

About the generic attribution of *Megatyloceras casei* HUMPHREY, 1949 (Ammonoidea, Ancyloceratina), from the Aptian of Mexico

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Abstract: In the present work we review the generic attribution of the Mexican ammonoid species *Megatyloceras casei* HUMPHREY, 1949, through a careful examination of the holotype housed in the University of Michigan and with reference to new biostratigraphic data from the type locality. We assign here this species to the subfamily Cheloniceratinae and to the genus *Epicheloniceras* CASEY, 1954.

Key Words: Ammonites; Cheloniceratinae; *Epicheloniceras*; Lower Cretaceous; Aptian; Mexico.

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Résumé : Sur l'attribution générique d'une ammonite de l'Aptien du Mexique: *Megatyloceras casei* HUMPHREY, 1949 (Ammonoidea, Ancyloceratina).- Dans ce travail, nous révisons l'attribution générique de l'espèce mexicaine d'ammonite *Megatyloceras casei* HUMPHREY, 1949. Grâce à un examen minutieux de l'holotype conservé à l'Université du Michigan et grâce aussi aux nouvelles données biostratigraphiques obtenues dans la localité-type, cette révision nous permet d'inclure maintenant cette espèce dans le genre *Epicheloniceras* CASEY, 1954.

Mots-Clefs : Ammonites ; Cheloniceratinae ; *Epicheloniceras* ; Crétacé inférieur ; Aptien ; Mexique.

Introduction

In Europe, the genus *Megatyloceras* HUMPHREY, 1949, is restricted to the *Roloboceras hambrovi* Subzone (REBOULET *et al.*, 2011) that coincides with the Oceanic Anoxic Event 1a (=OAE 1a) [e.g., MOULLADE *et al.*, 1998; RENARD *et al.*, 2005; BOVER-ARNAL *et al.*, 2010; MORENO-BEDMAR *et al.*, 2009, 2010; NAJARRO *et al.*, 2011]. Currently, this subzone and the OAE 1a are placed in the *Deshayesites forbesi* Zone (e.g., REBOULET *et al.*, 2011; MORENO-BEDMAR *et al.*, 2012a; GAONA-NARVAEZ *et al.*, 2013) or the *Deshayesites deshayesi* Zone (e.g., RENARD *et al.*, 2005; MOULLADE *et al.*, 2011). *Megatyloceras casei* HUMPHREY, 1949, is known from only a single specimen from the La Peña Formation in the Sierra del Rosario, Durango State, Northern Mexico. Based on the most recent research on the ammonoid record of Mexico (MORENO-BEDMAR *et al.*, 2012b, 2013), we propose assigning this species to the interval between the uppermost lower Aptian and the lowermost upper Aptian. The Mexican *Megatyloceras* is younger than the two possible ages of the *Roloboceras hambrovi*

Subzone proposed in Europe. This biostratigraphic inconsistency is reflected in the stratigraphy. The deposition of the La Peña Formation is related to the Ap 4 sequence (MORENO-BEDMAR *et al.*, 2011, 2012b) and the *Roloboceras hambrovi* Subzone is associated with the older sequence Ap 3 (GRADSTEIN *et al.*, 2012). In the present work we review the generic attribution of *Megatyloceras casei* HUMPHREY, 1949, by means of the taxonomic review of its holotype, specimen UMMP 21865 (Fig. 1) housed in the University of Michigan Museum of Paleontology (=UMMP).

Original description, dimensions and an excerpt of the remarks

HUMPHREY's (1949, p. 149-150) original description reads as follows:

"This species is represented by one large internal cast on which the inner whorls are imperfectly shown.

Form discoidal, depressed, evolute. Whorl section coronatiform, much wider than high, apparently embracing only one-fifth of the preceding

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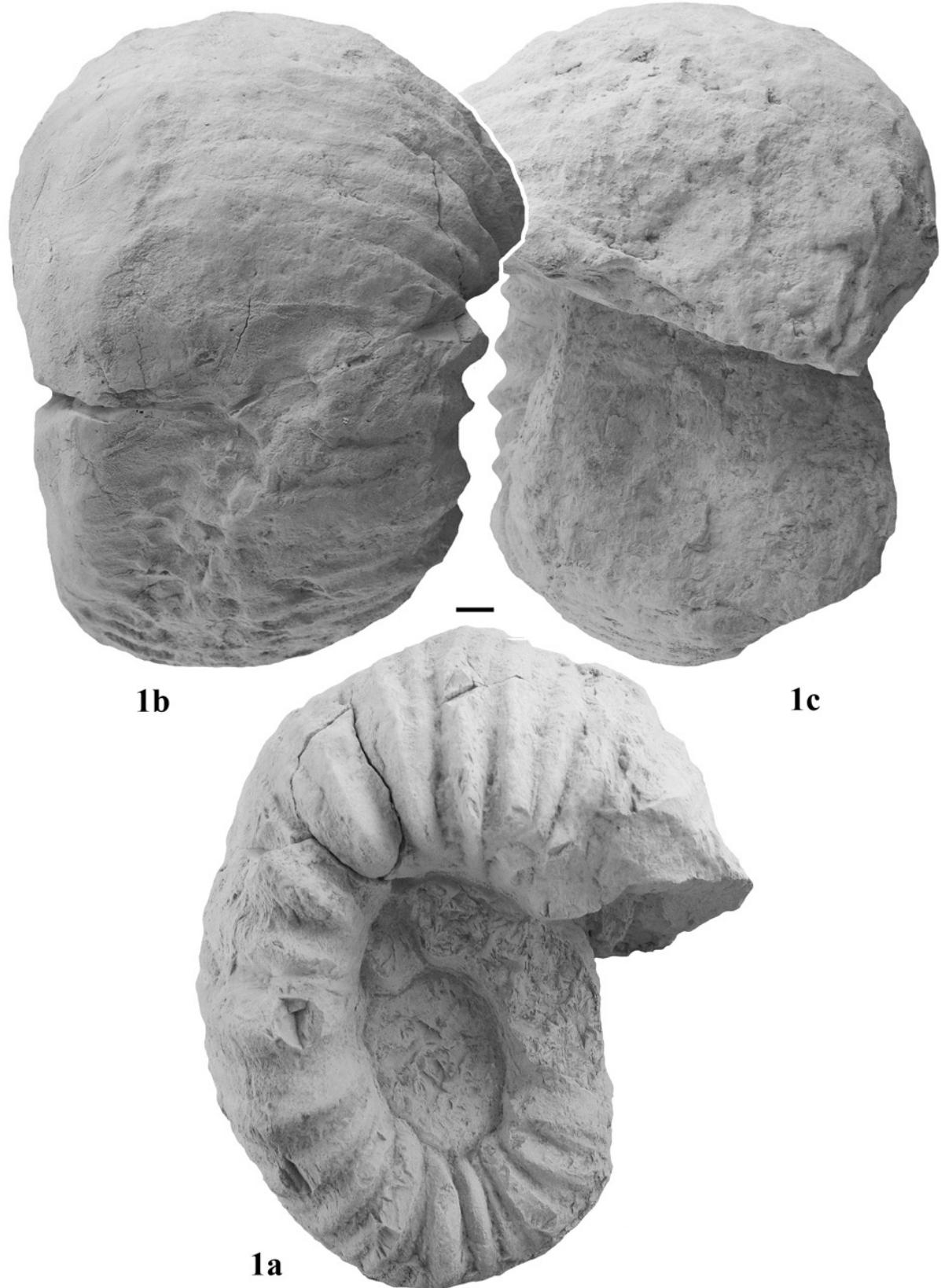


Figure 1: *Megatyloceras casei* HUMPHREY, 1949, lateral (1a), ventral (1b) and frontal (1c) views of the holotype, specimen UMMP 21865. Scale bar is 10 mm.

whorls. Flanks narrowly convex, venter broadly rounded. Umbilicus deep, rather wide; umbilical wall high, steeply inclined.

Shell ornamented by irregularly alternating primary and secondary ribs. Primaries begin on umbilical wall and form exaggerated lateral bullae from which, on posterior part of outer whorl, two or three rounded ribs may branch. One secondary may rise independently on broad venter between branching primaries. All ribs cross venter transversely without alteration, being somewhat irregularly spaced and subequal in size. On anterior portion of outer whorl, bifurcation from large bullae is rare, and two secondaries may be present between two simple primaries. On inner whorls there is suggestion that the bullae are represented by small, double nodes and that whorl height may be relatively greater. Suture lines not shown.

Holotype U.M 21865."

The dimensions (in mm), given by HUMPHREY, are: diameter = 176 mm, width of umbilicus = 85, whorl height = 68, whorl thickness = 150.

Remarks: "The new species is named in honor of Professor Emeritus Ermine Cowles CASE of the University of Michigan, Ann Arbor, Michigan."

Reboulet et al. (2011)

	Zones	Subzones	
Upper Aptian ↑	<i>Epicheloniceras martini</i>	<i>E. buxtorfi</i>	
		<i>E. gracile</i>	
		<i>E. debile</i>	
Lower Aptian	<i>Dufrenoyia furcata</i>	<i>D. dufrenoyi</i>	Megatyloceras spp.
		<i>D. furcata</i>	
	<i>Deshayesites deshayesi</i>	<i>D. grandis</i>	Roloboceras spp.
	<i>Deshayesites forbesi</i>	<i>R. hambrovi</i>	
	<i>Deshayesites oglanlensis</i>	<i>D. lupovi</i>	

Age assignment

The ammonoid record of the La Peña Formation contains three zones: the *Dufrenoyia justinae* Zone of the uppermost lower Aptian, the *Gargasiceras ? adkinsi* Zone that contains the boundary between the lower and upper Aptian and the *Caseyella aguilerae* Zone of the lowermost upper Aptian (MORENO-BEDMAR *et al.*, 2013). The oldest zone to which *Megatyloceras casei* HUMPHREY, 1949, can be assigned, *i.e.*, *Dufrenoyia justinae* Zone, is younger than the record of *Megatyloceras* in the *Roloboceras hambrovi* Subzone of Europe (Fig. 2). The older Aptian taxa, which come from the basal strata of the La Peña Formation, are referable to the genera *Dufrenoyia* and *Burckhardtites*, *Dufrenoyia justinae* Zone. HUMPHREY (1949) and HUMPHREY and DÍAZ (1956) reported some *Dufrenoyia* and *Burckhardtites* in the lower part of the La Peña Formation or laterally equivalent units including the Cuchillo Formation of Chihuahua State, the Sierra de los Muertos, Sierra de Parras, Cuesta del Cura, Puerto de las Palomas, Cañón de San Antonio and other localities of Coahuila State; some localities in Nuevo León State such as Cerro de la Silla and Arroyo de

Moreno-Bedmar
et al. (2013)

Zones	"M". casei
?	
<i>Caseyella aguilerae</i>	
<i>G. ? adkinsi</i>	
<i>D. justinae</i>	

◀ **Figure 2:** Tethyan lower Aptian and lowermost upper Aptian standard ammonite zonation of REBOULET *et al.* (2011) with the ranges of the species of *Megatyloceras* and *Roloboceras*, and Mexican uppermost lower Aptian and lowermost upper Aptian ammonite zonation of MORENO-BEDMAR *et al.* (2013) with the range of *Megatyloceras casei*.

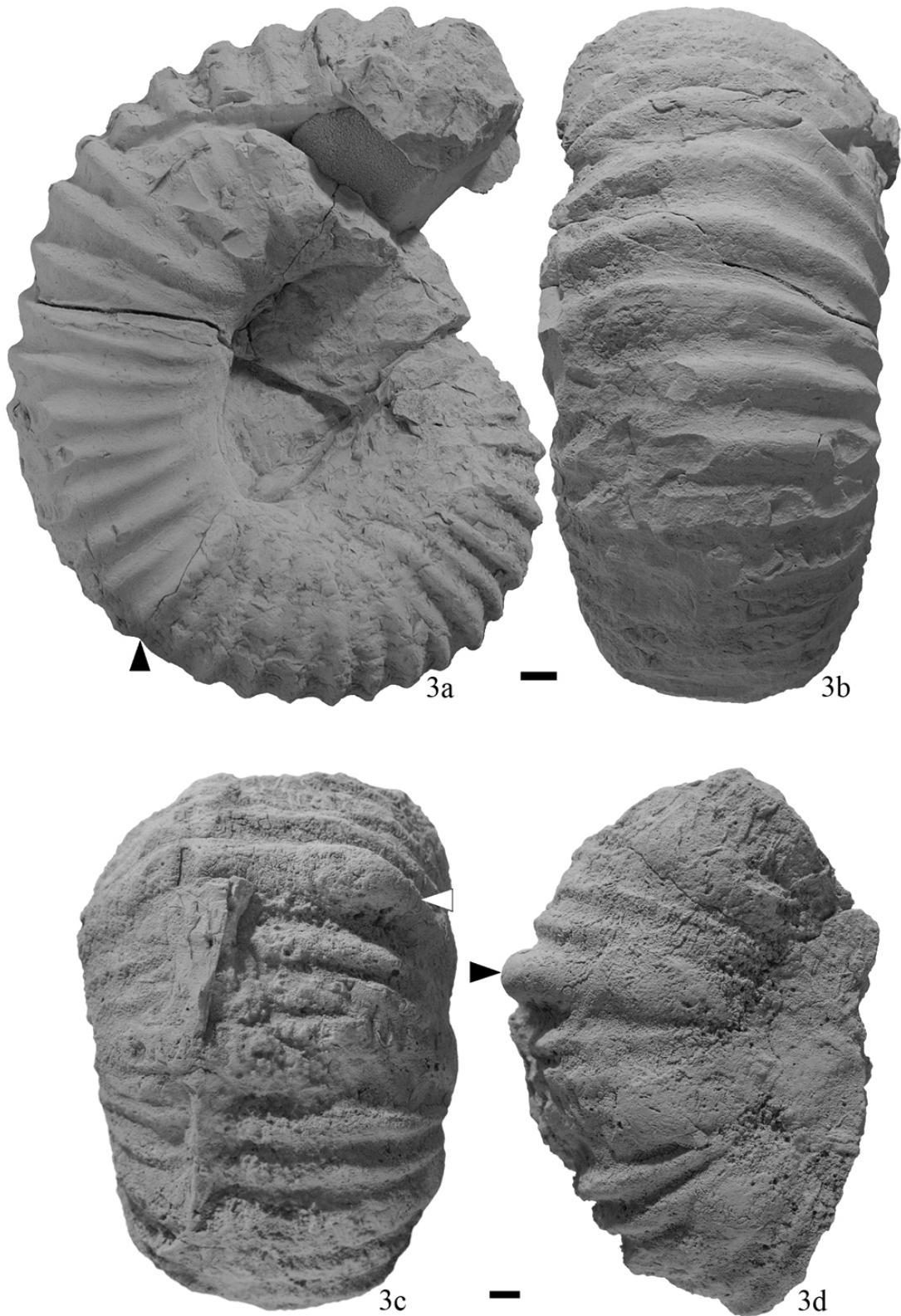


Figure 3: a-b) *Cheloniceras* sp. of 210 mm of maximum diameter lateral (3a) and ventral (3b) views of the specimen UMMP 16414. Black triangle indicates the end of the phragmocone. El Mulato Ranch, Durango State; **c-d)** *Epi-cheloniceras* sp., ventral (3c) and lateral (3d) views of the specimen UMMP 23215. White and black triangles indicate the equivalent ventral tubercle, characteristic of this genus. North of Rio Nazas Valley, Durango State. Scale bar is 10 mm.



Figure 4: **a)** *Cheloniceras* sp. of 175 mm of maximum diameter, lateral view of specimen UMMP 23458. South of Sierra del Rosario, Durango State; **b)** *Cheloniceras* sp. of 320 mm of maximum diameter, lateral view of the specimen UMMP 23479. Black triangle indicates the end of the phragmocone. Rio Nazas Valley, Durango State; **c)** *Cheloniceras* cf. *meyendorffi* of 160 mm of maximum diameter, lateral view of specimen UMMP 23485. West side of Sierra del Rosario, Durango State; **d)** *Cheloniceras* sp. of 225 mm of maximum diameter, lateral view of specimen UMMP 23480. North of Rio Nazas Valley, Durango State. Scale bar is 10 mm.

San Roque; and the El Mulato Ranch and several other localities in the Nazas River area of Durango State. Other authors have correlated the base of the La Peña Formation with the *Dufrenoyia justinae* Zone. Recently, MORENO-BEDMAR *et al.* (2011, 2012b) concluded that the base of La Peña Formation is isochronous and assignable to the *Dufrenoyia justinae* Zone. HUMPHREY (1949) does not specify the position where *Megatyloceras casei* HUMPHREY, 1949, was found within the La Peña Formation. Thus, *M. casei* could come from anywhere within the interval, uppermost lower Aptian to lowermost upper Aptian, that contains the ammonoid record of the La Peña Formation (Fig. 2). However, in the section of the La Peña Formation studied by MORENO-BEDMAR *et al.* (2013), three large fragments of a poorly preserved Cheloniceratinae were collected in beds 136 and 138 of the *Caseyella aguilerae* Zone (lowermost upper Aptian). In this particular section it seems that this is the only part of the La Peña Formation that provides large Cheloniceratinae. The dimensions and preservation of these large fragments of Cheloniceratinae resemble *Megatyloceras casei*. Accordingly, it is likely that *Megatyloceras casei* was collected from a similar position within the La Peña Formation and its age is probably earliest late Aptian. In order to test this probable age we reviewed all of the Cheloniceratinae of a similar size to *Megatyloceras casei* housed in the University of Michigan, Museum of Paleontology (UMMP), that come from the same or nearby areas to where *Megatyloceras casei* was collected. In this collection we recognize specimens of *Cheloniceras* (Fig. 3a-b; Fig. 4a-d), all of which must be assigned to the lower Aptian, as this genus is restricted to this interval. One of these specimens (Fig. 4c) with a high density of ribbing resembles *Cheloniceras meyendorffii* (d'ORBIGNY, 1845). In Europe this species is assigned to the uppermost lower Aptian (e.g., CASEY, 1961a; ROPOLY *et al.*, 2008; MORENO-BEDMAR *et al.*, 2012a). We also found one specimen that belongs to the genus *Epicheloniceras* (Fig. 3c-d). Given the particular ammonoid record of the PFZ section, the presence of *Cheloniceras* (uppermost lower Aptian) in the UMMP collection precludes a lowermost upper Aptian position for *Megatyloceras casei*. Thus, the range of *M. casei* is uppermost lower Aptian to lowermost upper Aptian (Fig. 2).

About the subfamilial attribution of *Megatyloceras casei*

The genus *Megatyloceras* HUMPHREY, 1949, possesses "but one row of prominent lateral bullae in the adult stages" (HUMPHREY, 1949, p. 149). The generic assignment of *Megatyloceras casei* is placed in doubt by HUMPHREY's (1949, p. 150) observation, "On inner whorls there is a suggestion that the bullae are represented by

small, double nodes". CASEY (1961b) comments that at 176 mm diameter this taxon is similar to the genus *Roloboceras* CASEY, 1954, CASEY (1961b) also remarks on the "double nodes" mentioned by HUMPHREY, which are problematic as *Roloboceras* has one tubercle, similar to a bulge, in the peri-umbilical position. CASEY (1961b) concludes that the Mexican taxon is more similar to the subfamily Cheloniceratinae SPATH, 1923, than the subfamily Roloboceratinae CASEY, 1961b, which includes the genera *Megatyloceras* HUMPHREY, 1949, and *Roloboceras* CASEY, 1954. Later, PAULIUC and GRĂDINARU (1970) make a similar argument in coming to the same conclusion as CASEY.

Megatyloceras casei HUMPHREY, 1949, cannot be assigned to the genus *Megatyloceras* because of some clear morphological differences. At the same diameter, the large mid-lateral tubercles that coronate the whorl section appear to be absent and the ribs do not bifurcate or trifurcate regularly as is common in species of *Megatyloceras*. In the Mexican taxon, ribs are clearly visible in the umbilical wall whereas in *Megatyloceras* and *Roloboceras*, ribs are more discreet or absent in this position. *Megatyloceras casei* HUMPHREY, 1949, cannot be included in the genus *Roloboceras* CASEY, 1954, because the majority of *Roloboceras* species of a similar size to the Mexican specimen possess the bulges characteristic of the genus. The only exception is *Roloboceras saxbyi* CASEY, 1961b, in which bulges disappear very early during ontogeny, but this species differs from the Mexican taxon because the ribs are stronger and have a more regular costulation pattern. In addition, the whorl section of *Megatyloceras casei* HUMPHREY, 1949, is of maximum width at the middle of the flank while in all species of *Roloboceras* the maximum width is located at the lower flank position.

The inner whorls of the Mexican species are very badly preserved (Fig. 5).

However, in the last whorl it seems that two very rudimentary tubercles occur in one rib, as indicated by the two white triangles in Fig. 5. This observation accords with the "double nodes" of HUMPHREY (1949). The presence of two such tubercles is a characteristic of Cheloniceratinae SPATH, 1923. The presence of two tubercles therefore enables us to eliminate the possibility that this ammonoid belongs to the genus *Megatyloceras* HUMPHREY, 1949, or the genus *Roloboceras* CASEY, 1954, from the Roloboceratinae, in accordance with the opinions of CASEY (1961b) and PAULIUC and GRĂDINARU (1970). Meanwhile, the fact that the whorl section of *Megatyloceras casei* HUMPHREY, 1949, has the maximum width at midflank is also characteristic of the genera *Cheloniceras* HYATT, 1903, and *Epicheloniceras* CASEY, 1954.

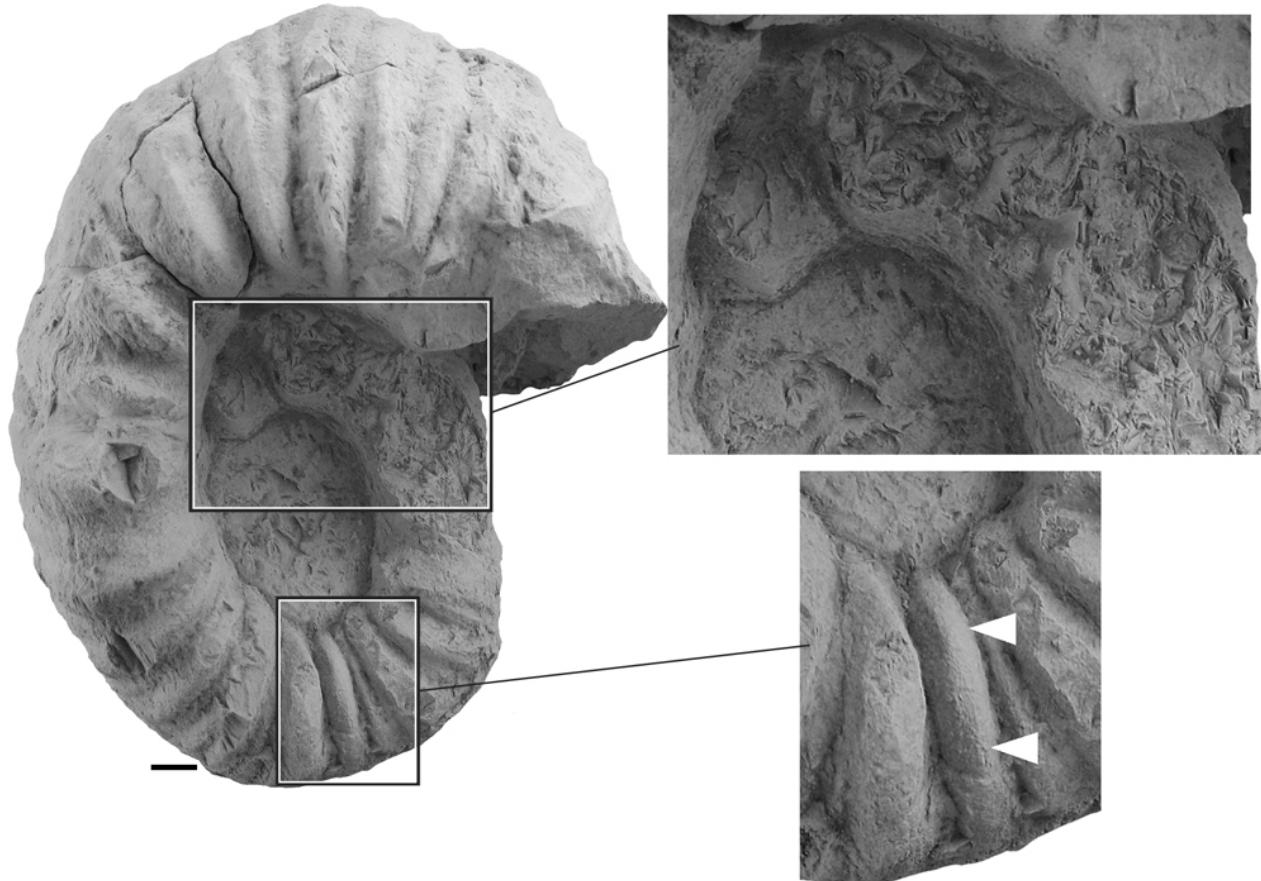


Figure 5: Lateral view of the holotype of *Megatyloceras casei* HUMPHREY, 1949, UMMP 21865 with two enlargements. The two white triangles show two very rudimentary tubercles. Scale bar is 10 mm.

About the generic attribution of *Megatyloceras casei*

The Mexican specimen is characterized by the irregularity of its ribbing pattern, especially of the secondary ribs. This important feature was also noted by HUMPHREY (1949): "Shell ornamented by irregularly alternating primary and secondary ribs". Species of the genus *Cheiloniceras* HYATT, 1903, have a more regular rib pattern. Species of the genus *Epicheloniceras* have a less regular rib pattern, especially in the secondary ribs. In juvenile specimens of the genus *Epicheloniceras* we can clearly see the characteristics of the genus *Epicheloniceras*: siphonal depression in the primary ribs and ventrolateral tubercles. In the current specimen, which is a subadult or adult, inner whorls are not visible and these characteristics cannot be observed. Therefore we compare our specimen with other subadult or adult specimens that belong to the genus *Epicheloniceras* CASEY, 1954. DUTOUR (2005) uses an interesting conception of the macroconch and microconch for the genus *Epicheloniceras*. According to DUTOUR (2005) *Epicheloniceras* microconchs are small forms with low costulation density, very regular rib pattern, less pronounced tuberculation and little difference between the primary and secondary ribs. In contrast, *Epicheloniceras* macroconchs

are larger specimens with higher costulation density, more irregular rib pattern especially in secondary ribs, well developed tuberculation during the first ontogenetic stages and a pronounced difference between the primary and secondary ribs. According to DUTOUR's conception, our specimen would be a subadult-adult macroconch. SINZOW (1906, Pl. 3, figs. 1-3) figured very well preserved specimens of macroconchs of *Epicheloniceras tschernyschewi* (SINZOW, 1906), the type species of the genus. In his Pl. 3, figs. 2 (diameter, D=100 mm) and 3, the high costulation density and the irregularity of the secondary ribs are clearly evident. Further, they show how, during the ontogeny, primary ribs become less tuberculated and more similar to the secondary ribs. On SINZOW's larger specimen (*op. cit.*, Pl. 3, fig. 1) the tuberculation virtually disappears; in its inner whorls it is difficult to see the initial tuberculated stages. NIKCHITCH (1915, Pl. 3, fig. 2) shows a larger specimen (D=174 mm) of the same species with identical features, but in this case the inner whorls are more distinct and it is possible to see the initial tuberculated stages. On the bigger specimen (D=215 mm) (NIKCHITCH, 1915, Pls. 4-5), the tuberculation seems to disappear completely. This absence of clear tuberculation, and the rib pattern of the large Mexican specimen (D=176 mm), resemble features of *Epicheloniceras* specimens of similar

size figured by NIKCHITCH (1915, Pls. 4-5). More recent authors show examples of large specimens of the genus *Epicheloniceras* with the same, previously noted features (e.g., CASEY, 1962, text-fig. 85c; ROPOLÓ *et al.*, 2008, Pls. 17, 19-20; Pl. 21, fig. 1; Pl. 22 & Pl. 24, fig. 3).

In addition, the Mexican specimen seems to have a big tubercle placed on a robust primary rib (Fig. 5). Robust primary ribs with a well developed tubercle can be seen on some specimens of DUTOUR (2005) e.g., Pl. 21, fig. 1b and Pl. 22, 2a & 2c. The comparison of the Mexican taxon with other *Epicheloniceras* specimens illustrated in the literature shows clear similarities.

Additionally, if we compare the species studied here with other Mexican Cheloniceratinae of a comparable size that come from the same or nearby areas to where *Megatyloceras casei* was collected, it is clear that the specimens assigned to the genus *Cheloniceras* (Fig. 3a-b; Fig. 4a-d) are very different in their regular rib pattern. The only specimen with an irregular rib pattern is assigned to the genus *Epicheloniceras* (Fig. 1c-d).

Conclusions

Despite poor preservation of the inner whorls, the morphological and ornamental features of *Megatyloceras casei* lead us to conclude that this taxon should be assigned to the subfamily Cheloniceratinae. Further, we consider it appropriate to place *M. casei* within the genus *Epicheloniceras* as *Epicheloniceras casei* (HUMPHREY, 1949). *E. casei* (HUMPHREY, 1949) is assigned to the uppermost lower Aptian.

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