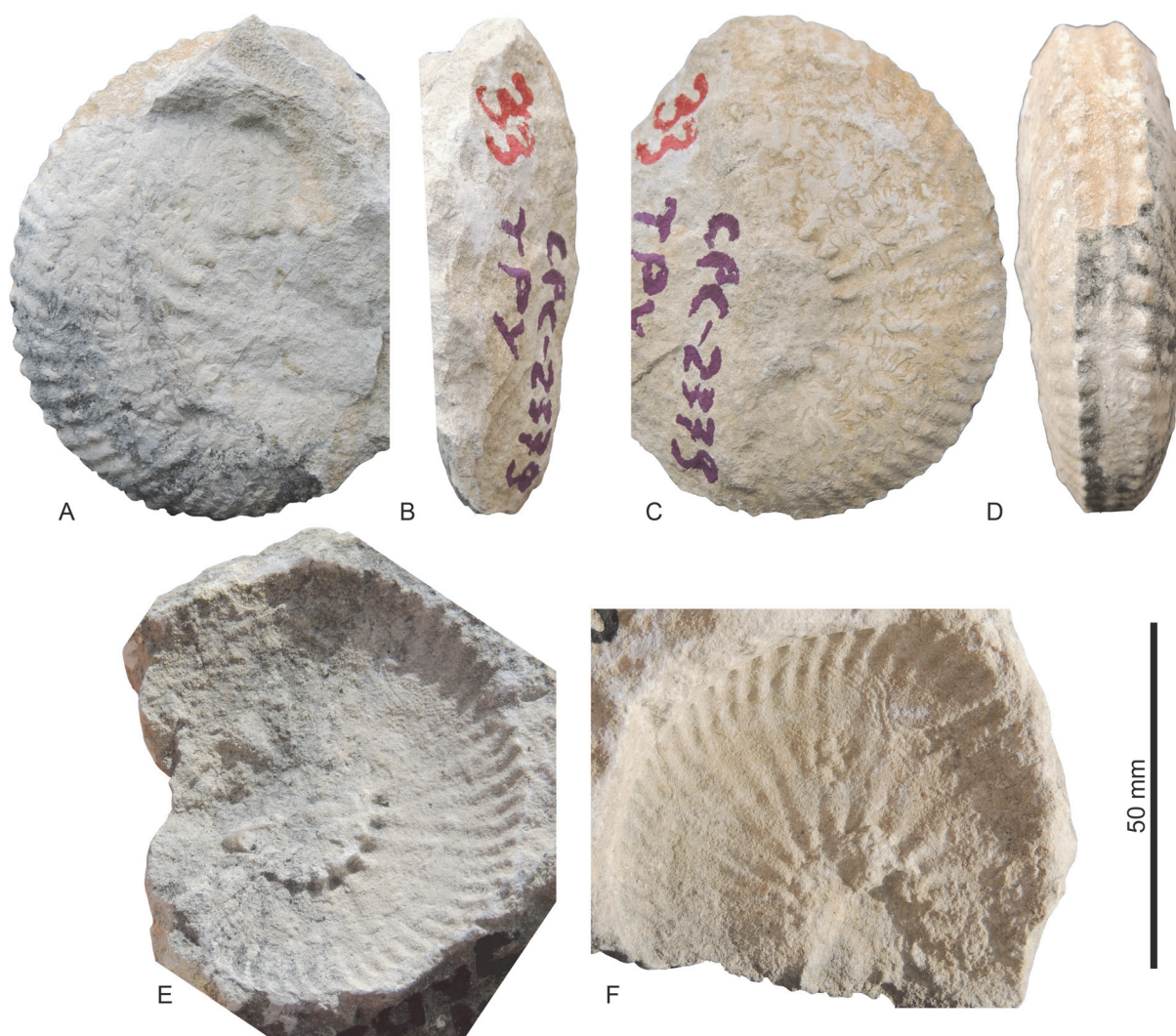
**Type.** The holotype is BEG–20478 by original designation by Young (1963, p. 104, plate 59, figure 3; plate 60, figures 1, 4–6; text-figure 14b, f). It is from

“the concretion horizon on the west side of Mariscal Mountain, Big Bend National Park, Brewster County,” Texas.

**Material.** Five specimens, CPC–2380, –2401, –2553, –2565, and –2566.

**Description.** Moderately compressed whorl with involute coiling, U/D is 0.16 to 0.19, WB/WH is 0.43 to 0.58, decreasing throughout ontogeny. The ornament is *vanuxemi*-like, with fine ribs rising from small umbilical tubercles, but ribs efface on the





**FIGURE 16.** *Menabites (Delawareella) vanuxemi* (Morton, 1830) from the middle Tepeyac section. A–D: CPC–2379, TPY33. E: CPC–2390, TPY50. F: CPC–2391, TPY50. Scale: 50 mm.

flanks so that the outer whorl is almost smooth. At  $D > 50$  mm, flanks and venter are smooth, and the venter is moderately wide and rounded. Only umbilical tubercles persist into this largest stage.

**Dimensions.** Table 8.

**Remarks.** *Submortonicerias mariscalense* Young, 1963 (p. 104, plate 59, figure 3, p1. 60, figures 1, 4–

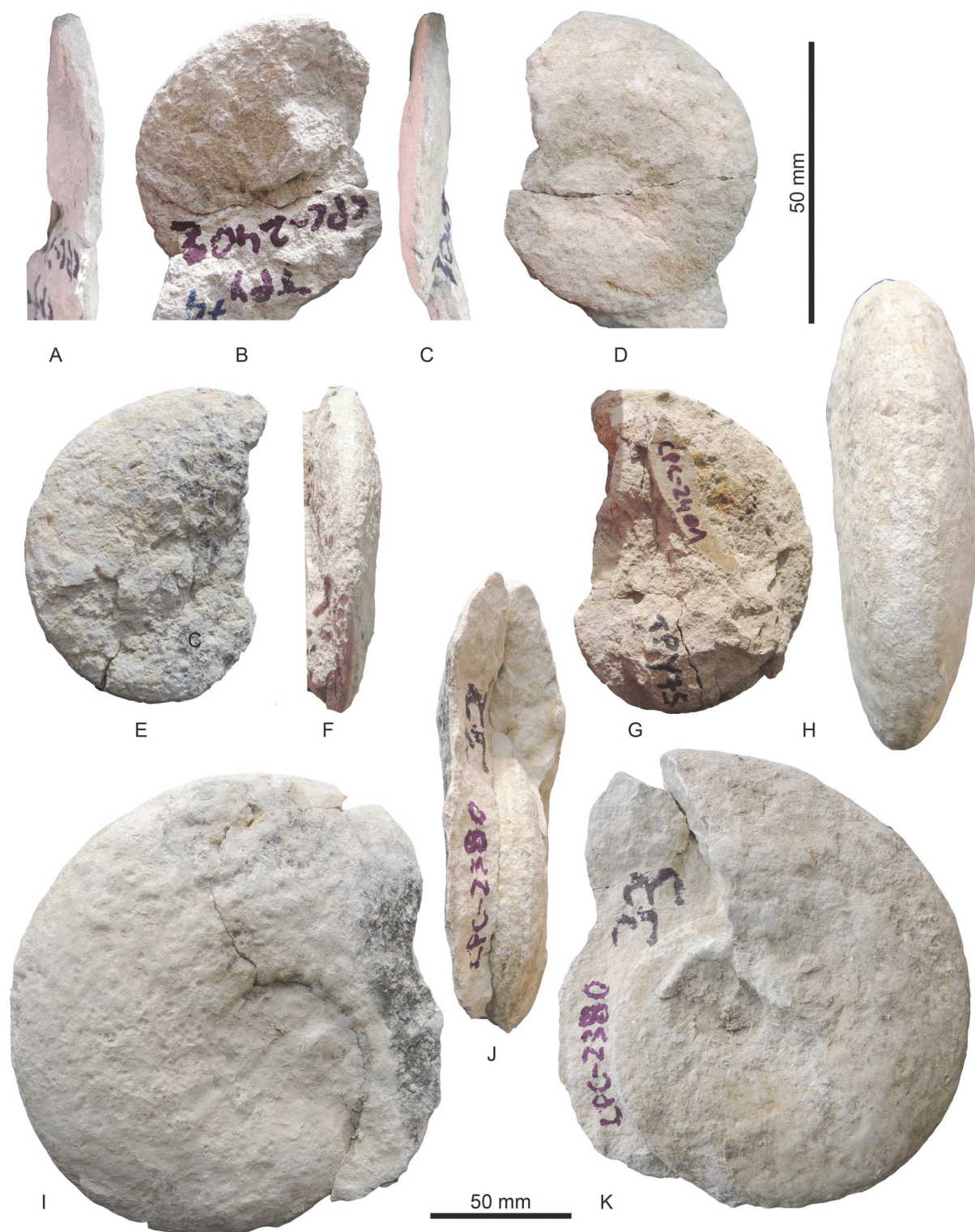
6, text-figures 14b, f) is based on a single specimen to which five more are added here. It is more evolute and smoother than all other species of the discoidal *Menabites (Delawareella)* group.

The species was hitherto included into *Submortonicerias*, but is here interpreted to have evolved from *Menabites (Delawareella) vanuxemi*. It

**TABLE 7.** Dimensions of *Menabites (Delawareella) vanuxemi*.

	bed of origin	D	WB	WB/D	WH	WH/D	WB/WH	U	U/D	number of ribs
CPC-2579	TPY77	48	9*	0.19	21	0.44	0.43*	13	0.27	52
CPC-2390	TPY50	51	-	-	27	0.53	-	8	0.16	-
CPC-2391	TPY50	68	-	-	37	0.54	-	12	0.18	-
CPC-2591	TPY69top	75	24	0.32	36	0.48	0.67	15	0.20	95
CPC-2379	TPY33	79	23	0.29	36	0.46	0.64	16	0.20	-





**FIGURE 17.** *Menabites (Delawareella) mariscalense* (Young, 1963) from the Tepeyac section. A–D: CPC–2402, from bed TPY74, E–G: CPC– 2401 from bed TPY75, H–K: CPC–2380 from bed TPY33. Scale: 50 mm.

**TABLE 8.** Dimensions of *Menabites (Delawarella) mariscalense*.

	bed of origin	D	WB	WB/D	WH	WH/D	WB/WH	U	U/D	number of ribs
CPC-2553	TPY77	43	9.5	0.22	19	0.44	0.50	10	0.23	65
CPC-2553	TPY77	57	16*	0.28*	25	0.44	0.64*	9	0.16	60
CPC-2587	TPY83	80	18*	0.23*	42	0.53	0.43	17	0.21	70
CPC-2380	TPY33	100	34	0.34	49	0.49	0.69	25	0.25	-
CPC-2566	TPY60	126	25	0.20	53	0.42	0.47	29	0.23	-
CPC-2401	TPY75	127	29	0.23	62	0.49	0.47	30	0.24	-
CPC-2565	TPY53	130	35	0.27	67	0.52	0.52	38	0.29	48
CPC-2380	TPY33	156	41	0.26	71	0.46	0.58	42	0.27	-
CPC-2565	TPY53	180	37	0.21	72	0.40	0.51	57	0.32	42

is therefore here assigned to this genus. However, both are also close to compressed species from Madagascar, potentially indicating another relationship.

**Occurrence.** This species is endemic to the lower Campanian of western Texas and across the border into northeastern Mexico.

*Menabites (Delawarella) vandaliense*  
(Young, 1963)  
Figure 18A–B

1963 *Submorticeras vandaliense*, n. sp.;  
Young, p. 102, pl. 55, figures 6, 7; text-  
figures 26a

?1993a *Submorticeras uddeni* Young, 1963;  
Kennedy and Cobban, p. 842, figures  
10.1, 12.3, 12.4, 12.7, 12.8

**Type.** The holotype is UT–30638, by original designation by Young (1963, p. 102, plate 55, figures 6, 7; text-figure 26a). It is from the Blossom Sand in Red River County, Texas.

**Material.** One specimen, CPC–2576 from bed TPY77.

**Description.** Involute. Whorl section compressed, with greatest width at mid-flank. Flanks converge moderately towards the subrounded venter. Nineteen pointed umbilical tubercles give rise to branching prorsiradiate ribs which efface on the flanks. They strengthen on the outer flank and form numerous fine oblique bullae on the ventrolateral shoulder. They terminate before reaching the siphonal keel so that the latter is accompanied by narrow smooth grooves.

**Dimensions.** CPC-2576, D: 90, WB: 12 (0.17), WH: 29 (0.42), WB/WH: 0.41, U: 11 (0.16), number of ribs: 50.

**Remarks.** This rare species was based on a single specimen with fine ribbing presented by Young (1963), to which another is added here. It differs

from *Menabites (Delawarella) vanuxemi* in the weakening of the outer tubercles at larger diameters and lateral effacing of the ribs. In this aspect it is similar to *M. (D.) uddeni*, but ventrolateral ornament is finer. Young (1963) already discussed that *Submorticeras vandaliense* and *S. sancarlosense* may be conspecific, but this question cannot be answered here.

The specimen described as *Submorticeras uddeni* Young, 1963, by Kennedy and Cobban (1993a, p. 842, figures 10.1, 12.3, 12.4, 12.7, 12.8) has finer ornament than the nominate species and is better placed in *Menabites (Delawarella) vandaliense*. It is from the Merchantville Formation exposed on the flanks of the Chesapeake and Delaware Canal 1.65 km (1 mi) east of Summit Bridge on the north side of the canal, New Castle County, Delaware, and thus lacks precise stratification.

**Occurrence.** Upper Santonian of Texas (but see discussion on the age of the Blossom Sand below), Merchantville Formation of New Castle County, Delaware, USA, and lower Campanian of Tepeyac, Mexico. Where precisely dated the species is from the lower Campanian.

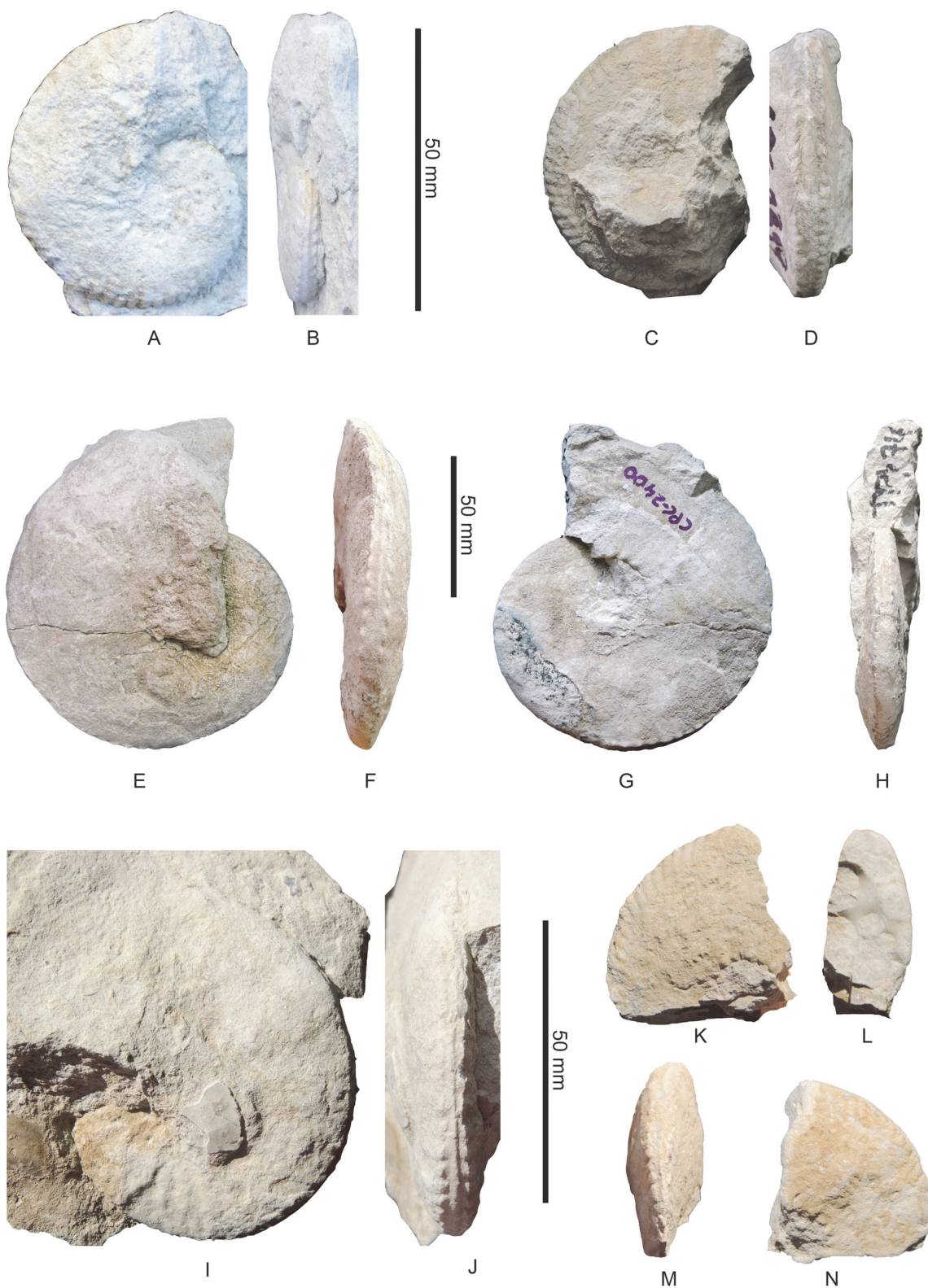
*Menabites (Delawarella) uddeni* (Young, 1963)  
Figure 18, Table 9

1963 *Submorticeras uddeni*, n. sp.; Young,  
p. 105, pl. 59, figures 1, 2, 4–9; pl. 60,  
figures 2, 3, 7, 9, 10; text-figures 14d, e,  
28c

non 1993a *Submorticeras uddeni* Young, 1963;  
Kennedy and Cobban, p. 842, figures  
10.1, 12.3, 12.4, 12.7, 12.8 [= possibly *M. (D.) vandaliense*].

**Type.** The holotype is USNM–130739, by original designation of Young (1963, p. 105, plate 59, figures 5, 7–9; text-figure 14e) from near the top of the





**FIGURE 18.** Compressed *Menabites* (*Delawareella*) from the Tepeyac section. A–B: *Menabites* (*Delawareella*) *vandalense* (Young, 1963), CPC–2576 from bed TPY77. *Menabites* (*Delawareella*) *uddeni* (Young, 1963) C–D: CPC–2399, E–H: CPC–2400, both from bed TPY74; I–J: CPC–2416, K–N: CPC–2415, both from bed TPY77. Scale: 50 mm.

**TABLE 9.** Dimensions of *Menabites (Delawarella) uddeni*.

	bed of origin	D	WB	WB/D	WH	WH/D	WB/WH	U	U/D
CPC-2396	TPY73	-	8.5	-	29	-	0.29	-	-
CPC-2399	TPY74	50	10	0.20	-	-	-	-	-
CPC-2402	TPY74	60	10	0.17	25.5	0.43	0.39	12	0.20
CPC-2416	TPY77	67.5	-	-	-	-	-	-	-
CPC-2405	TPY74	70	14	0.20	30	0.43	0.47	11	0.16
CPC-2575	TPY74	80	15*	0.19*	-	-	-	-	-
CPC-2415	TPY77	-	17.5	-	30	-	0.58	-	-
CPC-2574	TPY83	80	19	0.24	41	0.51	0.46	8	0.10
CPC-2400	TPY74	92	14	0.15	45	0.49	0.31	15	0.16
CPC-2400	TPY74	123	21	0.17	50	0.41	0.42	28	0.23

Terlingua Formation near the east end of Maverick Mountain, Brewster County, Texas.

**Material.** Eight specimens, CPC-2396, -2399, -2400, -2402, -2405, -2415, -2416, and -2574.

**Description.** Involute shell, U/D is between 0.2 and 0.1 and decreases with growth. The whorl section is compressed, with WB/WH ranging between 0.58 and 0.29. Rounded umbilical tubercles give rise to moderately prorsiradiate ribs, which efface on the flanks. Fifty-eight ribs are present on the last whorl at D=80 mm.

**Dimensions.** Table 9.

**Remarks.** This species is closely related to *Menabites (Delawarella) mariscalense*, but differs from the latter by a stronger and more prorsiradiate ventrolateral ornament and the absence of a rounded venter near the aperture. *M. (D.) vandaliense* is also closely related but differs by more delicate, more abundant, and more rounded and less prominent ventrolateral tubercles.

According to Young (1963), the species is restricted to the upper *Menabites (Delawarella) tequesquitense* zone, but at Tepeyac it occurs at higher levels of the lower Campanian.

**Occurrence.** Lower lower Campanian in Texas, upper lower Campanian at Tepeyac.

Subgenus BERERELLA Collignon, 1948

**Type species.** *Menabites (Bererella) bererensis* Collignon, 1948. Widely umbilicate and flat conchs with few, widely spaced ribs; discussed by Klingler and Kennedy (1980).

*Menabites (Bererella) walnutensis* (Young, 1963)

Figure 19A–G, Figure 20A–F, Figure 21A–F,

Figure 22, Figure 23A–C, Table 10

1963 *Menabites* s.l. *walnutensis* n. sp.; Young, p. 109, plate 58, figures 1, 4; text-figures 20e–f, 26k

1963 *Submortonicerias chicoense* (Trask, 1856), Young, p. 106, plate 57, figures 13; text-figures 11e–f, 12d

1993 ?*Menabites (Bererella)* sp., Kennedy and Cobban, p. 841, figures 14.36, 14.38, 14.39

1997b *Menabites (Bererella) walnutensis* (Young, 1963); Kennedy et al., p. 4, figure 3a–k, figures 4a–f, 5a–k, 6a–c

**Type.** The holotype is UT-18, by original designation by Young (1963, p. 109, plate 58, figures 1, 4; text-figures 20ef, 26k). It is from Bureau of Economic Geology locality 226-T-4 in Travis County, Texas.

**Material.** Twenty-eight specimens, CPC-2392, -2394, -2395, -2398, -2403, -2406 to -2414, -2417 to -2420, -2549, -2551, -2570, -2572, -2573, -2577, -2580, -2581, -2583, and -2589 from beds TPY46 upwards, but mostly in beds TPY73 to TPY77.

**Description.** Medium-sized, moderately involute shells (U/D between 0.21 and 0.46, increasing with D). The fifth, submarginal row of tubercles is always weak.

**Dimensions.** Table 10.

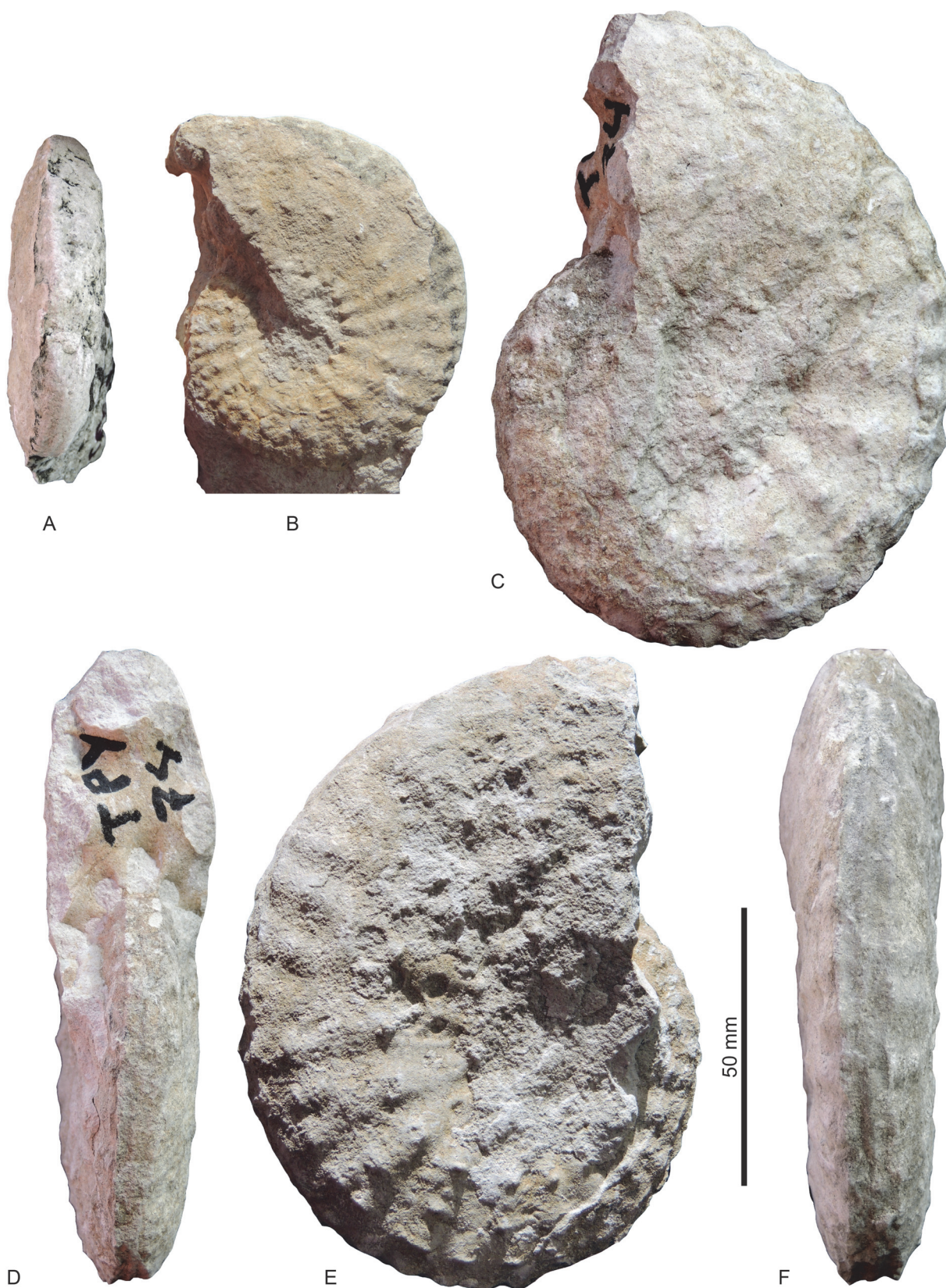
**Remarks.** *Menabites (Bererella) walnutensis* (Young, 1963) is based on a stout specimen (WB/WH ca. 0.9) with coarse ribbing and strong tuberculation. Nevertheless, Kennedy et al. (1997b) demonstrated a wide intraspecific variation and morphological dimorphism between stout and gracile forms of this species. Our specimens thus majorly correspond to the stout specimens and show a similarly wide range of morphologies (Figure 23). This suggests a wide intraspecific variation, as reported for *Pseudoschloenbachia (P.) mexicana* (see Ifrim et al., 2013). With this in mind





**FIGURE 19.** *Menabites (Bererella) walnutensis* (Young, 1963) from beds TPY54 to TPY60. A–B: CPC–2392, TPY54–56. C–D: CPC–2581, TPY60. E–G: CPC– 2549, TPY69top. Scale: 50 mm.





**FIGURE 20.** *Menabites* (*Bererella*) *walnutensis* (Young, 1963) from bed TPY74. A–B: CPC–2404. C–F: CPC– 2406. Scale: 50 mm.





**FIGURE 21.** *Menabites (Bererella) walnutensis* (Young, 1963) from bed TPY77. A–C: CPC–2394 from bed TPY73; D–F: CPC–2419 from bed TPY77. CPC– 2582 from bed TPY77. Scale: 50 mm.

we assign the Tepeyac specimens to *M. (B.) walnutensis*.

**Occurrence.** Merchantville Formation. New Jersey; central and western Texas (Young, 1963; Kennedy et al., 1997b), and now northeastern Coahuila.

Superfamily DESMOCERATOIDEA von Zittel,  
1895

Family MUNIERICERATIDAE Wright, 1952

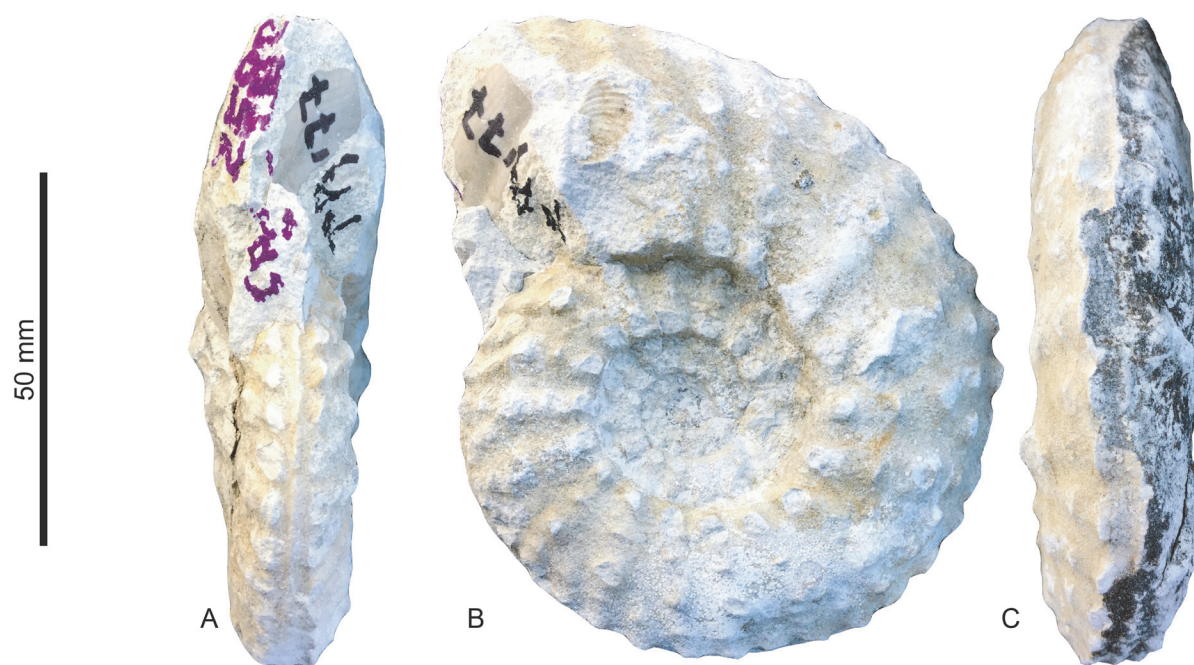
Genus and subgenus PSEUDOSCHLOENBACHIA

Spath, 1921

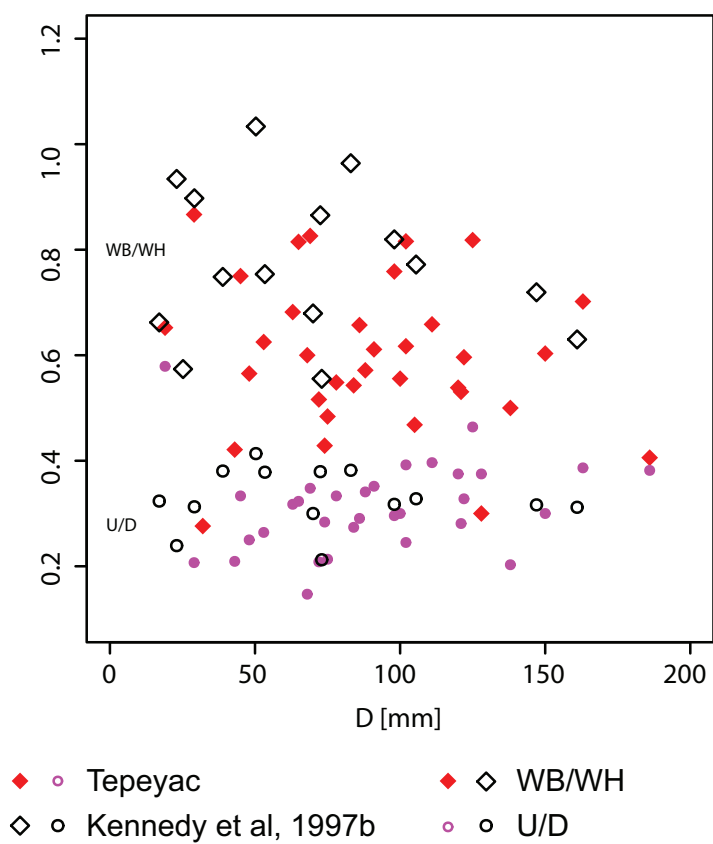
*Pseudoschloenbachia (Pseudoschloenbachia)*  
*mexicana* Renz, 1936  
Figures 24–26, Table 11

1936 *Schloenbachia bertrandi* de Grossouvre  
var. *mexicana* Renz, p. 6, plate 1, figure  
2; plate 3, figure 1

1963 *Pseudoschloenbachia mexicana* Renz;  
Young, p. 121, plate 29, figures 3–4; plate  
30, figures 1–7; plate 31, figures 1, 3–9;



**FIGURE 22.** *Menabites (Bererella) walnutensis* (Young, 1963) from bed TPY77. A–C: CPC–2580. Scale: 50 mm.



**FIGURE 23.** Morphometry of *Menabites (Bererella) walnutensis* (Young, 1963). Full Diamonds: WB/WH for TPY, empty diamonds: WB/WH from Kennedy et al. (1997b), full circles: U/D for TPY, empty circles: U/D from Kennedy et al. (1997b).

**TABLE 10.** Dimensions of *Menabites (Bererella) walnutensis*.

	bed of origin	D	WB	WB/D	WH	WH/D	WB/WH	U	U/D	number of ribs
CPC-2570	TPY77	19	7.5	0.39	11.5	0.61	0.65	-	-	-
CPC-2570	TPY77	29	6.5	0.22	7.5*	0.26*	0.87	6	0.21	-
CPC-2398	TPY74	32	5.8	0.18	21	0.66	0.28	-	-	-
CPC-2570	TPY77	43	8	0.19	19	0.44	0.42	9	0.21	-
CPC-2403	TPY74	48	13	0.27	23	0.48	0.57	12	0.25	-
CPC-2404	TPY74	53	15	0.28	24	0.45	0.63	14	0.26	-
CPC-2420	TPY77	63	15	0.24	22	0.35	0.68	20	0.32	-
CPC-2570	TPY77	65	22	0.34	27	0.42	0.81	21	0.32	-
CPC-2403	TPY74	68	18	0.26	30	0.44	0.60	10*	0.15*	-
CPC-2580	TPY77	69	19	0.28	23	0.33	0.83	24	0.35	32
CPC-2407	TPY74	72	16	0.22	31	0.43	0.52	15	0.21	-
CPC-2417	TPY77	74	15	0.20	35	0.47	0.43	21	0.28	-
CPC-2577	TPY77	75	15	0.20	31	0.41	0.48	16	0.21	62
CPC-2406	TPY74	78	17	0.22	31	0.40	0.55	26	0.33	-
CPC-2581	TPY60	84	19	0.23	35	0.42	0.54	23	0.27	40
CPC-2419	TPY77	86	23	0.27	35	0.41	0.66	25	0.29	-
CPC-2394	TPY73	88	20	0.23	35	0.40	0.57	30	0.34	-
CPC-2580	TPY77	91	22	0.24	36	0.40	0.61	32	0.35	34
CPC-2549	TPY69top	98	22	0.22	29	0.30	0.76	29	0.30	22
CPC-2408	TPY74	99	-	-	42	0.42	-	-	-	-
CPC-2413	TPY74	-	24	-	45	-	0.53	-	-	-
CPC-2395	TPY73	-	25	-	26	-	0.96	-	-	-
CPC-2414	TPY77	-	25	-	31	-	0.81	-	-	-
CPC-2570	TPY77	100	25	0.25	45	0.45	0.56	30	0.30	-
CPC-2409	TPY75	102	31	0.30	38	0.37	0.82	40	0.39	-
CPC-2407	TPY74	102	29	0.28	47	0.46	0.62	25	0.25	-
CPC-2583	TPY63	105	22	0.21	47	0.45	0.47	-	-	60
CPC-2549	TPY69	111	27	0.24	41	0.37	0.66	44*	0.40*	19
CPC-2411	TPY74	120	28	0.23	52	0.43	0.54	45	0.38	-
CPC-2570	TPY77	121	26	0.21	49	0.40	0.53	34	0.28	-
CPC-2410	TPY74	122	31	0.25	52	0.43	0.60	40	0.33	-
CPC-2392	TPY54-56	125	45	0.36	55	0.44	0.82	58	0.46	-
CPC-2551	TPY35	128	-	-	44	0.34	-	48	0.38	30
CPC-2589	TPY77	150	38	0.25	63	0.42	0.60	45	0.30	28
CPC-2412	TPY74	163	40	0.25	57	0.35	0.70	63	0.39	-
CPC-2572	TPY62	186	28	0.15	69	0.37	0.41	71	0.38	44
CPC-2573	TPY46	235	-	-	80	0.34	-	93	0.40	48

- 1963 plate 32, figures 1-6; plate 33, figures 1-3, 5-7, plate 44, figure 1; text-figures 13e, 28d, 29b, d
- 1967 *Pseudoschloenbachia mexicana* Renz; Wolleben, p. 1157, plate 149, figures 4-5
- 1991 *Pseudoschloenbachia (Pseudoschloenbachia) mexicana* Renz; Kennedy and Cobban, p. 172, figures 6.1-2, 7.5-39, 10.17-19, 10.22-23, 12.4
- 1963 *Pseudoschloenbachia* sp. juv. cf. *P. mexicana* Renz; Young, plate 30, figure 9; plate 31, figure 2; plate 33, figure 4





**FIGURE 24.** *Pseudoschloenbachia (P.) mexicana* (Renz, 1936) from the lower and middle Tepeyac section. A–C: CPC–2339, TPY13. D–F: CPC–2334, TPY48–50. Scale: 50 mm.





**FIGURE 25.** *Pseudoschloenbachia (P.) mexicana* (Renz, 1936) from bed TPY48 of the Tepeyac section. A–D: CPC–2337. Scale: 50 mm.





**FIGURE 26.** *Pseudoschloenbachia (P.) mexicana* (Renz, 1936) from the Jiménez region. A–C: CPC–2351. Scale: 50 mm.

**TABLE 11.** Dimensions of *Pseudoschloenbachia* (*P.*) *mexicana*.

	bed of origin	D	WB	WB/D	WH	WH/D	WB/WH	U	U/D
CPC-2339	TPY13	72	26	0.36	29	0.40	0.90	-	-
CPC-2334	TPY48-50	135	-	-	*29	*0.21	-	-	-
CPC-2335	TPY	-	31.5	-	64	-	0.49	-	-
CPC-2336	TPY33	-	-	-	-	-	-	-	-
CPC-2338	TPY53	153	41	0.27	64	0.42	0.64	35	0.23
CPC-2337	TPY48-50	208	58	0.28	102	0.49	0.57	-	-
CPC-2447	unknown	360	*75	*0.21	204	0.57	*0.37	-	-
CPC-2451	unknown	406	108	0.27	175	0.43	0.62	102	0.25
CPC-2450	unknown	678	158	0.23	383	0.56	0.41	67	0.10

2013 *Pseudoschloenbachia* (*Pseudoschloenbachia*) *mexicana* (Renz, 1936); Ifrim et al., p. 885, figures 4.9–4.17, 5.1–5.11, 6.1, 7

**Types.** Lectotype is NMBE 5024066, designated as holotype by Young (1963, p. 121). It is the original of Renz (1936, pl. 3, figure 1). The paralectotype, which corresponds to the original of Renz (1936, pl. 1, figure 2), was lost (U. Menkveld, NMBE, personal comm. 2018). The type specimens are from the Arroyo Tecolote and Arroyo del Fresno, i.e., a few to a maximum of 10 km north of our working area in northeastern Coahuila, Mexico. **Material.** Ten internal moulds, CPC–2334 to –2339 from beds TPY13 to TPY53; CPC–2447, –2450, and –2451 collected earlier from the working area.

**Description.** Oxyxcone, moderately involute. U is mostly covered with sediment, U/D is about 0.25, except for the largest specimen for which it is >670 mm. WB/WH ratio ranges from 0.4 to 0.9. The umbilical wall is short and steep. It bends towards the flanks in a narrow arch in juveniles and in a wide arch in adults. Greatest whorl width is at mid-flank in juveniles and in the umbilical half in adults. Flanks bend towards the acute venter ventrolaterally in a moderately wide arch in juveniles, in a wide arch in late juveniles, and they are flat and convergent in adults. Juvenile ornament consists of an umbilical row of distant tubercles that give rise to seven straight primary ribs per half whorl. In between, secondary ribs are intercalated rising at mid-flank. Tubercles along the ventrolateral shoulder accentuate this narrow edge in juveniles. Ventral to this row of tubercles, all ribs show equal strength and are prorsiradiate and straight, fading towards the venter. The narrow ventrolateral shoulder and the tubercles disappear at larger D, and ribs bifurcate; in adults the ribs are simple, broad, and shallow, with a broad tubercle in the center. The suture line shows an asymmetrically trifid L which

exceeds E in depth. Auxiliary lobes are also asymmetrically trifid.

**Dimensions.** Table 11.

**Remarks.** An exceedingly wide morphological variability of *Pseudoschloenbachia* (*P.*) *mexicana* (Renz, 1936) was documented by Ifrim et al. (2013) based on abundant pyritized moulds from the Union y Progreso site in western Coahuila. This full range of morphological variability is not identified in the Tepeyac material; while CPC–2339 is a rather stout specimen, most other individuals conform discoidal end members. The differences in the morphological habitus may relate to the larger sizes of Tepeyac specimens in comparison to the juveniles documented by Ifrim et al. (2013).

**Occurrence.** *Pseudoschloenbachia* (*P.*) *mexicana* Renz is restricted to the upper Santonian and lower Campanian of Texas, Chihuahua (Renz, 1936; Young, 1963; Wolleben, 1967; Kennedy and Cobban, 1991; Becker et al., 1998), western (Ifrim et al., 2013) and north-eastern Coahuila.

Family DESMOCERATIDAE von Zittel, 1895  
Subfamily PUZOSIINAE Spath, 1922

Synonymy of this subfamily after Wright and Kennedy (1984–1996). Their interpretation includes the Hauericeratinae Matsumoto, 1938.

Genus and subgenus PARAPUZOSIA  
Nowak, 1913

*Parapuzosia* (*Parapuzosia*) *leptophylla*  
Sharpe, 1857

This species was recently re-described by Kennedy (2019). The reader is referred to this paper for systematic description. Occurrences in Northeastern Mexico have been described by Ifrim et al. (in press).

**Occurrence.** Lower Santonian records of *Parapuzosia* (*Parapuzosia*) *leptophylla* exist from southern France (Musée de Paléontologie de Provence, 2010), Austria (Summesberger, 1978), and from



England (Kennedy, 2019). In the upper Santonian, the species is distributed in England and Mexico (Ifrim et al., in press).

*Parapuzosia (Parapuzosia) seppenradensis*  
Landois, 1895

This species was recently re-described by Ifrim et al. (in press). The reader is referred to this publication. All *Parapuzosia (P.)* specimens >> 1 m are exclusively Campanian in age.

**Occurrence.** Uppermost Santonian of the north-western Gulf of Mexico, lower Campanian of Germany, northern and western Gulf of Mexico and England. The age of the specimen from Montana is unknown. *Parapuzosia (Parapuzosia) seppenradensis* is abundant in the Tepeyac section and ranges from the Uppermost Santonian throughout the lower Campanian.

Family PACHYDISCIDAE Spath, 1922

Genus and subgenus PACHYDISCUS Spath, 1922

*Pachydiscus (Pachydiscus) duelmensis*  
(Schlüter, 1872)

Figure 27A–B, Figure 28A–B, Figure 29A–B, Figure 30B–E, Figure 31A, Figure 32A–B, Table 12

- 1872 *Ammonites dülmensis* Schlüter. p. 52. plate 16. figure 1-2
- 1894 *Pachydiscus dülmensis* Schlüter sp.; de Grossouvre. p. 199. plate 20
- 1920 *Pachydiscus dülmensis* Schlüter; Köpplitz. p. 69. plate 8. figure 25
- 1936 *Pachydiscus (Parapachydiscus) jimenezi* Renz. p. 3. plate 2. figure 4, 4a
- 1963 *Eupachydiscus jimenezi* Young. p. 59, plate 14, figures 1, 5; plate 16, figure 4; text-figure 10k
- 1963 *Parapuzosia paulsoni* Young. p. 53, plate 11. figures 3–5; plate 12. figures 1-4; plate 15. figure 10; plate 17. figure 9; plate 19. figures 3-4; text-figures 8a-b. 9g, j, r
- 1986 *Pachydiscus (Pachydiscus) duelmensis* (Schlüter, 1872); Kennedy. p. 35. text-figure 12
- 1989 *Pachydiscus (Pachydiscus) duelmensis* (Schlüter, 1872); Jagt. p. 7. plate 1-5. plate 6. figure 1
- 1992a *Pachydiscus (Pachydiscus) paulsoni* (Young, 1963); Cobban and Kennedy. p. 69, plate 1, figures 4-7; plate 4. figures 7-9; plate 5, figures 7-8; text-figures 3a-c, 4b
- 1992b *Pachydiscus* cf. *P. paulsoni* (Young, 1963); Kennedy et al., p. 441

- 1993a *Pachydiscus* sp.; Kennedy and Cobban. p. 831., figures 3-4
- 1995 *Pachydiscus (Pachydiscus) duelmensis* (Schlüter, 1872); Wippich, p. 52., plate 2. figures 1-2; plate 4. figures 1-2
- 1995 *Pachydiscus (Pachydiscus) duelmensis* (Schlüter, 1872); Kennedy and Kaplan, p. 27, plate 9. figures 1-2; plate 10, figures 1-2; plate 11; plate 12, figures 1, 2 (with synonymy)
- 1997 *Pachydiscus* cf. *P. paulsoni* (Young, 1963); Kennedy et al., p. 9
- 2005 *Pachydiscus (Pachydiscus) duelmensis* (Schlüter, 1872); Kaplan et al., p. 62, plate 6, figures 6-7; plate 10
- 2006 *Pachydiscus (Pachydiscus) duelmensis* (Schlüter, 1872); Kaplan et al., p. 34, plate 2, figures 1-3

**Type.** The lectotype is GPIB 47, the original of Schlüter (1872, pl. 16, figures 1-2) by subsequent designation by (Jagt, 1989, p. 7). It is from the lower Campanian Dülmen Formation, Westphalia, Germany, and was re-figured by Kennedy (1986, figure 12) and Jagt (1989, pl. 5).

**Material.** Five collected specimens, CPC–2193, –2195, –2197, –2545, and –2561 from bed TPY40 and upwards.

**Description.** Involute shell (U/D between 0.24 and 0.36) with compressed oval whorl section (WB/WH is around 1 but with variation). The shell is ornamented by narrow, sharp, shallow, moderately sinuous primary ribs separated by one or two long, narrow secondary ribs. The primaries show elongated bullae from the umbilical shoulder to the inner part of flank. All ribs cross the venter with forward arching. Distance of ribs is constant, with increasing D, so that the number of ribs increases linear with D.

**Dimensions.** Table 12.

**Remarks.** The specimens included here are characterized by numerous sharp, shallow primary and secondary ribs. These are also present on shells *Pachydiscus (Pachydiscus) jimenezi* (Renz, 1936), *P. (P.) paulsoni* Young, 1963 and *Pachydiscus (Pachydiscus) duelmensis* (Schlüter, 1872) from the lower Campanian of Mexico, Texas, and Germany.

Specimens from the Tepeyac-Jimenez area were first described by Renz (1936). The holotype of *Pachydiscus (P.) jimenezi* is the specimen of Renz (1936, p. 3, pl. 2, figure 4, 4a) by monotypy. Renz (op. cit.) states that it is specimen No. 1 in the Collection Böse-Staub, housed in the Geologi-



**FIGURE 27.** *Pachydiscus* (*Pachydiscus*) *duelmensis* (Schlüter, 1972) from bed TPY40. A–B: CPC–2561. Scale: 50 mm.





**FIGURE 28.** *Pachydiscus (Pachydiscus) duelmensis* (Schlüter, 1972) from bed TPY50. A–B: CPC– 2195. Scale: 50 mm.

cal Institute of the University of Bern. This collection has been transferred to the Naturhistorisches Museum Bern, but the holotype is untraceable there and is here regarded as lost.

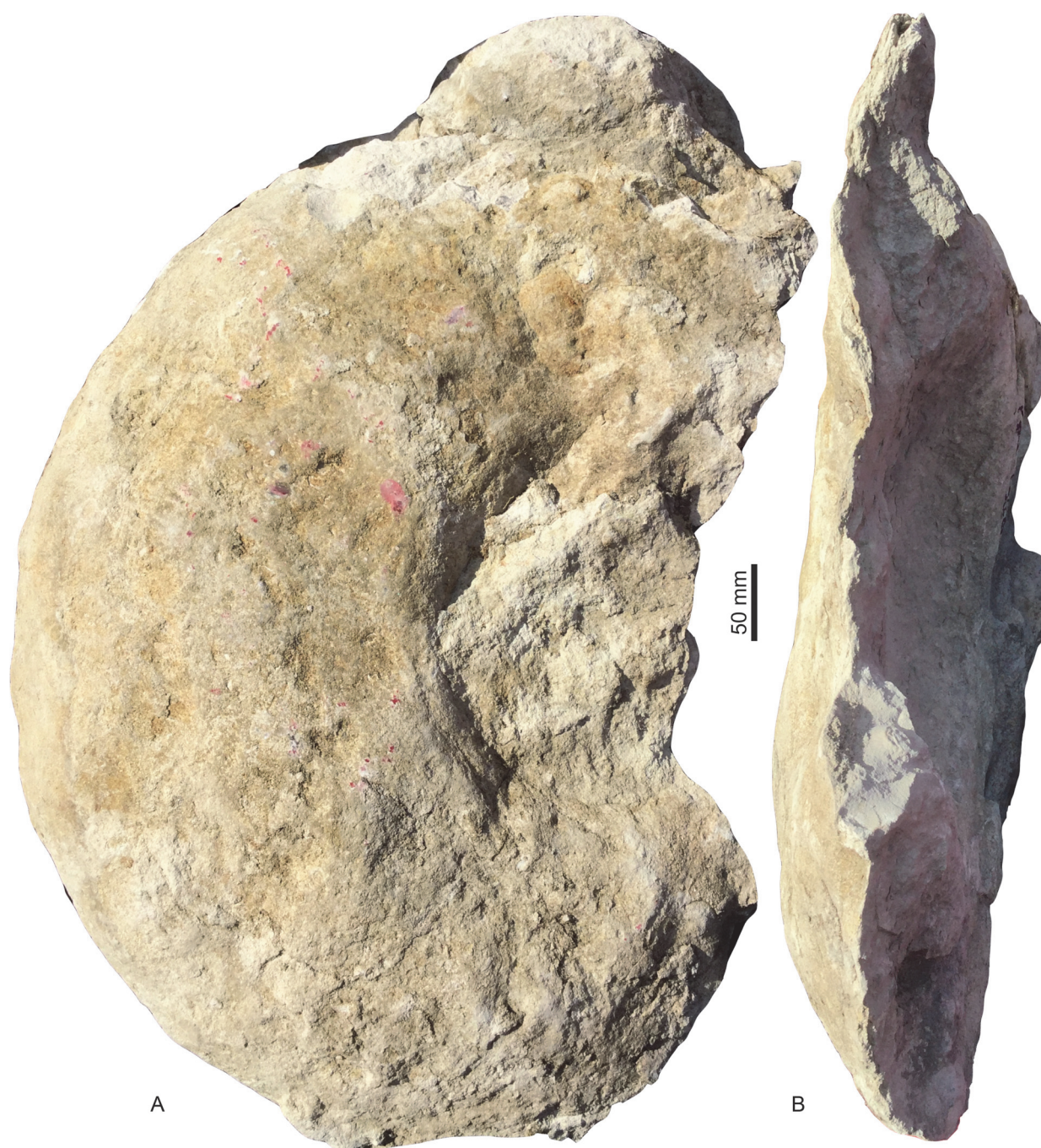
The morphology described here is also seen in *Parapuzosia paulsoni* Young, 1963 (p. 53ff). The holotype of *Parapuzosia paulsoni* is TMM 30625, from the “Gober chalk” in McCurtain County, Oklahoma. Specimens from Texas were described by Cobban and Kennedy (1992b), in addition to unfigured specimens from Texas Cobban and Kennedy (1992a) and Alabama (Kennedy et al. (1997a). Cobban and Kennedy (1992a) shortly mention similarities of *P. paulsoni* Young, 1963 with *Pachydiscus (Pachydiscus) duelmensis* (Schlüter, 1872, p. 52, Pl. 16, figures 1–2; see Kennedy, 1986a, text-figure 12). They suggested that the American species differed by weak bullae, a more compressed whorl section, and fewer, wider spaced ribs. However, these differences appear to be related to different ontogenetic stages. When plotting the morphometric data of all three species (Figure 31A–B), it becomes evident that no notable differ-

ences exist between the three closely related species regarding whorl dimensions and ribbing. Rather, each of the species is morphologically variable (Cobban and Kennedy, 1992a; Kaplan et al., 2005; Kaplan et al., 2006; Kennedy, 1986; Kennedy et al., 1997a; Kennedy and Kaplan, 1995). In fact, the holotypes of *Pachydiscus (P.) duelmensis* (Schlüter, 1872), *P. (P.) jimenezii* (Renz, 1936), and *P. (P.) paulsoni* (Young, 1963) plot together in all morphometric aspects (Figure 31A–B). As no other unequivocal characteristics exist between them, the three are considered to be conspecific, with *Pachydiscus (P.) duelmensis* as the homonym.

The low rib index in CPC–2193 is probably due to abrasion of the outer flanks and venter, also allowing for destruction of the secondaries. Specimen CPC–2545 shows a smooth adult body chamber, which excludes an assignation to the genus *Eupachydiscus*, because the latter presents prominent ribs on the terminal whorl.

Morphometric relations of *Menuites gordonii* Young, 1963 resemble those of *Pachydiscus (P.) duelmensis*. However, ribbing differs significantly





**FIGURE 29.** *Pachydiscus (Pachydiscus) duelmensis* (Schlüter, 1972) from bed TPY50. A–B: CPC–2545. Scale: 50 mm.

from the conspicuous ornament of *P. (P.) duelmensis*, and separation of the two taxa is here maintained.

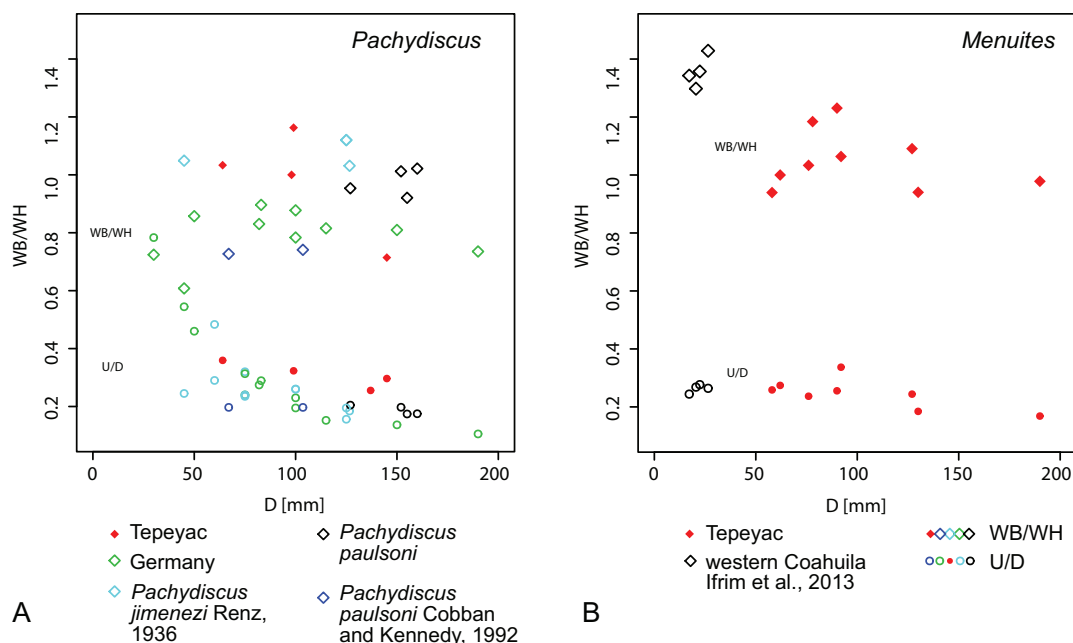
**Occurrence.** Basal to middle lower Campanian of Germany, Belgium, Netherlands, southwestern France, Oklahoma, Texas, Alabama, and Mexico.

In the Tepeyac section, the taxon occurs in bed TPY40 and above this layer, i.e., in the *Menabites (Delawarella) tequesquitense*, *M. (D.) delawarensis* and *Baculites taylorensis* zones, and thus throughout the lower Campanian.





**FIGURE 30.** *Pachydiscus (Pachydiscus) duelmensis* (Schlüter, 1972) from the Tepeyac section. A: CPC–2545, imprint of inner whorl. B–E: CPC–2197, bed TPY76. Scale: 50 mm.



**FIGURE 31.** Morphometry of lower Campanian *Menuites* and *Pachydiscus*. A: WB/WH and U/D against D for *Pachydiscus* (*P.*) *duelmensis* from Tepeyac (red) and Germany (green), the holotype of *Pachydiscus jimenezi* Renz, 1936 (turquoise) and *Pachydiscus paulsoni* of Young (1963, grey) and Cobban and Kennedy (1992b, blue). B: WB/WH and U/D against D for *Menuites stephensoni* from Tepeyac (red) and western Coahuila (Ifrim et al., 2013, black). Morphometric data of Young (1963) are implausible and thus not shown.

Genus MENUITES Spath, 1922  
*Menuites stephensoni* Young, 1963  
 Figure 31A–B; Figure 32C–F; Figure 33A–B, Table 13

- 1932 *Menuites* n. sp., Adkins, p. 467  
 1963 *Menuites stephensoni*, n. sp.; Young, p. 57, p1. 15, figures 1-2, text-figures 7o, 9n  
 1963 *Menuites* juv. sp., Young, p. 58, plate 15, figures 6, 7, 9, 11, 12; plate 20, figures 11, 11; text-figure 9q  
 1999 *Menuites* sp.; Kennedy and Cobban, p. 70  
 p.2005 *Menuites portlocki portlocki* (Sharpe, 1855); Kaplan et al, p. 76, plate 33, figure 3 only  
 p.2005 *Pachydiscus pseudostobaei* (Moberg [sic], 1885); Kaplan, et al., p. 66, plate 31, figures 1-2 only

**Type.** The holotype is WSA-69 by original designation by Young (1963, p. 57, plate 15, figures 1, 2; text-figures 7o, 9n). It is from a horizon with calcareous concretions in the upper Taylor Marl in Travis County, Texas.

**Material.** Four specimens, CPC-2194,–2349, –2554, and –2562, from beds TPY17, 50, 52, and 62.

**Description.** Involute (U/D with moderate growth rate). Juveniles with rounded whorl sections and 28 to 32 distant, sharp, straight to slightly prorsiradiate ribs. At D >120 mm lateral and lateroventral rounded bullae develop and whorl section is gradually subrectangular. In large adults ribs become irregular and finally disappear. Suture line with a trifid L that is equal in depth to E.

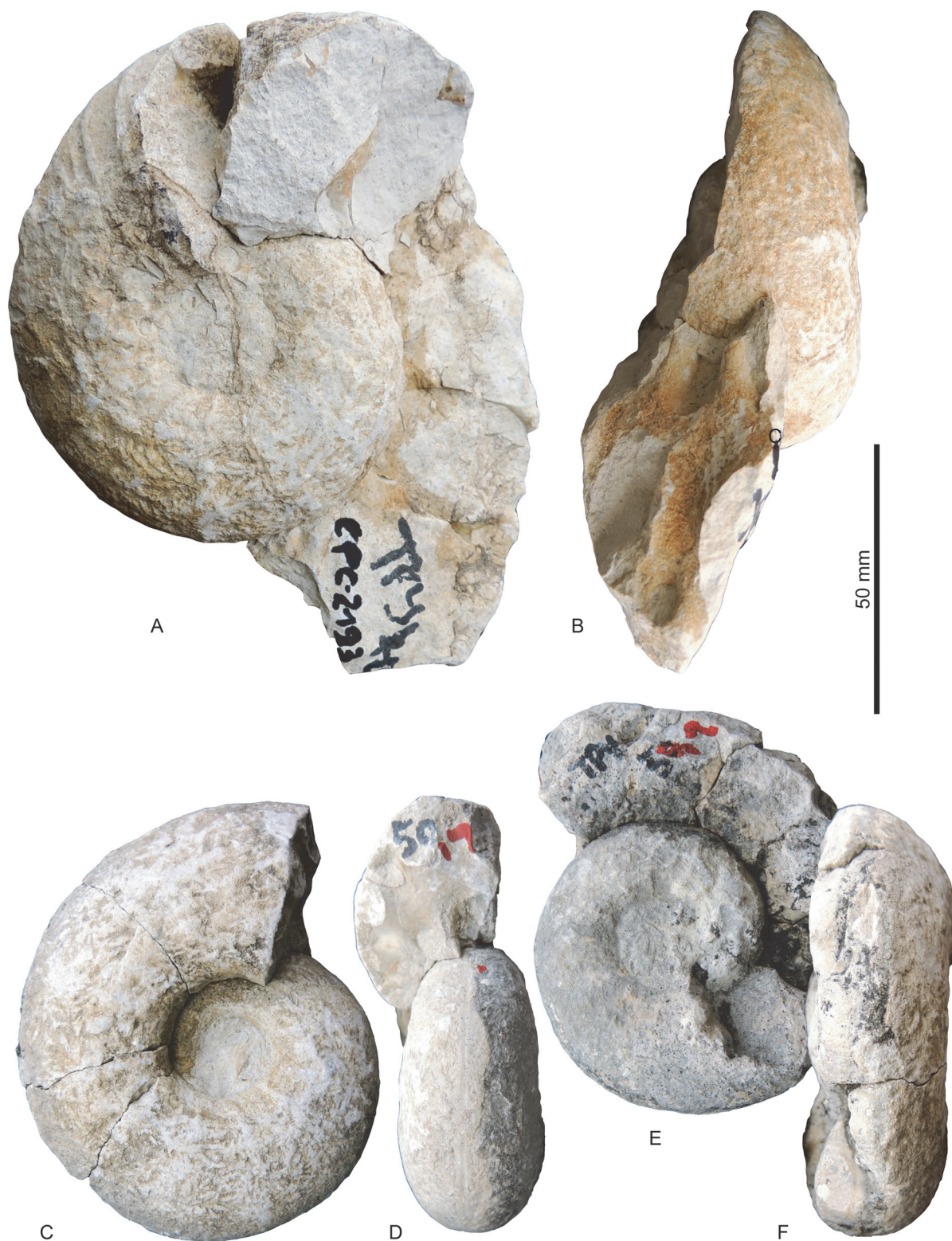
**Dimensions.** Table 13.

**Remarks.** The taxon is characterized by high morphologic variability. Juveniles assigned to *Menuites* juv. sp. by (Ifrim et al., 2013) may differ from *Menuites stephensoni* with respect to their U/D ratio and rib index (Figure 31A–B) and are kept separately until intermediate growth stages are known.

Specimen RE A 4214 from questionable lower Campanian sediments of Germany was described as *Menuites portlocki portlocki* (Sharpe, 1855) by Kaplan et al. (2005), but rather agrees with *M. stephensoni* than with the upper Campanian species (compare plate 32, op. cit.).

Specimen RE A 4193 from the lower Campanian of Germany described as *Pachydiscus pseu-*





**FIGURE 32.** Pachydiscids from the Tepeyac section. A–B: *Pachydiscus (Pachydiscus) duelmensis* (Schlüter, 1972), CPC–2193 from bed TPY40; C–F: *Menuites stephensoni* Young, 1963, CPC–2194 from bed TPY50. Scale: 50 mm.



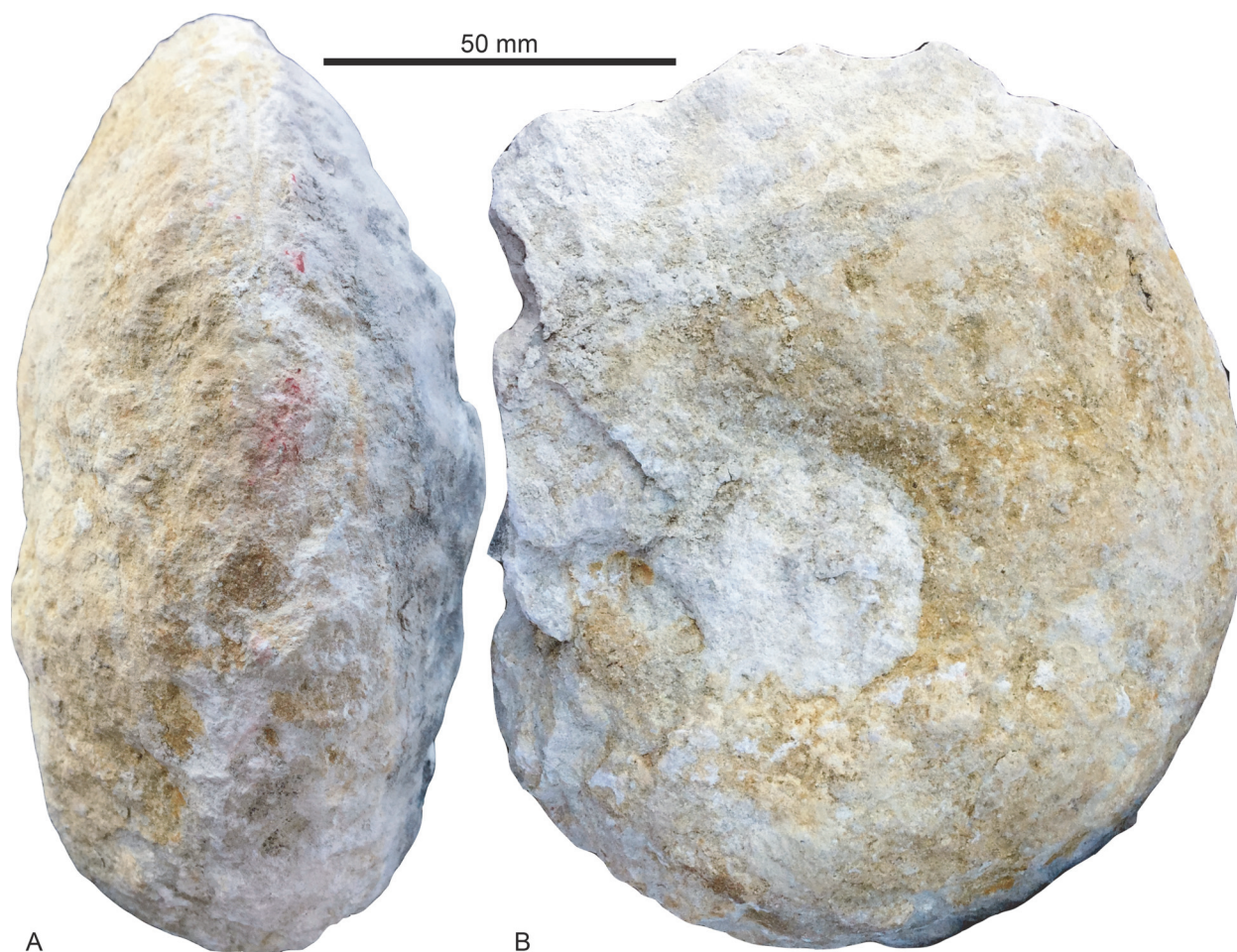
**TABLE 12.** Dimensions of *Pachydiscus (P.) duelmensis*.

	bed of origin	D	WB	WB/D	WH	WH/D	WB/WH	U	U/D	number of ribs
CPC-2193	TPY40	64	31	0.48	30	0.47	1.03	23	0.36	-
CPC-2561	TPY40	98	54	0.55	41	0.42	1.32	24	0.24	-
CPC-2197	TPY76?	98	45	0.46	45	0.46	1.00	-	-	52
CPC-2193	TPY40	99	50	0.51	43	0.43	1.16	32	0.32	-
CPC-2561	TPY40	127	50	0.39	58	0.46	0.86	32	0.25	-
CPC-2193	TPY40	137	-	-	67	-	-	35	0.26	25
CPC-2197	TPY76?	145	50	0.34	70	0.48	0.71	43	0.30	62
CPC-2195	TPY50.2	170	-	-	66	-	-	-	-	53
CPC-2545	TPY50	370	-	-	160	0.43	-	93	0.25	-

*dostobaei* (Möberg, 1885) by Kaplan et al. (2005) also rather shows characteristics of a juvenile *Menuites stephensoni* as understood here.

The species is closely related to, and most probably the ancestor, of the upper Campanian

*Menuites portlocki* (Sharpe, 1855) known from North America. *Menuites portlocki* differs from *M. stephensoni* by a stronger ornamentation (compare e.g., Błaszkiwicz, 1980), although morphometry is similar between the two species.

**FIGURE 33.** *Menuites stephensoni* Young, 1963 from bed TPY62. A–B: CPC–2562. Scale: 50 mm.



**TABLE 13.** Dimensions of *Menuites stephensoni*.

	bed of origin	D	WB	WB/D	WH	WH/D	WB/WH	U	U/D	number of ribs
CPC-2194	TPY50.1	62	31	0.50	31	0.50	1.00	17	0.27	13.3
CPC-2194	TPY50.1	90	56	0.62	45.5	0.51	1.23	23	0.26	14
CPC-2554	TPY52	76	31	0.41	30	0.39	1.03	18	0.24	-
CPC-2562	TPY62	92	50	0.54	47	0.51	1.06	31	0.34	-
CPC-2562	TPY62	127	60	0.47	55	0.43	1.09	31	0.24	9

**Occurrence.** Upper Santonian to lower Campanian of the Tepeyac section. Young (1963, p. 57) states that the holotype from Texas is upper Campanian in age, but without providing further details or age calibration. In central to western Europe the taxon is known from the lower Campanian. The record from Tepeyac is thus the oldest.

*Menuites* sp.

Figure 34 A–D, Table 14

**Material.** Four specimens, CPC–2196, –2544, –2554, and –2562.

**Description.** The shells are moderately involute with a moderate expansion rate. Ornament in the inner whorls of CPC–2544 is similar to *Pachydiscus* (*P.*) *duelmensis* at similar D, but ribs are more numerous and more irregular, and the shell is more involute. Each specimen presents a deep constriction.

**Dimensions.** Table 14.

**Remarks.** This morphotype differs from *Menuites stephensoni* by the absence of ribbing except at small diameters and by the presence of deep constrictions. The material may represent more than one species but specimens are not comparable as they represent different ontogenetic stages.

Suborder ANCYLOCERATINA Wiedmann, 1966

Superfamily TURRILITOIDEA Gill, 1871

Family DIPLOMOCERATIDAE Spath, 1926

Subfamily DIPLOMOCERATIDAE Spath, 1926

Genus GLYPTOXOCERAS Spath, 1925

Shafts are more or less curved, no straight shafts, simple ribs, circular to oval cross section

*Glyptoxoceras texanum*

Kennedy, Landman, and Cobban, 2001

Figure 35A–H

1992 *Glyptoxoceras* sp.; Cobban and Kennedy, p. 80, plate 4, figures 10–11; plate 6, figures 5–6; plate 7, figures 7–8

1997a *Glyptoxoceras* sp.; Kennedy et al., p. 35, figure 22c–e

2001 *Glyptoxoceras texanum* Kennedy, Landman and Cobban, p. 7, figure 4

**Type.** The holotype is USNM 490970, by original designation by Kennedy, Landman and Cobban (2001, figure 4c–e). It is from the top of the Blossom Sand at USGS Mesozoic locality 18120, between Detroit and Bagwell, Red River County, Texas

**Material.** Two fragments, CPC–2349 from bed TPY48–50 and CPC–2610 from bed TPY73.

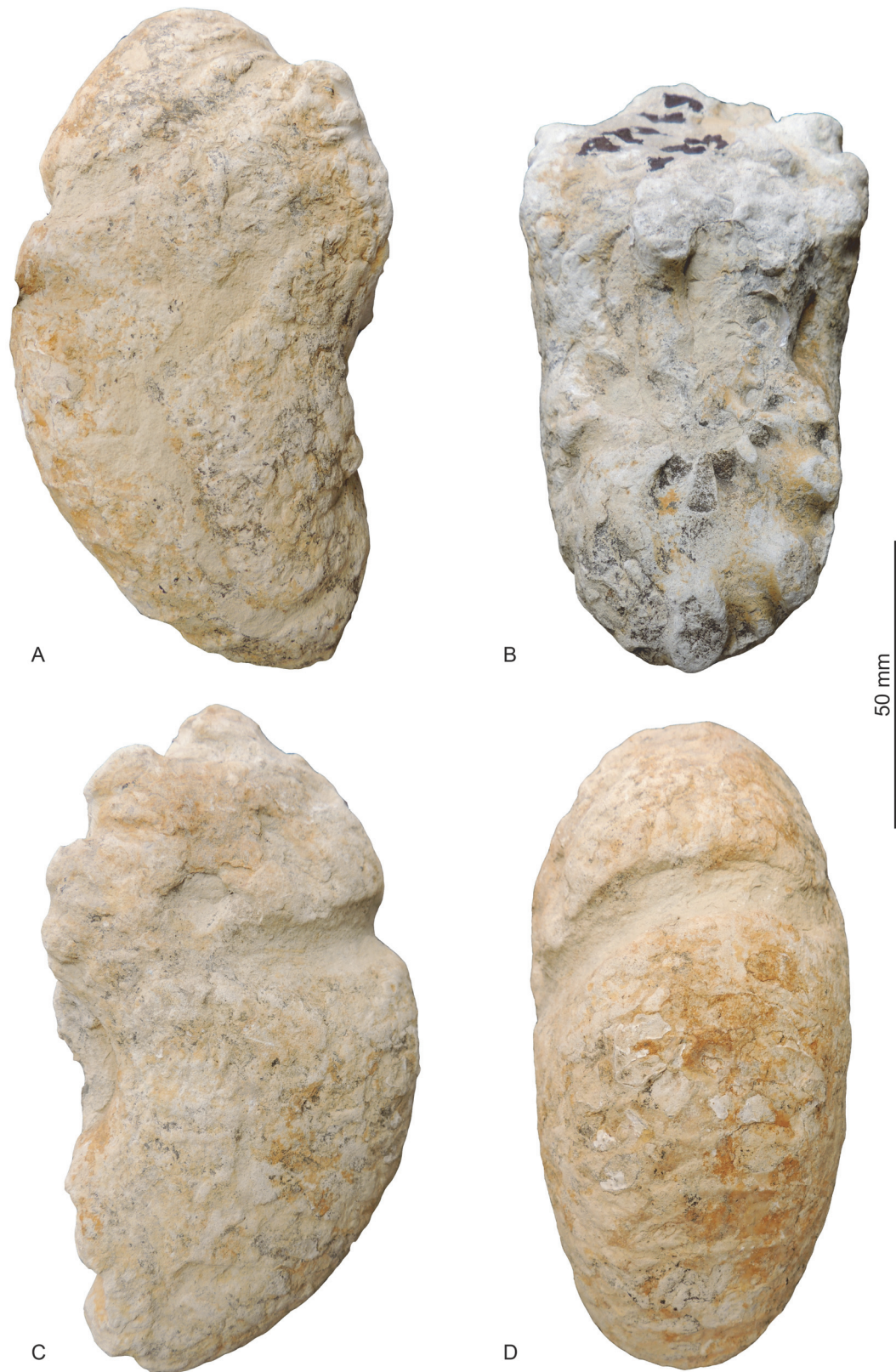
**Description.** Open coil with different intensities of coiling, moderately helicoidal. Whorl section is ovoid, WB/WH is between 0.60 and 0.74, but the ratio may be distorted due to crushing of the shell. Ribs are closely spaced, with a rib index of between 8 and 10, increasing with WH. Ribs are weak and straight across the dorsum, strong and slightly convex across the dorsolateral margin, strong, straight, and rursiradiate on the flanks, and transverse on the venter where they reach their maximum height. CPC–2349 shows a deep constriction which is flanked by a flared adapertural rib.

**Dimensions.** CPC–2346, WB: 14, WH: 19, WB/WH 0.74, L: 15, ribs per WH: 8. CPC–2610, smaller end, WB: 12, WH: 20, WB/WH: 0.60, ribs per WH: 10, L: 65 to larger end, there WB: 15, WH: 24, WB/WH 0.63.

**Remarks.** Our specimens are closely resemble the lower Campanian *Glyptoxoceras* sp. described by Kennedy et al. (1997b) and Cobban and Kennedy (1992b), which are here included in the present species.

*Glyptoxoceras retrorsum* (Schlüter, 1972) from the lower Campanian of Germany is similar to our specimens with respect to ribbing and dimensions near the aperture (e.g., Kaplan and Kennedy 2005, p. 310, plate 46, figures 1–3; plate 49, figures 1–2), but lacks flared ribs. *Glyptoxoceras novimexicanus* (Reeside, 1927) is morphologically indistinguishable from *G. retrorsum* and is here regarded as a synonym.

The present material is ribbed more finely than the upper Santonian *Glyptoxoceras* sp. of (Kennedy and Cobban, 1991). *Glyptoxoceras aquisgranense* (Schlüter, 1972) from the lower Campanian of Germany has a lower rib index and a more



**FIGURE 34.** *Menuites stephensoni* sp. from the Tepeyac section. A–D: CPC–2196 from bed TPY69–89. Scale: 50 mm.



TABLE 14. Dimensions of *Menuites* sp.

	bed of origin	D	WB	WB/D	WH	WH/D	WB/WH	U	U/D	number of ribs
CPC-2544	TPY50	58	31	0.53	33	0.57	0.94	15	0.26	32
CPC-2562	TPY62	92	50	0.54	47	0.51	1.06	31	0.34	-
CPC-2562	TPY62	127	60	0.47	55	0.43	1.09	31	0.24	9
CPC-2196	TPY69-89	78	45	0.58	38	0.49	1.18			
CPC-2196	TPY69-89	130	63	0.48	67	0.52	0.94	24	0.18	
CPC-2196	TPY69-89	190	90	0.47	92	0.48	0.98	32	0.17	13.3

rounded whorl section (Kennedy and Kaplan, 1995). This species was also recorded from lower Campanian of the Atlantic Coast (Kennedy et al., 1997b). A more circular section and significantly coarser ribs are present in *Glyptoxoceras ellisoni* Young, 1963 and *Glyptoxoceras rubei* (Reeside, 1927).

Two groups may thus be distinguished within lower Campanian members of the genus *Glyptoxoceras*, i.e., delicately ribbed taxa including *Glyptoxoceras retrorsum* and *G. texanum*, and coarsely ribbed ones such as *G. aquisgranense* and *G. ellisoni*. The presence, or absence, of constrictions may distin-

guish species in these two groups of *Glyptoxoceras*, but this cannot be decided to date.

**Occurrence.** Uppermost Santonian of northeastern Texas, *Menabites (Delawarella) delawarensis* zone of New Jersey, lower Campanian of northeastern Coahuila, and middle Campanian of Texas.

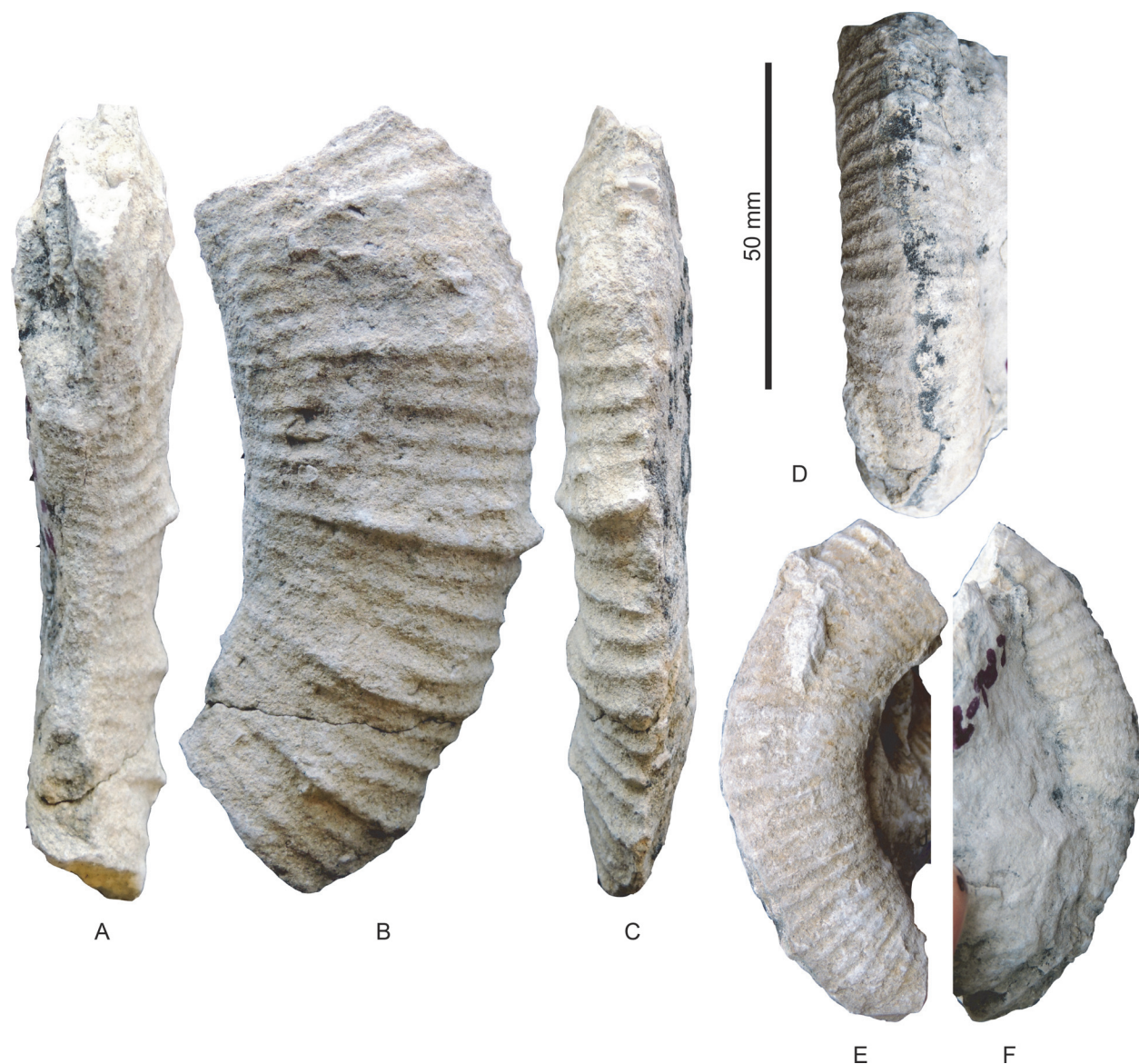
Family NOSTOCERATIDAE

Genus AMAPONDELLA Klinger and Kennedy, 1997

**Type species.** *Heteroceras amapondense* van Hoepen, 1921 by original designation of Klinger and Kennedy (1997).



FIGURE 35. *Glyptoxoceras texanum* Kennedy, Landman and Cobban, 2001 from the Tepeyac section. A–D: CPC–2349, bed TPY48–50; E–F: CPC–2610, bed TPY73. Scale: 50 mm.



**FIGURE 36.** *Amapondella amapondense* (van Hoepen, 1921) from bed TPY50 of the Tepeyac section. A–C: CPC–2345, D–E: CPC–2346. Scale: 50 mm.

*Amapondella amapondense* (van Hoepen, 1921)  
Figure 36A–E, Figure 37A–E, Table 15

- |      |   |      |  |
|------|---|------|--|
| 1921 | <i>Heteroceras amapondense</i> van Hoepen, p. 17, plate 4, figures 1, 2   | 1983 | <i>Hyphantoceras amapondense</i> (van Hoepen); Lewy, p. 24, figures 1-6 (with synonymy)                          |
| 1969 | <i>Anaklinoceras</i> (?) <i>stephensoni</i> Collignon, p. 50, plate 532 (figure 2096)   | 1985 | <i>Hyphantoceras</i> ( <i>Madagascarites</i> ) <i>amapondense</i> (van Hoepen, 1921); Klinger, p. 6, figure 41-k |
| 1969 | <i>Hyphantoceras reussianum</i> d'Orb.; Collignon, p. 29, plate 523 (figure 2064), p. 38, plate 527 (figures 2079–2080); p. 48, plate 531 (figure 2095) | 1991 | <i>Hyphantoceras</i> (?) <i>amapondense</i> (van Hoepen, 1921); Kennedy, p. 181, figure 9.9, 9.10                |
| 1978 | <i>Hyphantoceras</i> ( <i>Madagascarites</i> ?) <i>amapondense</i> (van Hoepen); Summes-  | 1997 | <i>Eubostriochoceras</i> ( <i>Amapondella</i> ) <i>amapondense</i> van Hoepen; Klinger and                       |



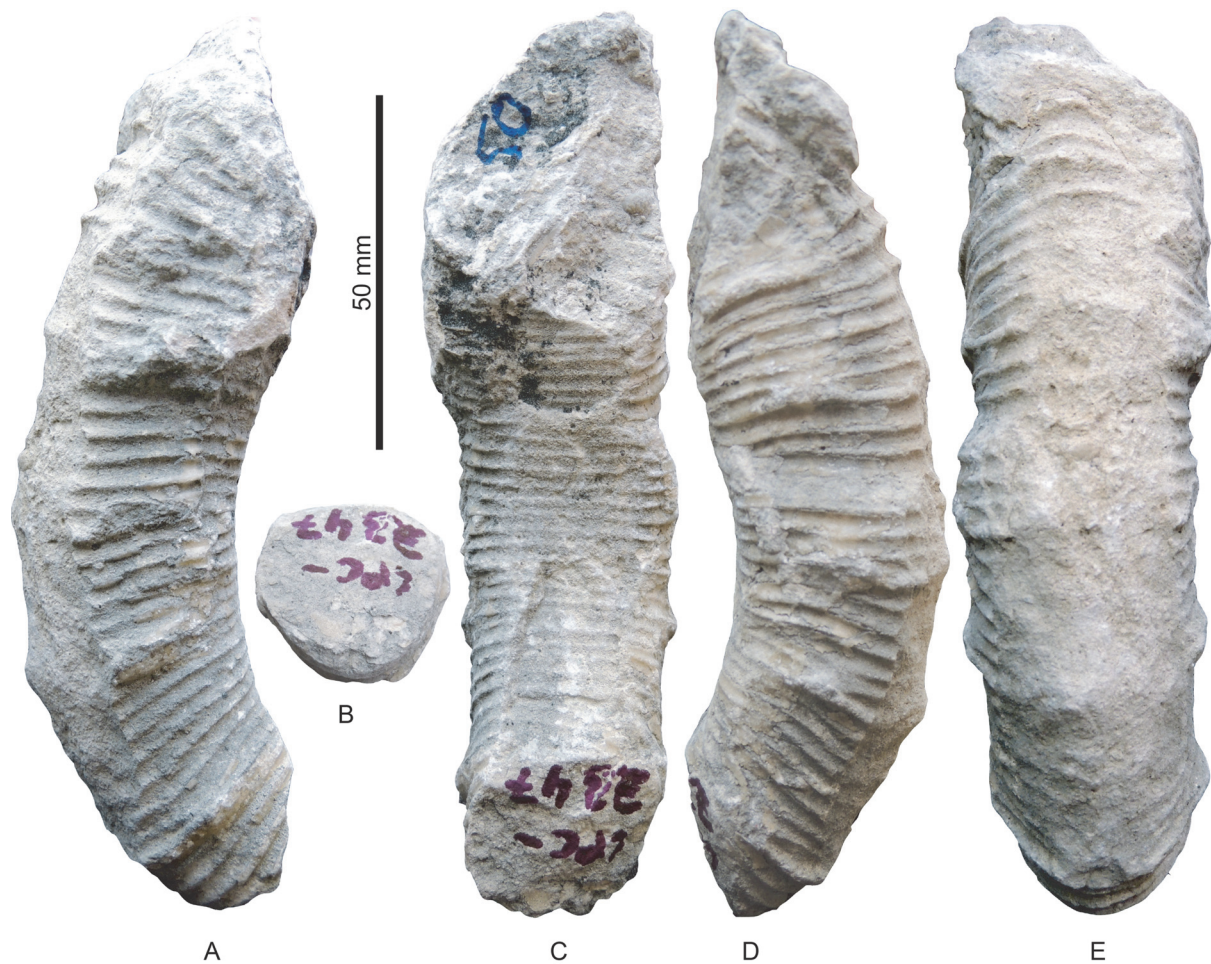


FIGURE 37. *Amapondella amapondense* from bed TPY 50 of the Tepeyac section. A–E: CPC–2347. Scale: 50 mm.

2003 Kennedy, p. 244, figures 12- 14a, 15a-d, 17a-c  
*Eubostrychoceras (Amapondella) amapondense* (van Hoepen); Klinger and Kennedy p. 235, figures 5–6, 7a, 8a–d, 9a–c (with synonymy)

2007 *Amapondella amapondense* (van Hoepen, 1921); Klinger and Kennedy, p. 101, figures 5a–c, 10i–j, 11, 12b–i, 13a–e, m

**Type.** Holotype is the specimen figured by van Hoepen (1921, plate 4, figures 1–2) by original designation. It is from the upper Santonian or lower Campanian of the Mzamba Formation at the type section (locality 1), Eastern Cape Province, South Africa. SAM-PCZ18722 is a cast of the holotype.

**Material.** Five specimens, CPC–2345 to 2347 from bed TPY50, CPC–2351 to –2352 from bed TPY25.

**Description.** Open, slightly helicoidal, more or less even coiling, U/D is ca. 0.47. Circular to more sub-quadrade whorl sections at larger D, while ovoid whorl sections may result from deformation. Ribs

TABLE 15. Dimensions of *Amapondella amapondense*.

	bed of origin	D	WB	WH	WB/WH	U	rib index	L
CPC-2345	TPY50			45			10	75
CPC-2346	TPY50		22	20	1.10		8	45
CPC-2347	TPY50		30	30	1.00		9	55
CPC-2351	TPY25	116	15 (0.13)	28 (0.24)	0.54	55 (0.47)	8	

are weak, feebly prorsiradiate, sweep back and strengthen on both upper and lower whorl faces; they are markedly oblique and reach their maximum strength on the outer whorl face. Every fourth to sixth rib is strengthened, forming a pronounced flare; these are conspicuous on the lateral, ventrolateral and ventral whorls.

**Dimensions.** Table 15.

**Remarks.** This species was extensively discussed by Lewy (1983), and additional comments were provided by Klinger and Kennedy (2003) and Klinger et al. (2007). The latter authors discussed dimorphism in this species.

**Occurrence.** Middle Santonian to lower upper Santonian of France, middle Santonian to lower Campanian of South Africa, upper Santonian of Israel, Austria, and Mississippi, uppermost Santonian to lower Campanian of Coahuila, lower Campanian of Madagascar.

Family BACULITIDAE Gill, 1871

Genus BACULITES Lamarck, 1799

*Baculites taylorensis* Adkins, 1929

Figure 38A–B, G–H, Table 16

- 1929 *Baculites taylorensis* Adkins, p. 204, plate 5, figures 9–11
- 1993a *Baculites taylorensis* Adkins; Kenney and Cobban, p. 93, figures 10.1–9, 10.11–12, 10.16, 10.18–19, 11.1–2 (Kennedy and Cobban, 1993b)
- 1993b *Baculites taylorensis* Adkins; Kennedy and Cobban, p. 143, plate 6, figures 1–9, plate 7, figures 1–6, 10–13; text-figure 8b, d (Kennedy and Cobban, 1993c)
- 1994 *Baculites taylorensis* Adkins; Cobban and Kennedy, p. D6, plate 3, figures 5–19; text-figure 7 (Cobban and Kennedy, 1994)
- 2001 *Baculites taylorensis* Adkins; Kennedy and Cobban, p. 25, plate 6, figures 8–9 (Kennedy and Cobban, 2001) (with synonymy)
- 2013 *Baculites taylorensis* Adkins, 1929; Ifrim et al., p. 234, figure 5b–f, figure 6f–y, figure 7a–l, figure 8a–k, figure 9a–l

**Type.** The holotype is TMM 21014 by monotypy. This specimen is from the basal Pecan Gap Chalk, Travis County, Texas.

**Material.** Two specimens, CPC–2198 and –2199, both internal moulds, from beds TPY64 and 77, respectively.

**Description.** Shell substraight with a low expansion rate. Whorl section is stout and ovate, with a widely-rounded dorsum, dorsolaterally parallel and

ventrolaterally convergent flanks which terminate in a moderately narrow rounded venter. Rib index is 1 to 0.5. These nodes arise at the dorsolateral shoulder and increase in size on the dorsal third to half of the flank; they are rounded and weak in CPC–2183 and stronger in CPC–2199. Ribs and nodes fade markedly on both the dorsum and the ventral portion of the flank.

**Dimensions.** Table 16.

**Remarks.** The two specimens and their ornamentation match the abundant specimens described from Arkansas, Texas and Coahuila.

**Occurrence.** Lower-upper Campanian of the northern and north-western Gulf coast. The FAD of the species marks the base for an uppermost lower Campanian biozone in this region.

*Baculites* cf. *haresi* Reeside, 1927

Figure 38C–F, I–L

- 1927 *Baculites ovatus* var. *haresi*, Reeside, p. 10, plate 6, figures 5–10, plate 7, figures 9–10 (with synonymy)
- 1992a *Baculites haresi* Reeside; Cobban and Kennedy, p. 449, figures 6.5–6.8, 6.11–6.13, 6.16–6.24, 7.1 (with additional synonymy)
- 1993a *Baculites haresi* Reeside, 1927; Kennedy and Cobban, p. 844, figures 14.18–14.35, 14.37, 15.2, 16.1–16.6 (with additional synonymy)
- 1997 *Baculites haresi*, Reeside; Larson, p. 20
- 2013 *Baculites haresi* Reeside, 1927; Ifrim et al., p. 890, figures 8.1–8.13, 9.1–9.6, 10.1–10.7, table 5

**Type.** The lectotype is USNM 73296, the original of Reeside (1927, pl. 6, figs 5–6), by subsequent designation of Cobban and Kennedy (1992a, p. 449). It comes from the Elk Basin Sandstone Member of the Telegraph Creek Formation, Wyoming, USA.

**Material.** Four specimens, CPC–2604 to –2607, from beds TPY52, 57, and 77.

**Description.** Compressed whorl section with rounded dorsum and venter. The shell is smooth or ornamented by faint bullae and falcate ribs in dorsolateral position.

**Remarks.** Our specimens are deformed. Their characteristics correspond to the lectotype of Reeside (1927, pl. 6, figures 5–6) with respect to whorl section, as far as reconstructible, and the faint ornament. The suture is little incised. Superficially, *B. haresi* Reeside, 1927 resembles *B. scotti* Cobban, 1958 and *B. eliasi* Cobban, 1958, but the latter two species differ in the shape and higher complexity of their sutural elements.





**FIGURE 38.** *Baculites* from the Tepeyac section. A–B, G–H: *Baculites taylorensis*, A–B: CPC–2198, bed TPY64; G–H: CPC–2199 before extraction from bed TPY77; C–F, I–L: *Baculites haresi*, C–F: CPC–2607, bed TPY52; I–L: CPC2606, bed TPY77. Scale: 50 mm.

**TABLE 16.** Dimensions of *Baculites taylorensis*.

	bed of origin	WB	WH	WB/WH	L
CPC-2198	TPY64	22	-	-	140
CPC-2198	TPY64	20	0	-	0
CPC-2199	TPY77	15	34	0.44	150
CPC-2199	TPY77	15	30	0.50	0

**Occurrence.** *Baculites haresi* is widely distributed in lower Campanian strata of the Western Interior Seaway, from Wyoming to Texas (Larson et al., 1997), and also present in Coahuila (Ifrim et al., 2013, and herein). Isolated records also exist from the lower Campanian of New Jersey (fide Klinger and Kennedy, 2001) and Greenland (Birkelund, 1965).

Superfamily SCAPHITOIDEA Gill, 1871

Family SCAPHITIDAE Gill, 1871

Subfamily SCAPHITINAE Spath, 1926

Genus and subgenus SCAPHITES Parkinson, 1811

*Scaphites* (*Scaphites*) *hippocrepis* (DeKay, 1828)  
III Cobban, 1969  
Figure 39A–P

- 1828 *Ammonites hippocrepis* DeKay, p. 273, plate 5, figure 5.
- 1969 *Scaphites hippocrepis* (DeKay) III; Cobban, plate 3, figures 1-25; plate 4, figures 35-49; plate 5, figures 36-40; text figures 2, 4, 10, 11 (with synonymy)
- 1986 *Scaphites* (*Scaphites*) *hippocrepis* (DeKay, 1828); Kennedy, p. 118, plate 13, figure 5; plate 19, figures 1-34; plate 20, figures 1-6, 9, 10; plate 21, figures 1-11; plate 23, figures 2, 3 (with synonymy)
- 1992 *Scaphites* (*Scaphites*) *hippocrepis* (DeKay) III; Cobban and Kennedy, p. 451, figures 4.1-4.3, 4.13-4.20, 4.22-4.23, 4.28, 4.92, 6.1-6.4, 6.10, 7.2
- 1993 *Scaphites* (*Scaphites*) *hippocrepis* (DeKay, 1828); Kennedy and Cobban, p. 845, figures 15.1, 17.1-17.32
- 1995 *Scaphites* (*Scaphites*) *hippocrepis* (DeKay, 1828) form III; Jagt, Burnett and Kennedy, p. 57, plate 3, figure 3
- 1996 *Scaphites* (*Scaphites*) *hippocrepis* (DeKay, 1828), form III of Cobban, 1969; Kennedy and Christensen, p. 115, figure 32
- 2000a *Scaphites hippocrepis* (DeKay) III; Küchler, plate 8, figures 3-6

2004 *Scaphites* (*Scaphites*) *hippocrepis* (DeKay, 1828), III *sensu* Cobban, 1969; Jagt, Walaszczyk, Yazykova, and Zaton, p. 577, plate 1, figure 4

2005 *Scaphites hippocrepis* (DeKay, 1828), Kaplan et al., p. 138, plate 57, figures 1-30; plate 58, figures 1-15; plate 62, figure 5 (with synonymy)

?2013 *Scaphites* sp. ex gr. *S. hippocrepis* (DeKay, 1828); Ifrim et al., p. 895, figures 9.23-9.28, 12.1-12.15, table 7

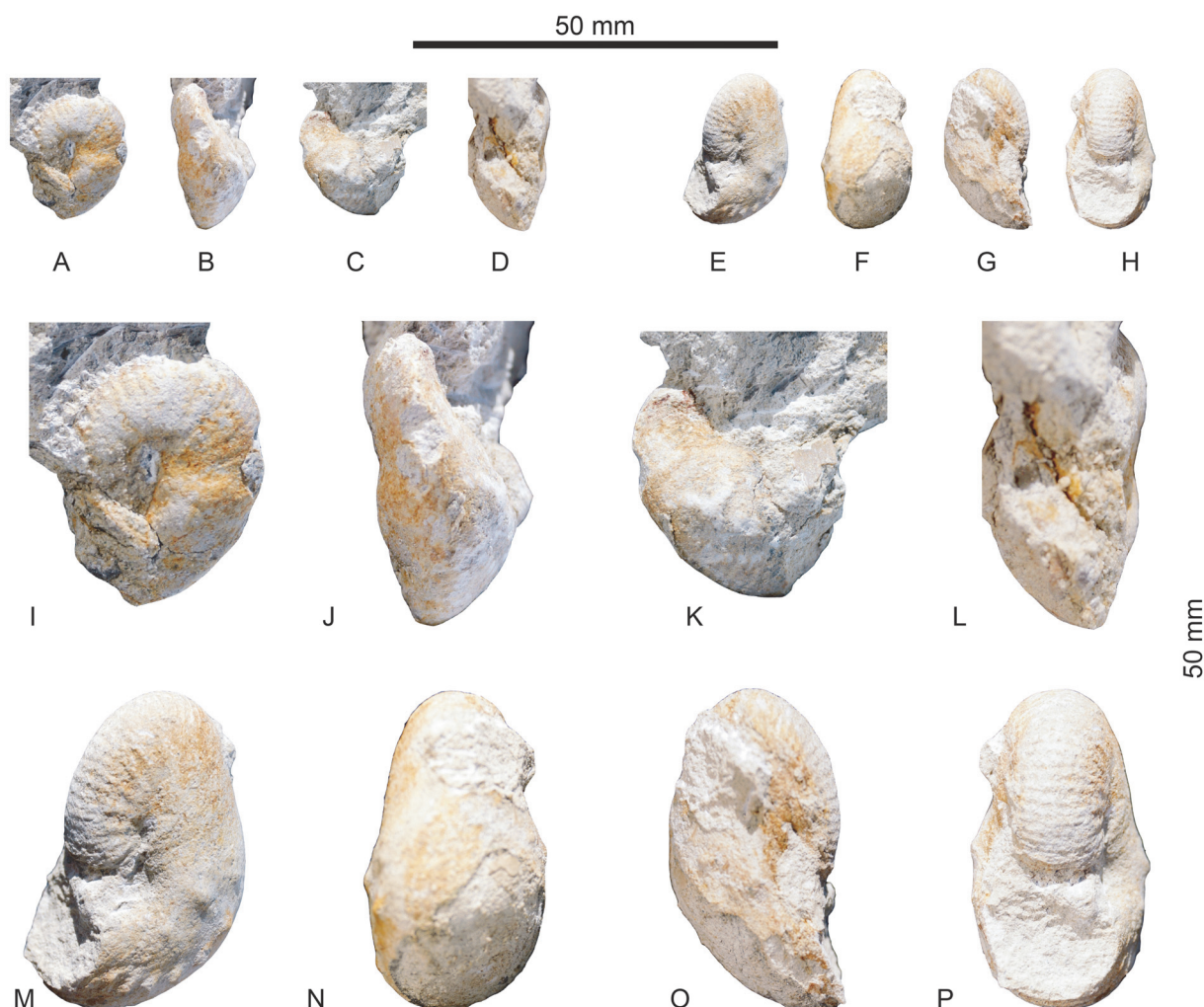
**Type.** Neotype, designated by (Kennedy, 1986, p. 118), is no. 19483 in the collections of the Philadelphia Academy of Sciences. It is the holotype of *Scaphites cuvieri* Morton, 1834, p. 109, p1. 7, figure 1, refigured by Whitfield, 1892, p1. 44, figure 8, Richards, 1953, text-figure 224, and Reeside, 1962, p1. 71, figures 1-5. The specimen is from the deep cut of the Chesapeake and Delaware Canal, Delaware.

**Material.** Two specimens, CPC-2599 and -2600, both from bed TPY732.

**Description.** Inflated to globular whorl section. WB/WH is <1.76 in juveniles but decreases to 1.03 in shells with D >16 mm. Maximum width is reached at mid-flank. The expansion rate is high in early growth stages but decreases at larger diameters, as indicated by similar WBs of the early and later whorl. The final whorl section grades towards a subtriangular shape. U is small, with U/D decreasing from 0.2 in early juveniles to 0.1 at large D. The umbilicus is deep. Umbilical walls are rounded and grade into rounded flanks, which are short due to a widely rounded venter. Eight tubercles are present per half whorl and give rise to bullae that each grade into pairs of moderately prorsiradiate convex ribs. These are occasionally intercalated by secondaries, resulting in ca. 17 primaries and secondaries per half whorl. The suture is simple, with shallow, subrectangular, asymmetrically bifid elements. Only E/L and L are asymmetrically trifid.

**Dimensions.** CPC-2599, D: 17.0; CPC-2600, D: 21.5, WB: 12.0 (0.6), WH: 8.0 (0.4), WB/WH: 1.50, U: 6.0 (0.28), ribs per whorl: 38.





**FIGURE 39.** *Scaphites* (*S.*) *hippocrepsis* III from bed TPY73 of the Tepeyac section. A–D, I–L: CPC–2599; E–H, M–P: CPC–1600, both from bed TPY72. Scale: 50 mm.

**Remarks.** Ornament, particularly the type of ribbing, relates our specimens to morphotype III of *S. hippocrepsis*. This morphotype is the most widespread which provides good biostratigraphic control in both North America and Europe. Size differences exist between CPC–2599 and –2600 and suggest that the two represent a micro- and a macroconch.

**Occurrence.** In North America *S. hippocrepsis* III is known from the middle lower Campanian of the Western Interior, Gulf Coast and Atlantic Coast Plan (Cobban, 1969; Cobban and Kennedy, 1992a, 1992b), western Coahuila (Ifrim et al., 2013) (Pervinquière, 1907), and the North American Pacific coast (Anderson, 1958). Records are also from France (Kennedy, 1986), Poland, Germany, and Netherlands (Jagt et al., 2004; Kaplan et al., 2005), Sweden (Kennedy and Christensen, 1997), and

Tunisia. Lower middle Campanian records of *S. hippocrepsis* III also exist from Spain (Küchler, 2000) and Germany (Kaplan et al., 2005).

#### AMMONID ZONATION AND THE SANTONIAN-CAMPANIAN BOUNDARY

Young (1963, 1985) and Kennedy et al. (1997a) used the first occurrence (FO) of *Mena-bites* (*Delawareella*) *tequesquitense* to define the base of the Campanian in Texas (Figure 40), but their biozonation within the lower Campanian provides slight differences (Figure 40). Gale et al. (2008) noted, that the FO of *Uintacrinus anglicus* was to be placed slightly above the FO of *M. (D.) tequesquitense*, within this ammonite zone. This crinoid is another good index for the base of the Campanian, similar to the LO of *Marsupites testu-*

	Young, 1963	Wolleben, 1967	Young, 1985	Kennedy, Cobban and Landman, 1997	Tepeyac
<b>middle Campanian</b>	<i>H. marroti</i>	no data	<i>H. marroti</i>	<i>B. taylorensis</i>	no data
<b>lower Campanian</b>	<i>M. (D.) sabinalensis</i>		<i>M. (D.) sabinalensis</i>	<i>M. (D.) delawarensis</i>	<i>B. taylorensis</i>
	<i>M. (D.) delawarensis</i>		<i>M. (D.) delawarensis</i>		<i>M. (D.) delawarensis</i>
	<i>S. tequesquitense</i>		<i>S. vanuxemi</i>		<i>M. (D.) tequesquitense</i>
		<i>S. tequesquitense</i>	<i>S. tequesquitense</i>	<i>S. tequesquitense</i>	<i>(B. bevahensis)</i>
<b>upper Santonian</b>	<i>T. shiloensis</i>	<i>T. shiloensis</i>	<i>B. bevahensis</i>	<i>P. shiloensis</i>	<i>P. shiloensis</i>

**FIGURE 40.** Biozonations used for the upper Santonian to lower Campanian stages in the northwestern Gulf Coast Plain.

*dinarius* (Gale et al., 1995; Kennedy et al., 1997a; Gale et al., 2008), which is also placed within the *M. (D.) tequesquitense* zone (Kennedy et al., 1997a). Another good marker for the base of the Campanian is provided by the stable carbon isotope curve which shifts from a generally increasing towards a decreasing trend in the Santonian-Campanian Boundary Event (SCBE, Thibault, 2016 #1045, and Figure 2). This excursion is the best marker for the base of the Campanian in bed 30 of the Tepeyac section.

The FO of the giant ammonite *Parapuzosia* (*Parapuzosia*) *seppenradensis* provides to be another event close to the Santonian-Campanian boundary, which was identified, at Tepeyac, in bed 30 (Ifrim et al., in press) and at the base of the Campanian. At Waxahachie, Texas, however, a small specimen of *P. (P.) seppenradensis* was found below the Santonian-Campanian boundary, i.e., 0.7 m below the LO of *Marsupites testudinaris* and the FO of *Uintacrinus anglicus* (Gale et al., 2008; but see discussion in Ifrim et al., in press). At Tepeyac, a gap exists between the LO of *Parapuzosia* (*P.*) *leptophylla* (loose specimen near bed 12) and the FO of *P. (P.) seppenradensis* in bed 30. The FO of this giant ammonite thus also seems to be a suitable secondary marker. However, this exceptional ammonite is abundant in the upper half of the Tepeyac section but rare elsewhere (Ifrim et al., in press); it thus does not meet general abundance as requirement for a reliable index ammonite.

The original definition of the base of the Campanian of de Grossouvre (1894) was the lowest level with *Placenticerus bidorsatum*. The FO of this ammonite provides a good approximation for the Santonian-Campanian boundary level in central Europe, but the taxon has not been found elsewhere (Kennedy, 1986; Kennedy and Kaplan, 1995). In North America, *Placenticerus syrtale* [including the endemic subspecies of Chihuahua and adjacent Trans-Pecos-Texas described by Hyatt (1903) and Wolleben (1967)] occurs below and above the boundary in Chihuahua, Texas, Alabama, Mississippi, New Mexico, Colorado, Wyoming, Montana, and Utah. The taxon seems to be a good proxy to determine the boundary in clastic facies of the Western Interior, but not a single specimen of *Placenticerus* was found at Tepeyac, likely due to its absence in carbonate environments of the Gulf of Mexico, so other index species are needed there.

The ammonoid biozonations for the upper Santonian and lower Campanian stages in Texas and northeastern Mexico (Tepeyac) are summarized in Figure 40. Young (1963: 18, table 7) first presented a biozonation for the Santonian and Campanian of the Gulf Coast region (Figure 40). Based on data from central Texas to Tepeyac, the *Menabites* (*Delawarella*) *tequesquitense* zone represents the lowermost Campanian and underlies the *Menabites* (*Delawarella*) *delawarensis* zone. Subsequent work has shown that *Menabites* (*Delawarella*) *delawarensis* has a long range in the Gulf



Coast region (Cobban and Kennedy, 1992a, 1992b). Therefore, the *delawarensis* zone was extended to encompass the entire interval between Young's (1963) zones of *tequesquitense* and *marroti*, with the latter renamed *Baculites taylorensis* zone by Kennedy et al. (1997a). The *Texanites shiloensis* zone was changed to the *B. bevahensis* zone by Young (1985), due to the wide geographical occurrence of this species from Texas to Madagascar. Although not explicitly stated, the authors appear to have used these zones in the sense of ranges, thus allowing them to modify their zonation as shown in Figure 40, but actually, these zones have never been defined formally.

Collignon (1948, p. 85) states that *Bevahites bevahensis* occurs at the boundary between the uppermost Santonian and the lower Campanian. This matches the occurrence of *B. bevahensis* in the lower *tequesquitense* zone at Tepeyac. *Texanites shiloensis* occurs lower in the section, notably below the FO of *tequesquitense* in Chihuahua (Wolleben, 1967), although it was only found in a single bed. Young (1959) suggested to use *B. bevahensis* as index species for the upper Santonian in Texas. Elsewhere, its occurrence is, however, not calibrated with other index species. A single specimen of *Bevahites bevahensis* was discovered in bed TPY31, i.e., from the lowermost *Menabites (Delawarella) tequesquitense* zone. We maintain the *Plesiotexanites shiloensis* zone of Young (1963) and Cobban and Kennedy (1992a, 1992b), which is documented by various specimens.

Given the numerous different zonations, the absence of a formal biozonal definition, and the fact that Tepeyac is the only section in the Americas where ammonoid zonation across the Santonian-Campanian boundary is calibrated by a stable carbon isotope curve (Ifrim et al., in press), we propose the following ammonoid zonation for this interval of the Upper Cretaceous in the northern and northwestern Gulf Coast (Figure 2):

#### ***Plesiotexanites shiloensis* Interval Zone**

The base of this zone is defined by the first occurrence (FO) of the index species. At Tepeyac, this species first occurs in bed 12, but layers below this level are little exposed and the fossil record is scarce. We suggest that the FO of *Plesiotexanites shiloensis* may even reach to below the base of the Tepeyac section. Species co-occurring with *Plesiotexanites shiloensis* are *Parapuzosia (P.) leptophylla*, *Pseudoschloenbachia (P.) mexicana*, and *Texanites lonsdalei*, whereas *Menuites stephensoni* has its FO in this zone.

#### ***Menabites (Delawarella) tequesquitense* Interval Zone**

The base of this zone is defined by the first occurrence (FO) of the index species in bed 25 at 10.7 m of the Tepeyac section. The zone is 5.3 m thick. Co-occurring species are *Amapondella amapondense*, *Plesiotexantes shiloensis*, *Pseudoschloenbachia (Pseudoschloenbachia) mexicana*, *Menuites stephensoni*, and *Texanites lonsdalei*. *Bevahites bevahensis*, *Menabites (Delawarella) mariscalense*, *Menabites (Delawarella) vanuxemi*, and *Parapuzosia (Parapuzosia) seppenradensis* have their FOs within this zone. The index is an endemic species. Even though, *Menabites (Delawarella) tequesquitense* is chosen as the index here because it occurs in several beds, whereas *B. bevahensis*, the other potential zonal marker, is scarce and only found in bed 33, at 14.5 m of the section.

#### ***Menabites (Delawarella) delawarensis* Interval Zone**

The base of this zone is defined by the first occurrence (FO) of the index species in bed 35 at 16.0 m of the section. The zone is 6.6 m thick. *Amapondella amapondense*, *Bevahites costatus coahuilaensis*, *Menabites (Delawarella) tequesquitense*, *Menuites stephensoni*, *Plesiotexantes shiloensis*, *Texanites lonsdalei*, and the index species have their last occurrences (LO) in this zone, while *Parapuzosia (Parapuzosia) seppenradensis*, *Pseudoschloenbachia (Pseudoschloenbachia) mexicana*, *Menabites (Delawarella) mariscalense*, and *Menabites (Delawarella) vanuxemi* range throughout the zone, and *Glyptoxoceras texanum*, *Baculites haresi*, *Menabites (Bererella) walnutensis*, *Menabites (Delawarella) danei*, *Pachydiscus (P.) duelmensis*, and *Menuites* sp. have their first occurrences (FO). This zone may correspond to a full range of the index fossil, but we suggest definition as an interval zone.

#### ***Baculites taylorensis* Interval Zone**

The base of this zone is defined by the first occurrence (FO) of the index species in bed 64, at 22.6 m of the section. The zone is 5.7 m thick at Tepeyac and cut off upsection by a disconformity. Co-occurring taxa are *Glyptoxoceras texanum*, *Baculites haresi*, *M. (B.) walnutensis*, *Menabites (Bererella) walnutensis*, *Menabites (Delawarella) danei*, *Menabites (Delawarella) mariscalense*, *Menabites (Delawarella) uddeni*, *Menabites (Delawarella) vandaliense*, *Menabites (Delawarella) vanuxemi*, *Menuites* sp., *Pachydiscus (P.) duel-*

*mensis*, *Parapuzosia* (*Parapuzosia*) *seppenradensis*, *Pseudoschloenbachia* (*Pseudoschloenbachia*) *mexicana* and *Scaphites* (*S.*) *hippocrepis* III.

### Other Occurrences

*Submortonicer* *uddeni* was previously known only from a single specimen collected by L.W. Stephenson, in 1932, along the Chesapeake and Delaware Canal. Its occurrence was suggested to correlate with the lowest Campanian *Submortonicer* *tequesquitense* zone, documented for Texas fide Kennedy et al. (1997b), based on a statement by Young (1963, p. 106), who nevertheless did not refer to this correlation explicitly. The view of Kennedy et al. (1997b) is also challenged here because the species is recorded, at Tepeyac, from beds yielding *Scaphites* (*S.*) *hippocrepis* III and above, and thus not from the lowest Campanian, nor co-occurring with *Menabites* (*Delawarella*) *tequesquitense*.

Sohl and Mello (in Owens et al., 1970, table 5) documented *Submortonicer* *uddeni* and *Menabites* (*Delawarella*) *delawarensis* from spoil heaps along the Atlantic seaboard of New Jersey and Maryland. In figure 23 of the authors, the two species are interpreted as co-occurring in strata stratigraphically older than those containing *S. hippocrepis* III. At Tepeyac, however, they clearly co-occur with *Scaphites* (*S.*) *hippocrepis* III.

A single specimen of *Menabites* (*Delawarella*) *vandaliense* was recorded from the Blossom Sand, Texas. The unit was assigned to the upper Santonian by Kennedy et al. (2001), although *Glyptoxoceras texanum*, *Placenticer* *syrtale* and *Baculites* cf. *haresi* oppose this view. These species do not reliably indicate a Santonian age, and correlation of the Blossom Sand to the upper Santonian therefore appears questionable. At Tepeyac, *G. texanum* and *Baculites* *haresi* first appear in the early Campanian, along with *Menabites* (*Delawarella*) *vandaliense*, while *Placenticer* *syrtale* is absent. The Blossom Sand deposit may therefore be early Campanian in age. The occurrence of Young's (1963) high-whorled *Submortonicer* in the Blossom Sand deposit would then be coeval to the upper part of the lower Campanian at Tepeyac, where these morphotypes also occur in large numbers.

### PALAEOBIOGEOGRAPHIC RELATIONS

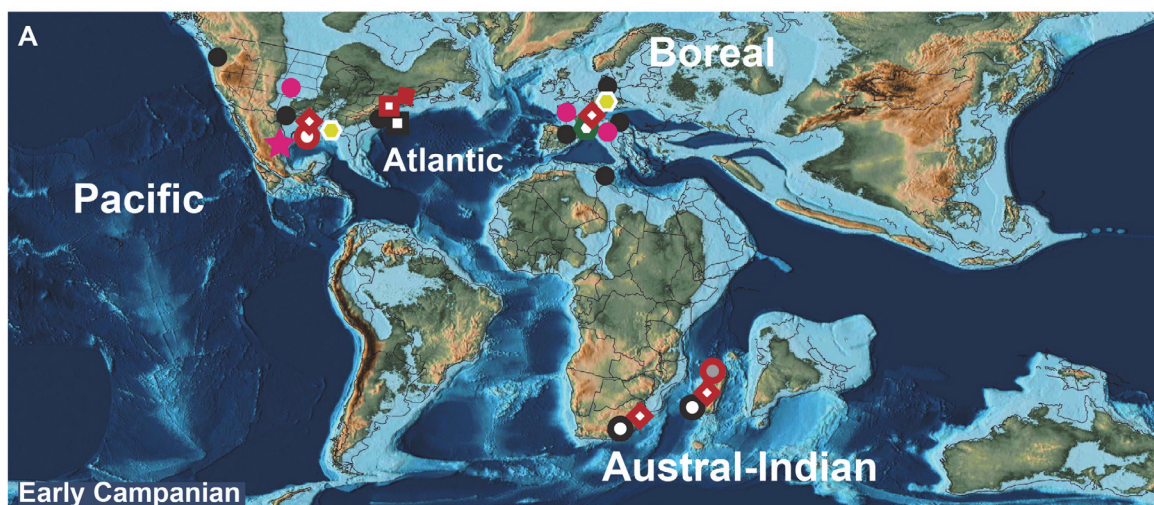
Upper Santonian and lower Campanian *Placenticer* *syrtale* and *Placenticer* *placenta* are absent at Tepeyac. These widely distributed species developed lower Campanian endemic subspe-

cies in the Ojinaga region of Chihuahua, about 300 km west of Tepeyac, an area previously identified as an endemic center for bivalves (Kauffman, 1973). Restriction of *Placenticer* to siliciclastic facies, as prevailing in Chihuahua and western and central Texas (Hyatt, 1903; Young, 1963; Wolleben, 1967; Kennedy et al., 2001; Kennedy et al., 2004) and the northern Gulf Coast (Kennedy et al., 1997a), has already been suggested. High-whorled morphotypes, such as *Placenticer*, are frequently interpreted to have adapted to wave movements and shallow water (Jacobs and Chamberlain, 1996; Ifrim and Stinnesbeck, 2010). The absence of *Placenticer* in the Tepeyac limestones may therefore reflect palaeoenvironmental factors.

The "high-whorled" oxycone and smooth *Menabites* (*Delawarella*) *sancarlosense* (Young, 1963) from the upper Santonian of western Texas and Ojinaga, Chihuahua, and its potential descendants *M. (D.) candelariae* (Young, 1963), *M. (D.) mariscalense* (Young, 1963) and *M. (D.) uddeni* (Young, 1963) from the lower Campanian of the Big Bend area, Texas, but also the coarsely ornamented *M. (D.) densinodosus* (Young, 1963) from the Lower Campanian of the northern Gulf area of Texas, seem to be endemic species of the subgenus *Delawarella* with occurrences in a restricted area reaching from southern Texas to eastern Chihuahua. This interpretation of an early Campanian endemic event is supported by the absence of coarsely ornamented *Menabites* (*Australiella*) (Ifrim et al., 2013) and of *M. (D.) sabinalensis*, an index species for a upper part of the lower Campanian which may also be endemic to Texas. *Texanites candelariae*, originally documented from the Big Bend area of southern Texas, and *Submortonicer punctatum* from the Atlantic seaboard of New Jersey and Maryland, are further endemics to the region of their first description. There was little geographical interchange between texaniids of the region during the late Santonian and early Campanian.

On the other hand, there is also evidence for faunal connections between Tepeyac and other palaeobiogeographic provinces, as summarized in Figure 41. The genus *Menuites* evolved in high southern latitudes (see discussion in Ifrim et al., 2013). An early Campanian *Menuites* from western Coahuila was interpreted by Ifrim et al. (2013) to be the earliest representative in North America, but some specimens from Tepeyac are even older. This includes late Santonian occurrences of *Menuites stephensoni*, a species previously known only





★ *Bacultis taylorensis*, *Menabites (Delawareella) danei*, *Menabites (Delawareella) mariscalense*, *Menabites (Delawareella) n. sp.*, *Menabites (Delawareella) uddeni*, *Menabites (Delawareella) vandaliense*, *Menabites (Delawareella) vanuxemi*, *Pseudoschloenbachia (P.) mexicana*, *Texanites lonsdalei*

○ *Plesiotexanites shiloensis*

● *Bevahites costatus*

◇ *Menabites (Delawareella) delawarensis*

■ *Menabites (Bererella) walnutensis*

● *Parapuzosia seppenradensis*

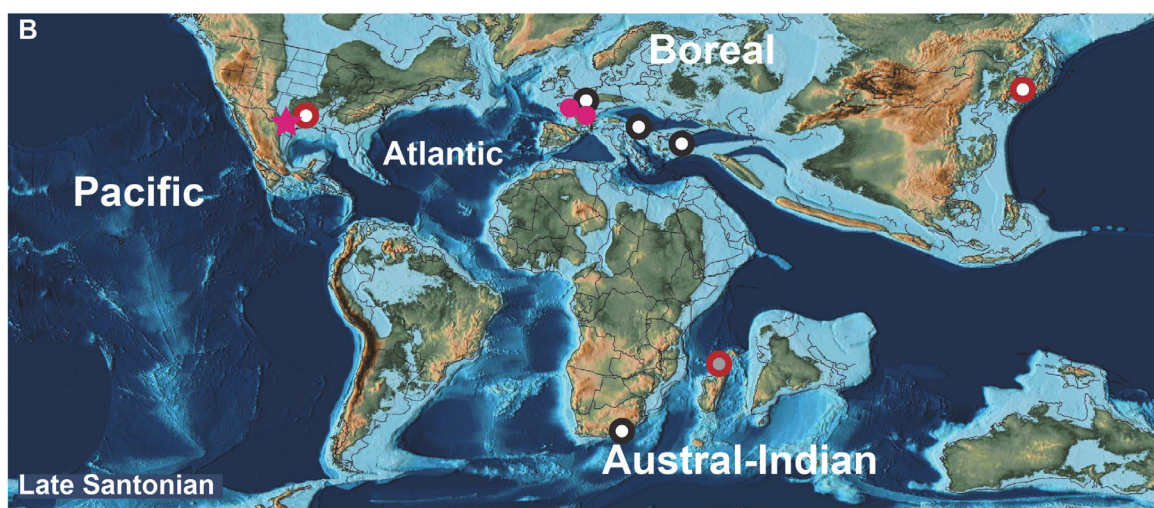
● *Pachydiscus duelmensis*

● *Menuites stephensoni*

■ *Glyptoxoceras texanum*

○ *Amapondella amapondense*

● *Scaphites hippocrepis* III



★ *Menuites stephensoni*, *Pachydiscus (P.) mexicana*, *Texanites lonsdalei*

○ *Plesiotexanites shiloensis*

● *Bevahites bevahensis*

● *Parapuzosia leptophylla*

○ *Amapondella amapondense*

**FIGURE 41.** The early Campanian World with localities presenting ammonites with affinities to northeastern Coahuila (e.g., Tepeyac). Endemic species are summarized in the asterisk. Species with a wider occurrence are marked in other regions, but not in the northwestern Gulf region. Map courtesy of Scotese (2021).

from the early Campanian of southern North America and Central Europe, but also *Parapuzosia* (*Parapuzosia*) *seppenradensis*, which is here documented from the basal Campanian on and thus earlier than in Europe (Ifrim et al., in press). Faunal exchange must have existed with Europe, although these connections have been little evident to date. *Parapuzosia* (*P.*) *leptophylla* is known from the lower Santonian of South France, the Santonian of Austria, and the upper Santonian of England. Its appearance in the northwestern Gulf of Mexico is now dated to the late Santonian. Although frequent at Tepeyac, the species has never been recorded in the Chihuahua area, at only a few hundred kilometres to the west along the same broad shelf. *Parapuzosia* (*P.*) *leptophylla* evolved into the even larger species *Parapuzosia* (*P.*) *seppenradensis* at the end of the Santonian, a species now known to be present on both sides of the North Atlantic (Ifrim et al., in press). This latter gigantic species may have been mobile enough to cross the North Atlantic into the European Basin. Nevertheless, there are also other species recorded from both sides of the North Atlantic, such as *Amapondella amanpondense*, *Menuites stephensoni*, and *Pachydiscus* (*P.*) *duelmensis*. These taxa are known from the Lower Campanian of Germany and Tepeyac. *Glyptoxoceras texanum* occurs in Texas and adjacent areas in the late Santonian but was also found at the Atlantic coast of New Jersey in the early Campanian. It is a close relative of *Neoglyptoxoceras retrorsum* (Schlüter, 1972) from the lower Campanian of Germany. However, *N. retrorsum* and its synonym *N. novimexicanus* (Reeside, 1927) occur in Germany (Kaplan et al., 2005), Austria (Kennedy and Summesberger, 1984; Summesberger et al., 2017), Poland (Błaszkiwicz, 1980; Machalski et al., 2004), the Crimea (Arkadiev et al., 2000), Belgium (Kennedy, 1986; Kennedy, 1993), France (Kennedy, 1986), but also the US Western Interior (Reeside, 1927). *Glyptoxoceras texanum* appears at Tepeyac shortly after *Pachydiscus* (*P.*) *duelmensis*, i.e., during the lower Campanian, which further supports the interpretation of a temporal connection to Europe. After this phase, FOs at Tepeyac are from endemic and North American species, which indicates that the connection to Europe was again lost.

Other faunal connections existed with the Southern hemisphere, and in particular with South Africa and Madagascar. This is indicated by the genus *Pseudoschloenbachia*, known from endemic upper Santonian and lower Campanian species of Texas, Coahuila, and Chihuahua, but also from a

variety of lower Campanian species from Madagascar (Collignon, 1969).

The two *Submortonicer* – *Delawarella* lineages of South Africa – Madagascar on one side, and the Gulf of Mexico on the other, are closely connected. Interchange between the two is seen in the late Santonian, based on the close relation between the *Texanites soutoni* – *Submortonicer* *woodsii* lineage and the emergence of *Menabites* (*Delawarella*) *tequesquitense*. *Amapondella amanpondense*, *Bevahites costatus*, and *Menuites stephensoni* first appear in these levels in both Tepeyac and Madagascar, and possibly *Bevahites bevahensis* in Texas. During the early Campanian, *Menabites* (*Delawarella*) *delawarensis* dispersed to Europe and is documented for this interval from France and Spain. *Menabites* (*Bererella*) *walnutensis* (Young, 1963), present in the Gulf of Mexico region including Tepeyac, and along the North American Atlantic coast, also has equivalents in the lower Campanian of Madagascar (Collignon, 1969). The subgenus may there even be more diverse than in Texas, New Jersey (Kennedy et al., 1997b), and Coahuila.

*Amanpondiella amanpondense* is another widespread taxon known from the Santonian of Israel (Lewy, 1983), France (Kennedy et al., 1995), South Africa (Klinger and Kennedy, 2003) and Madagascar (Klinger et al., 2007), and the Campanian of Germany, and now Coahuila.

*Scaphites* (*S.*) *hippocrepis* III is even wider distributed. The taxon evolved in the Western Interior but dispersed into the northern Gulf (Kennedy et al., 1997a) and to the Atlantic Coast of New Jersey (Kennedy et al., 1997b). It crossed to Europe and is documented from Spain (Küchler, 2000), France (Kennedy, 1986), Poland, Germany, the Netherlands (Jagt et al., 2004; Kaplan et al., 2005), and Sweden (Kennedy and Christensen, 1997). Beyond Europe, the species occurs in late early Campanian sediments of Tunisia (Pervinquier, 1907) and the North American Pacific coast (Anderson, 1958).

The Tepeyac faunal assemblage thus provides evidence for repeated and increasing faunal exchange with Europe and southern latitudes, but also includes intervals of faunal cut-off and endemic evolution. It is difficult to date to explain these unusual faunal connections of the Gulf of Mexico ammonite assemblage with Europe, South Africa, and even Madagascar, but we suggest that these may have been triggered by geotectonic changes during the Santonian-Campanian stages. During this period of the Late Cretaceous, the Cre-



taceous Supergreenhouse ended and was followed by a long-term gradual cooling. This cooling trend has been interpreted to be a consequence of changes in the global ocean circulation system due to the opening of the Equatorial Atlantic Gateway in the late Santonian to early Campanian (Wagner and Pletsch, 1999; Pletsch et al., 2001). The sediments exposed at Tepeyac formed during this phase, and the palaeobiogeographic analysis reflects this palaeoceanographic event. Faunal exchange with other provinces, especially with the Southern Ocean, i.e., Madagascar and Antarctica, increased considerably during this phase. Faunal exchange across the Atlantic was also intensified. It is likely that the final deep ocean opening of the Atlantic Gateway between Brazil and North Africa allowed for the connection to the South and immigration of southern hemisphere taxa during the late Santonian. Intensified oceanic circulation may then have improved the connection with Europe during the early Campanian. Intercontinental faunal exchange in the late Santonian - early Campanian was thus significantly more intense than hitherto known (compare Ifrim et al., 2015a).

## CONCLUSIONS

Twenty-four species of ammonites assigned to 12 genera are described from Tepeyac near Jiménez, northern Coahuila, north-eastern Mexico. The faunal assemblage is late Santonian-early Campanian (Upper Cretaceous) in age and allows for detailed biozonation for Gulf coast ammonoids across the stage boundary. Outstanding outcrop conditions, the abundance and diversity of ammonites in the new section, and their biozonal completeness distinguish Tepeyac as a potential reference section for the Santonian-Campanian boundary in the Americas.

Three phases of faunal interchange are identified in the Tepeyac section: (1) In the late Santonian, with the FO of *M. (D.) tequesquite* along with other species or genera from the Southern Ocean. (2) In the early Campanian. FO of *M. (D.) delawarensis*. Regional to endemic lineages evolved from immigrating ammonoids, thus indicating a subsequent phase of cut-off. (3) The dispersal of *Scaphites (S.) hippocrepis* III ended the

endemic phase during the late early Campanian and led to a phase of increasing dispersal of species and better connectivity between provinces.

Faunal connections between Tepeyac and the Southern hemisphere (e.g., South Africa, Madagascar) may have resulted from the opening of the Atlantic Gateway during the late Santonian, while early Campanian exchange with Europe is interpreted as related to intensified oceanic circulation, another consequence of rapid opening of the Atlantic.

*Placenticer*, a genus frequently used as a proxy to determine the Santonian-Campanian boundary, is absent at Tepeyac, but this is explained as facies-controlled. This genus appears to have preferred clastic depositional environments and avoided carbonate-dominated environments, as present in Tepeyac.

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