



Perisphinctid Some Perisphinctid Ammonites of the Tithonian (Jurassic) from Eastern Mexico – Systematic Considerations

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Abstract.- The perisphinctid ammonites *Mazatepites arredondense* and *Volanoceras chignahuapense* were proposed as new taxa in the Upper Jurassic (Tithonian), from outcrops of the Pimienta Formation in the Mazatepec and Chignahuapan villages, eastern Mexico (Cantú-Chapa, 1967, 1990). Interpretation of these taxa generated controversy about their systematic classification and stratigraphic position. For this reason, these taxa and a specimen of *Kossmatia victoris* from the same bed that *Mazatepites* are here revised.

fueron propuestos como nuevos taxa en la Formación Pimienta (Tithoniano, Jurásico); proceden de afloramientos de los pueblos de Mazatepec y Chignahuapan, Estado de Puebla, Este de México (Cantú-Chapa, 1967, 1990). Esas propuestas generaron controversias relacionadas con las clasificaciones sistemáticas y la posición estratigráfica de *Mazatepites*. Por esa razón, esos taxa son de nuevo discutidos. La clasificación sistemática de un ejemplar de *Kossmatia victoris*, procedente de la misma capa que *Mazatepites*, es aquí analizada.

A new family and three new subfamilies are herein proposed: Nebroditidae n. fam., Mazatepitinae n. subfam., Cuetzalaninae n. subfam., and Chignahuapinae n. subfam. *Chignahuapites* n. gen. and *Cuetzalanites tonatiuhoides* n. gen. and sp., and *Chignahuapites fosyi* n. gen. and sp. are also proposed. The penultimate taxa has the same age and geographic provenance of *Mazatepites*. Last taxa is from Hungary.

Una nueva familia y tres nuevas subfamilias son propuestas, Nebroditidae, Mazatepitinae, Cuetzalaninae y Chignahuapinae. *Chignahuapites* género nuevo y *Cuetzalanites tonatiuhoides* género y especie nuevos y *Chignahuapites fosyi* género y especie nuevos también son propuestos. El penúltimo taxa es de la misma edad y localidad que *Mazatepites*. El último taxa es de Hungría.

Key-words: México, Mazatepec-Chignahuapan, Tithonian ammonites, *Mazatepites*, *Cuetzalanites*, *Kossmatia*, *Chignahuapites*.

Palabras clave: México, Mazatepec-Chignahuapan, Amonitas titonianos, *Mazatepites*, *Cuetzalanites*, *Kossmatia*, *Chignahuapites*.

Resumen.- ALGUNAS AMONITAS PERISFINCTIDOS DEL TITONIANO (JURASICO) DEL ESTE DE MEXICO- CONSIDERACIONES SISTEMATICAS.

PREVIOUS STUDIES

Las amonitas perisfinctidos *Mazatepites arredondense* y *Volanoceras hignahuapense*

The purpose of this report is to provide new information of the Tithonian perisphinctids *Mazatepites arredondense* Cantú-Chapa, 1967; *Kossmatia victoris* Burckhardt, 1906; and *Volanoceras chignahuapense* Cantú-



Chapa, 1990; they were formerly known from Mazatepec and Chignahuapan, eastern Mexico (Cantú-Chapa, 1967, 1990).

Because the original systematic classifications and ages generated some controversy (Callomon, *in* Hillebrandt *et al.*, 1992; Cecca, 1999; Oloriz, *in* López-Caballero *et al.*, 2007), the discussion presented in this paper is supported by new illustrations that include the suture lines from these specimens. Hopefully, this new information will help in future systematic studies and also in the chronostratigraphic correlation of these ammonites.

The discussion about the stratigraphic position and systematic classification of *Mazatepites* and *Kossmatia* is also related with the Jurassic-Cretaceous boundary in Mazatepec (Stinnesbeck *et al.*, 1993; López-Caballero *et al.*, 2007) (Fig. 1). This important section was proposed as the stratotype for the Jurassic-Cretaceous boundary, and was characterized by ammonites in this locality; it was later confirmed by subsurface data of cores from Petróleos Mexicanos (Pemex) wells in eastern Mexico (Cantú-Chapa 1967, 1976, 1982, 1989, 1999, 2001, 2003, 2008a-b).

Systematic classification.- The Tithonian ammonites above mentioned were collected from the base of the Pimienta Formation in Mazatepec. This unit consists of an alternating clayey limestone and black shale, with lenses of yellowish-green bentonite dominant and chert at the top. It includes in ascending order the following chronostratigraphic zones in this locality (Cantú-Chapa, 1967): the *Kossmatia victoris*-*Pseudolissoceras zitteli* Zone (6 m), the *Suarites bituberculatum* Zone (19 m), and the *Parodontoceras aff. calistoides* Zone (48 m).

One of the fossils herein discussed is *Mazatepites arredondense* Cantú-Chapa (1967: pl. 1: 1, 1a, 4), which was characterized by two specimens, they were assigned as holotype and paratype. The original illustrations were not good enough and the suture lines were not shown; its systematic classification is here discussed based on new illustrations, including the suture lines. Both specimens were collected from the

Mazatepec sequence in a single bed, they were found associated with *Pseudolissoceras zitteli* and *Kossmatia victoris*.

These species were proposed to characterize a biostratigraphic zone of the Lower Tithonian from eastern Mexico sequences (Cantú-Chapa, 1967, 1989), and compared with specimens previously described from Argentina, Cuba and Mexico (Burckhardt, 1930; Imlay, 1942; Leanza, 1945).

Mazatepites was assigned to the subfamily *Virgatospinctinae* Spath, 1923, and compared with *Anavirgatites* Spath, 1925, and *Phanerostephanus* Spath, 1950, in the original description. However, the two last genera differ from the former by their different style of ribbing (Cantú-Chapa, 1967). *Mazatepites* was later suspected as a synonym of *Virgatosimoceras* Spath, 1925, by Callomon (*in* Hillebrandt *et al.*, 1992); however, this suggestion was not supported by additional evidences. Furthermore, two ammonites from Mazatepec were later assigned and illustrated as *Mazatepites arredondense* by Stinnesbeck *et al.* (1993); they are different, and are discussed below.

In addition, *Volanoceras chignahuapense* Cantú-Chapa, 1990, was erected from a small and well preserved specimen which shows its suture line; it is of the same age as *Mazatepites*, from a neighbor locality, the Chignahuapan village, Eastern Mexico. This taxonomic proposition was refused without explanation by Cecca (1999), who considered it as a junior synonym of *Simoceras aesinense* Meneghini, 1885.

Volanoceras was proposed by Geysant (1985), but it was not accepted by Cecca (1999), neither by Oloriz *et al.* (1999), and Villaseñor *et al.* (2000). Concerning *V. chignahuapense*, the point of view of Cecca (1999) was also followed by Schweigert *et al.* (2002); this taxa is discussed below.

Stratigraphic discussion.- The ammonite zones proposed by Cantú-Chapa (1967) in the Mazatepec sequences was accepted by Imlay (1980) and Callomon (*in* Hillebrandt *et al.*, 1992). Unfortunately, the Zitteli-Victoris Zone containing *Mazatepites* of the Lower Tithonian was reassigned to the Upper



Tithonian by López-Caballero *et al.* (2007), after confusing determinations of some fragmentary ammonites from Mazatepec, which were previously identified by Stinnesbeck *et al.* (1993).

These last authors only illustrated some specimens that were apparently collected from the same bed 4 with *Mazatepites*; they were assigned to *Proniceras* sp., *Suarites bituberculatum* Cantú-Chapa, 1969, *Suarites* sp., *Berriasella* sp., and *Kossmatia* sp. The age of *Mazatepites* was also discussed by López-Caballero *et al.* (2007); the conclusions of these authors are inaccurate and misleading, they will be here analysed.

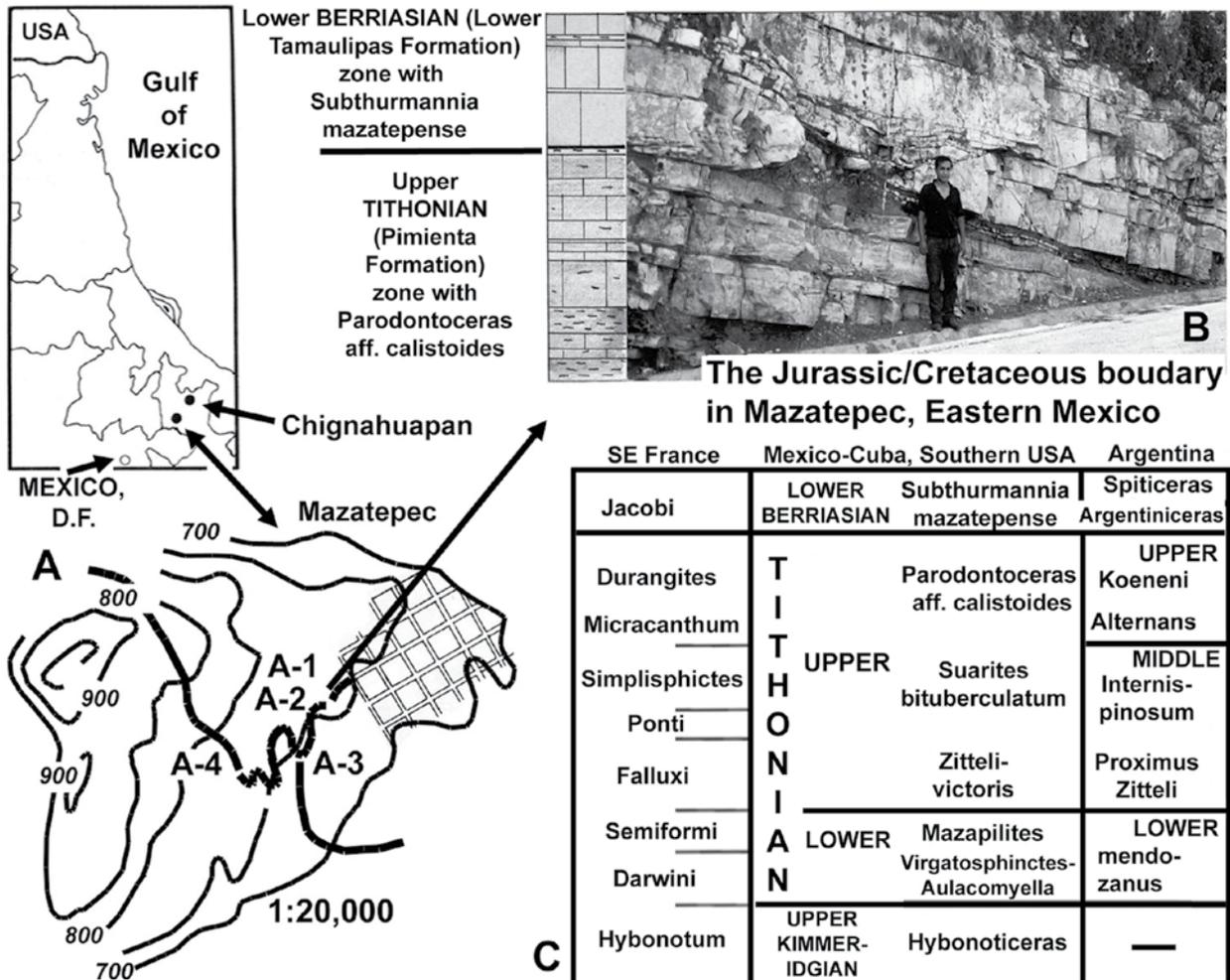
The supposedly Upper Tithonian specimen so-called *Proniceras* sp. does not show the periumbilical lamellar tubercles and the

ventrolateral ribs are not projected forward (see Stinnesbeck *et al.* 1993 : pl. 3: 4), which characterize *Proniceras* Burckhardt (1919).

From this bed with *Mazatepites*, Stinnesbeck *et al.* (1993) also collected some eroded and fragmentary specimens of *Suarites* which were only illustrated. Two of them are preserved as negative moulds, such as *S. bituberculatum* and *Suarites* sp. (Stinnesbeck *et al.* 1993: pl. 4: 6, 10 respectively). The so-called *S. bituberculatum* has no looped ribs and shows only two rows of lateral and probably ventro-lateral tubercles; the looped ribbing characterizes the genus *Suarites*. This type of ribbing is not developed in these specimens.

Two fragmentary specimens were assigned to *Kossmatia* and *Berriasella* and were only illustrated by Stinnesbeck *et al.* (1993: pl. 4:

Figure 1. A, C: map showing the Mazatepec ammonite locality, bed 4, base of the Upper Tithonian (Pimienta Formation). B: Photograph of the Jurassic-Cretaceous boundary in same locality, D: biostratigraphical zones of the Tithonian-Kimmeridgian, eastern Mexico.



7, 11, respectively). Both specimens do not show the ventral ribbing that characterizes these genera. Unfortunately this material is insufficient for any biostratigraphic study.

In addition, another specimen was collected from the bed 4 with *Mazatepites*, and was assigned to *Kossmatia victoris* of the Lower Tithonian by Cantú-Chapa (1969). López-Caballero *et al.* (2007) did not accept the age previously assigned for this bed, proposing to change it to the Upper Tithonian. This proposition is unreliable and importantly affects the recognition of the position of the Jurassic-Cretaceous boundary in Mazatepec by biostratigraphic correlation. The systematic position of a specimen assigned as *Kossmatia victoris* is below revised, it was collected in association with *Mazatepites* (Cantú-Chapa 1967, 1999, 2006) (Fig 1).

In fact, the stratigraphical sequence from Mazatepec was previously disregarded by Remane (*in Steinnsbeck et al.*, 1993) to recognize the Upper Tithonian rocks; in this paper is insisted in reassigning to the Berriasian several unquestionably Upper Tithonian ammonites, based on a supposed predominance of calpionellids over those fossils from this Mexican locality. By the way, the Jurassic-Cretaceous boundary would not be present in this locality, neither the Upper Tithonian beds, corresponding to the zone with *Parodontoceras aff. calistoides*. It represents a bizarre biostratigraphical explication, as was presented by López-Caballero *et al.* (2007).

The Lower Tithonian age originally proposed for *Mazatepites* was later confirmed by Parent (2001), when he studied *Pseudolissoceras zitteli* from Argentina; specimens of this species from several countries, including Mexico were compared by this author. Both taxa were collected in the same bed from Mazatepec (Cantú-Chapa 1967).

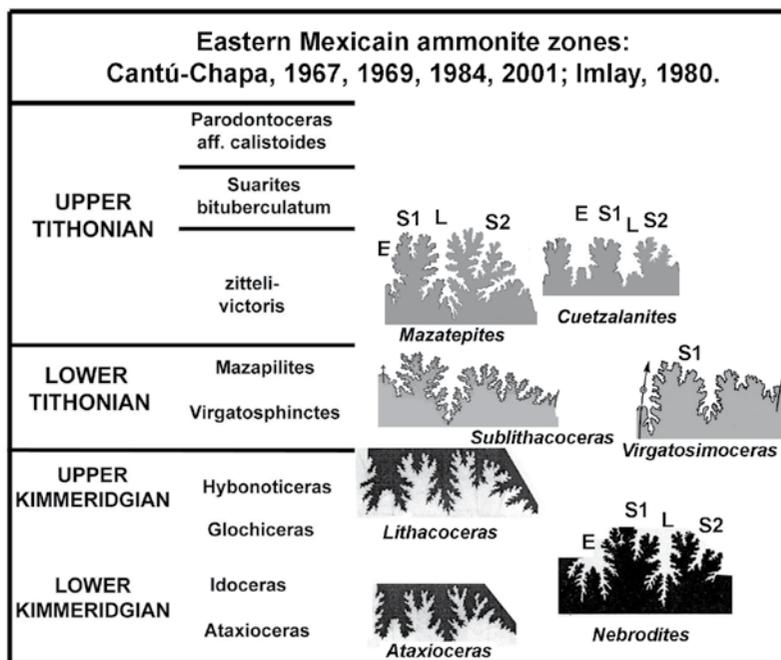
The Tithonian subdivisions in Mexico. - The ammonites are the primary biostratigraphic tool for definition of the Mesozoic periods and their stages on the basis of the ammonite zones. The Tithonian is subdivided in two or three substages in Europe (e.g., Arkell *et al.*; 1956, Enay, 1964; Enay & Geysant,

1975; Cecca *et al.*, 1988; Schweigert & Scherzinger, 2004). Some of the zonations proposed in those papers have been used for time-correlation of Mexican sequences (Imlay, 1980; Cantú-Chapa, 1967, 1984, 2001; Oloriz *et al.*, 1990).

However, different biostratigraphic criteria are invoked for subdividing the Tithonian. For instance, the presence of berriasellids allow to propose a bipartite division from this stage in Cuban sequences (Myczynski, 1990). Some perisphinctids are used to subdivide it in two substages in German sequences (Schweigert & Scherzinger, 2004). Also, bipartite or tripartite Tithonian subdivisions have been used in France, based on different ammonite assemblages (Enay & Geysant, 1975; Cecca *et al.* 1988; Cecca & Enay, 1991).

On the other hand, the Zone of *Mazapilites* (Fig. 1) represents the lower Tithonian top in Mexico; it characterizes a limited and important biostratigraphical zone that allows subdivide the Tithonian in two chronostratigraphical substages; it represents an important break in this biostratigraphic succession (Cantú-Chapa, 2001). *Mazapilites* Burckhardt, 1919, is a conspicuous oppellid with a wide geographical distribution in México (Burckhardt, 1930; Imlay, 1980; Cantú-Chapa, 1984; Villaseñor *et al.* 2005) and

Figure 2. Phylogenetic sequence of suture lines from selected Kimmeridgian-Tithonian Perisphinctoidae genera. After Geysant & Zeiss, 1978; Zeiss, 1968; Geyer, 1961; and the author. Without scale.





it also recognized in Cuba and Germany (Myczynski, 1990; Berckheimer & Hölder 1959).

Finally, it must be pointed that the ammonite zones of the Mexican Upper Jurassic which were proposed by Callomon (*in* Hillebrandt *et al.*, 1992), and Oloriz (Villaseñor *et al.*, 2000; López-Caballero *et al.*, 2007) are theoretical and inconsistent. They represent simple transactions from the European zones to distant countries like Mexico; these zones have not the relationship with the biostratigraphical bases that are used to generate new propositions; by the way unaccountable hiatus are represented in them.

SYSTEMATIC PALEONTOLOGY

Morphologic terminology follows Wright *et al.* (1996). All dimensions are given in millimeters; D = shell diameter; H = whorl height measured from umbilical seam to venter; W = whorl width; U = umbilical diameter. Specimens described in this paper are housed in the author collection, and are abbreviated Ac; casts are deposited in Instituto Politécnico Nacional de México (IPN).

Order Ammonoidea Zittel, 1884
Suborder Ammonitina Hyatt, 1889
Superfamily Perisphinctoidea Steinmann, 1890

Discussion.-This superfamily includes also families of the Kimmeridgian-Tithonian, some of them are insufficiently defined; they are characterized by a supposedly regional distribution and an hypothetical intrageneric dimorphism, but lacking clear definitions based on their morphological characters (Donovan *et al.*, 1981).

Genera from the above mentioned age are grouped in two families, they include specimens characterized by subinvolute shell and subrounded whorl section, flanks and narrow venter are also subrounded. The family Ataxioceratidae Buckman, 1921, represents forms with sharp and distant, prorsiradiate primary ribs, or they are weakly curve forward on the internal part of the flanks. Primary ribs divide in fine secondaries on the external flank of the outer whorl, and cross transversely the ventral

region. Suture line with S1 subrectangular, narrow and irregularly subdivided; S2 very narrow, frequently trifurcated at top, U2 with small elements; E is as large as S1 and is divided by a small and subrectangular ventral saddle; L is superficial and irregularly trifold (Fig. 2).

This family includes the subfamilies Ataxioceratinae Buckman, 1921, Lithacoceratinae Zeiss, 1968, and Virgatosphinctinae Spath, 1923, from the Kimmeridgian-Lower Tithonian (Donovan *et al.* 1980). By contrary, the tribe "Sublithacoceratinae" which was proposed by Zeiss (1968), is considered unnecessary to distinguish it as a different subfamily by the above mentioned authors. Therefore, this last subfamily must be reestablished because of its particular suture line that is centred in its L which is deeper than E, and by its S1 which is higher than S2; both elements differ from those of Ataxioceratinae representatives (Fig. 2).

Another systematic classification is represented by the family Lithacoceratidae which was discussed by Zeiss (2001: 39); it was previously considered at subfamily level by the same author (Zeiss, 1968). This family includes the subfamilies Torquatisphinctinae and Paralaucostephaninae (Tavera, 1985), and Sublithacoceratinae and Richterellinae Sapunov, 1977.

The Richterellinae was emended by Cantú-Chapa (2006) and assigned to the family Berriasellidae Spath, 1922, by its suture line which differs from the lithacoceratids. Representatives of Richterellinae exhibit principal ribs bifurcate on the flanks and projected forward on the venter, S1 with a wide base differs from the same structure with a narrow base in the lithacoceratids.

There is also a small group of Kimmeridgian perisphinctid with an uncertain systematic position such as *Idoceras* Burckhardt, 1912, and *Nebroditis* Burckhardt, 1912. Both genera are discussed below.

Family Lithacoceratidae Zeiss, 1968

Discussion.- This family includes subevolute shell with rectiradiate and primary ribs

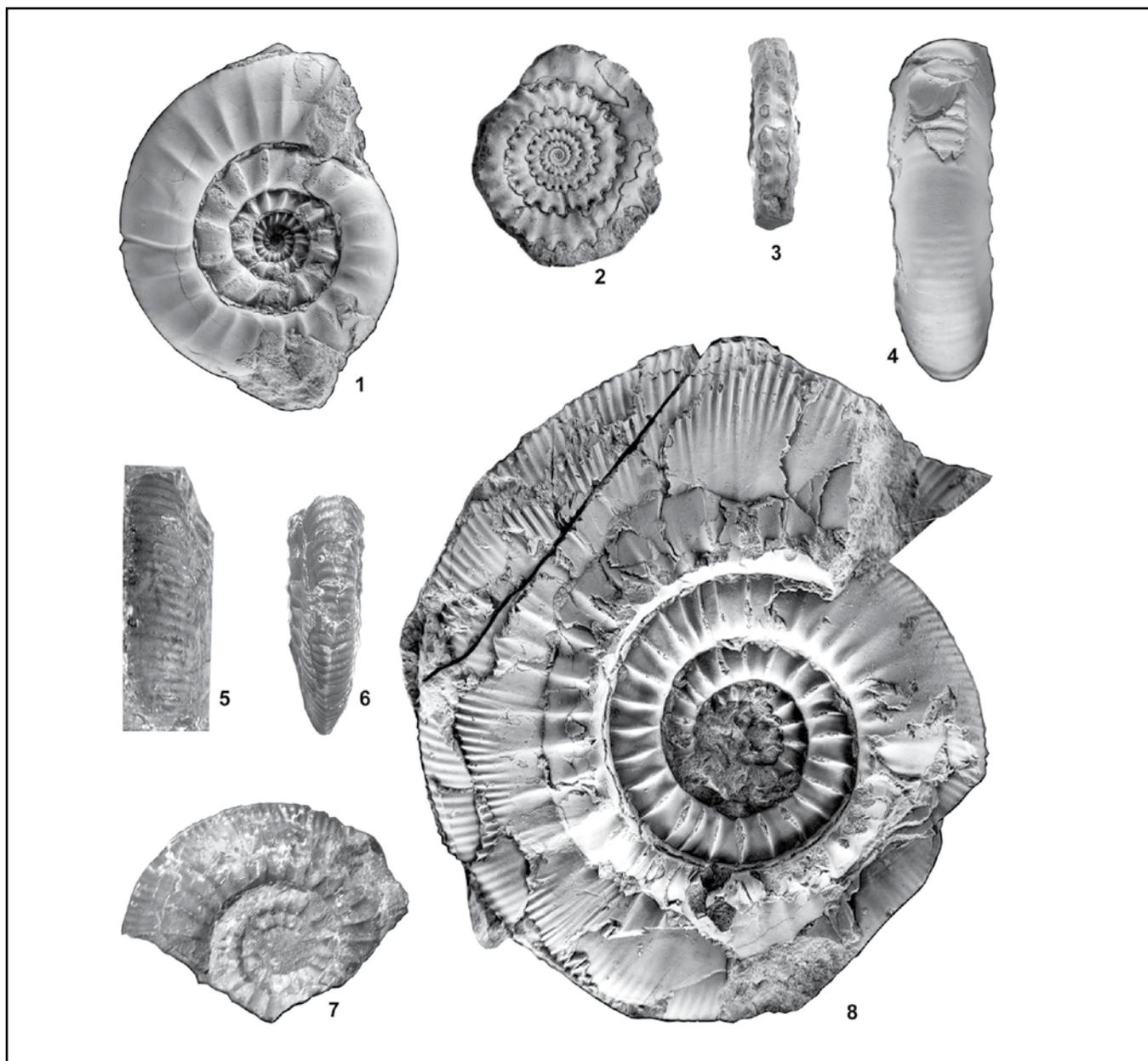


Figure 3.1, 4: Lateral and ventral views of *Cuetzalanites tonatiuhoides* n. gen. et n. sp., holotype (Ac-89).
 2, 3: Lateral and ventral views of *Chignahuapites chignahuapense* (Cantú-Chapa, 1990), holotype (Ac-1001).
 5, 8: Ventral and lateral views of *Mazatepites arredondense* Cantú-Chapa, 1969, holotype (Ac-89).
 6, 7: Ventral and lateral views of *M. arredondense* Cantú-Chapa, 1969, topotype (Ac-130), Mazatepec, Puebla, bed 4. Base of the Upper Tithonian, *Pseudolissoceras zitteli*-*Kossmatia victoris* Zone. Pimienta Formation. All Specimens x0.9. Specimens coated with ammonium chloride, except 6-7. (Ac = collection of the author).

that are separated on the inner part of the flanks; ribs are subdivided on outer flanks, crossing normally the subrounded venter. Suture line with trifurcated and deep L, and subrectangular, S1 irregularly bifurcated. The representatives of this family are Kimmeridgian-Tithonian in age.

Subfamily Mazatepitinae new subfamily

Type genus.- *Mazatepites* Cantú-Chapa, 1967.

Age.- Base of the Upper Tithonian.

Diagnosis.- Shell subevolute, subrounded whorl section, flanks slowly subrounded. Rectiradiate, sharp and lamelliform, widely distant primary ribs on inner whorls; divided in fine secondary ribs in a palmate pattern from the mid-outer part of the flanks, crossing normally the narrow venter; sporadic constrictions. Suture line with S1 subrectangular, somewhat narrow base, irregularly bifurcated at top; S2 larger and

higher than S1, with narrow base, strongly bifurcated by a secondary and oblique lobe projected toward the internal shell; its external branch larger and prominent than the internal one; L trifurcate, base slightly inclined to the umbilical area, deeper than E.

Discussion.- Mazatepitinae n. subfam. has its own, characteristic morphological features associated with those typical of the family Lithacoceratidae:

- subevolute shell with subrounded venter;
- sharp and rectiradiate and widely distant primary ribs on inner whorls which become subdivided at outer flank in the external whorls;
- S1 large, subrectangular and subdivided by a secondary lobe at top.
- S2 prominent, divided from the narrow base by a secondary lobe that is projected toward the umbilical area; its external branch higher than S1 (Fig. 2).

Taxonomy within the new subfamily is based essentially on the above mentioned features; its suture line exhibits a prominent and strongly S2 with two divergent branches and a narrow base. They must therefore be considered as the basic unifying element that links it with the family Lithacoceratidae.

Mazatepitinae n. subfam. differs from Lithacoceratinae and Sublithacoceratinae by its rectiradiate, lamelliforme and distant primary ribs on inner whorls, and by S2 larger and higher than S1, it is subdivided by a deep, oblique and secondary lobe. By contrary, genera from the two latter subfamilies have a fine and dense ribbing on the inner whorls, and S2 is subdivided normally.

The descriptions of the suture lines of these subfamilies are incomplete in systematical studies. However, one of the most important difference between them lies in L, that is narrow, regularly trifurcate, and twofold in deep than E in the Sublithacoceratinae, contrary to representatives of the Lithacoceratinae and Mazatepitinae in which L is as long as E. The former also differs from the two latter by the prominence of S1 over S2. Mazatepitinae n. subfam. includes the monospecific genus *Mazatepites*.

Genus *Mazatepites* Cantú-Chapa, 1967

Type species.- *Mazatepites arredondense* Cantú-Chapa, 1967; by OD.

Emended diagnosis.- Subevolute shell, subrounded whorl section, flanks slowly subrounded; inner whorls with sharp, lamelliform, and widely spaced rectiradiate primary ribs arising from the subrounded umbilical wall; outer whorl with primary and rectiradiate ribs originate fine, and palmate secondary ribs, crossing normally the narrow and subrounded venter. Suture line with E narrow, divided by a narrow and small saddle; L regularly trifurcate, long, narrow, base slightly inclined to the umbilical area. S1 subrectangular, irregularly divided at top, with somewhat narrow base; S2 large, with narrow base, higher than S1, irregularly and strongly divided by an oblique secondary lobe project toward the internal shell; external branch higher than internal one; U2 with small and low elements.

Discussion.- *Mazatepites* was proposed with a type-species based on two specimens with different form of shell and type of ribbing (Cantú-Chapa, 1967). *Mazatepites* was later considered with doubts as synonym of *Virgatosimoceras* Spath, 1925, by Callomon (in Hillebrandt et al., 1992); it was not specified which one of the two specimens, originally included in *M. arredondense*, could be assigned to *Virgatosimoceras*. However, the study of the original material, including the suture lines which have not been shown before, suggests that they must be separated in two different genera; they are described below.

Virgatosimoceras shows the typical suture line of Simoceratidae (Geysant & Zeiss, 1978), it consists of S1 rectangular, with a wide base, small incisions, and a weak division at top. L is narrow and irregularly trifurcated; the umbilical external lobes (U2) are very superficial (see Fig. 2).

Mazatepites may be distinguished from *Virgatosimoceras* by its ornamentation and suture line. In the former primary ribs are simple, lamelliform, well spaced, and rectiradiate on inner whorls; they branch in several fine and closely spaced secondary

ribs in outer whorls, crossing without interruption the narrow and subrounded ventral region, even in the internal mould; in the latter this kind of ventral ribbing is not present.

Mazatepites is also distinguished from *Virgatosimoceras* by its suture line, S1 is subrectangular with a somewhat narrow base, and asymmetrically bifurcated at top by a secondary lobe; by contrary, in *Virgatosimoceras* S1 is rectangular with a large base and a weakly subdivision at top.

The most important difference between these genera lies in S2; *Mazatepites* has a narrow base and is strongly bifurcated in two long and divergent branches, by a deep and inclined secondary lobe, that is projected toward the internal shell; S2 is larger at top than S1. By contrary, this structure is short, rectangular, and superficial in *Virgatosimoceras* (Fig. 2).

***Mazatepites arredondense* Cantú-Chapa, 1967**

Figs. 2; 3.5-8.

1967 *Mazatepites arredondense* n. sp.- Cantú-Chapa, p 7, pl. 1, fig. 4; non figs. 1, 1a.

non 1993 *Mazatepites arredondense* Cantú-Chapa.- Stinnesbeck *et al.*, pl. 3, figs. 2, 3.

Types.- Holotype (Ac-89) figured in Cantú-Chapa (1967: 7, pl. 1: 4), herein refigured in Fig. 3.5, 8. Topotype (Ac-130) (Fig. 3.6, 8).

Diagnosis.- Same as for the genus.

Description.- Sculpture ontogeny is composed by the succession of two styles of ribbing: inner whorls with sharp, lamelliform, distant and rectiradiate ribs; outer whorls with primaries palmate from the mid-flank, and crossing perpendicularly the narrow and subrounded venter. The umbilical wall is low and the flanks are gently subrounded.

A small topotype specimen is crushed (Fig. 3.6, 7), and was collected by the author in the same bed of the Pimienta Formation as the holotype; it was not considered in the original description (Cantú-Chapa, 1967), it is here illustrated. In this topotype the last whorl is subevolute with flanks subrounded,

showing the same style of ornamentation that the holotype. It consists of simple, sharp, lamelliform, and distant primary ribs on the inner whorls; the ribs become palmate from the mid-flank on the outer whorl, and cross normally the subrounded and narrow ventral region. Both specimens with different sizes are similar in U/D = 0.4.

Discussion.- The two specimens from Mazatepec mentioned and illustrated as *M. arredondense* by Stinnesbeck *et al.* (1993: pl. 3: 2-3), do not belong to this genus. One of them (Stinnesbeck *et al.*, 1993: pl. 3: 2), although poorly preserved, differs by its fine and dense ribbing on the inner whorls; it may be assigned to the Lithacoceratinae by this style of ornamentation, most likely representing a still indescribable taxa. The other specimen (Stinnesbeck *et al.*, 1993: pl. 3: 3) is discussed below as a new genus.

Age and occurrence.- *Mazatepites* is known from the base of the Upper Tithonian. Pimienta Formation.

Family Nebroditidae new family

Type genus.- *Nebrodites* Burckhardt, 1912.

Diagnosis.- Evolute, serpenticonic, planulate shell with wide umbilicus; subquadrate to subrounded whorl section; simple or bifurcated, rectiradiate or weakly curving forward primary ribs, somewhat raised on the ventrolateral edges; irregular occurrence of constrictions. Suture line with S1 subrectangular and irregularly bifurcated at top; S2 with a large base, asymmetrically divided at top by an accessory lobe; internal branch inclined forward to umbilical region, external branch irregularly bifid, as high as S1; U2 with small elements, E narrow with a small and low ventral saddle, L trifurcate.

Discussion.- Nebroditidae n. fam. is proposed for including evolute shells, with simple, rectiradiate or gently curved ribs, some of them are irregularly bifurcated. The genus *Nebrodites* was assigned to the family Aspidoceratidae Zittel, 1895, subfamily Simoceratinae Spath, 1924, by Arkell *et al.* (1957). Later, it was considered as a monotypic genus and placed in the family Perisphinctidae Steinmann, 1890, subfamily

Idoceratinae Spath, 1924, by Ziegler (1959) and Brochwicz-Lewinski (1973).

More recently, it was placed together with *Idoceras* in the family Ataxioceratidae Buckman, 1921, subfamily Idoceratinae by Callomon *in* Donovan *et al.* (1981). Both genera are very important, their representatives are known in Mexican sequences of the Lower Kimmeridgian (Burckhardt, 1930; Imlay, 1980; Cantú-Chapa, 2001).

They represent a small group with an uncertain systematic position that must be revised. Their inclusion in the family Ataxioceratidae is artificial, they have different morphological features, such as the attitude of coiling, the style of ribbing, and the pattern of the suture line; all them differ from this family. By the way, they must be separated from the family Ataxioceratidae and reassigned each one of them into different taxa. *Nebroditites* has a very evolute and planulate shell, large umbilicus, subrectangular whorl section and venter plane; its simple, rectiradial or weakly curved primary ribs are irregularly bifurcated at the outer part of the flanks.

Idoceras differs from this genus by its subevolute shell, the diversity types of lateral ribbing and its attitude at the ventral region, and by the suture line; primary ribs are divided from the mid part of the flanks in bifurcate to polyfurcate patterns, crossing the ventral area gently projected forward. It differs also from *Nebroditites* and representatives of Ataxioceratids by this last morphological feature.

The most important morphological feature to distinguish the ataxioceratids from *Idoceras* is their suture lines, which S2 varies from very narrow in the former to subrectangular and higher than large in the latter (Cantú-Chapa, 1992). Lithacoceratidae, Sublithacoceratinae and *Nebroditites* have similar subrectangular S1, exceptly representatives of Ataxioceratidae which S1 and S2 were already mentioned (Fig. 2). For the above reasons the Nebroditidae n. fam. is here proposed to includes the monotypic genus *Nebroditites*.

In addition, it is here must be pointed out that the Upper Oxfordian *Passendorferia*

Brochwicz-Lewinski, 1973, was considered as a subgenus of *Nebroditites* by this author. However, it was later excluded from it by Meléndez-Hevia (1989). By contrary, *N. rohdaenensis* Ziegler (*in* Hölder & Ziegler, 1959: 191, pl. 21: 1-3), does not belong to this genus considering its palmate and fine ribbing on the outer part of the flanks; it is a representative of Lithacoceratidae.

Nebroditidae n. fam. could be related with the following systematic unity by its evolute and planulate shell, radial ribbing, and by its similar attitude of the suture line in S1 and S2 (Fig. 2).

Subfamily Cuetzalaninae new subfamily

Type genus. - *Cuetzalanites* n. gen.

Diagnosis. - Shell evolute, planulate, with wide umbilicus and subrounded whorl section; umbilical wall subrounded and low. Venter moderately wide and subrounded; with a constriction in the last whorl. Simple, lamelliform, rectiradial, and very widely spaced primary ribs, weakly divided at the outer flanks, crossing normally the ventral region. Suture line with E shallow and narrow; L asymmetrically trifurcate; S1 subrectangular, irregularly divided at top, with somewhat narrow base; S2 with narrow base, divided irregularly by an inclined and narrow accessory lobe, external branch bifurcated at top, higher than S1; U2 with small elements (Fig. 2).

Etymology. - Derived from the Cuetzalan village near Mazatepec, northern State of Puebla, eastern Mexico.

Discussion. - The Cuetzalaninae n. subfam. includes the monotypic genus *Cuetzalanites* n. gen. Taxonomy of the proposed Cuetzalaninae n. subfamily within the Nebroditidae n. family is based essentially on the characteristics of the same type of evolute and planulate shell, with wide umbilicus, rectiradial ribbing, and suture line consisting in a subrectangular S1 that is irregularly bifid at top, with a somewhat narrow base; S2 is here considered as formed by a wide base, that is divided by two branches, the internal one inclined forward the umbilical area.

This subfamily could be related with representatives of the Simoceratinae, by its evolute shell and the style of ribbing, that is based on simple and rectiradiate principal ribs. However, they differ by their suture lines that correspond to different subfamilies, as following (Fig. 2):

- (a) S1 subrectangular with a somewhat narrow base, and S2 wide at top, and bifurcate in Cuetzalaninae, eg. *Cuetzalanites*;
 (b) S1 very rectangular with a base as wide as the top; S2 very small, close to U2 in Simoceratinae, eg. *Virgatosimoceras*.

Phylogeny of the Cuetzalaninae n. sub- fam.- The origin of the proposed subfamily Cuetzalanitinae could be rooted in Nebroditidae, by its similar attitude of coiling, that is evolute and planulate, and by its rectiradiate primary ribs. However, the Tithonian Cuetzalaninae have widely spaced ribs, contrary to the Kimmeridgian nebroditids, which have dense, rectiradiate or gently curved ribbing on the inner whorls, some of them are bifurcate on the outer whorl. The former represents a biostratigraphic element younger than nebroditids, a short time interval separates them.

It could be considered that similarities in their suture lines link them. It consists of S1 which is rectangular and bifurcate at top; S2 is larger, more strongly divided than S1, with large base, and divided by a inclined secondary lobe in both taxa (Fig. 2).

Age.- Tithonian.

Genus *Cuetzalanites* new genus

Type-species.- *Cuetzalanites tonatiuhoides* new genus and sp.

Diagnosis.- Evolute and planulate shell with subrounded whorl section; flanks, umbilical wall, and venter subrounded. Simple, rectiradiate, lamelliform and very widely spaced primary ribs, arise from the umbilical shoulder and weaken on outer flanks; ribs irregularly trifurcate at the ventro-lateral edges, the secondaries are weak and cross normally the ventral area on the internal mould and on the shell; a single constriction on the bodychamber. Suture line with E

narrow, as deep as L, subdivided by a small and narrow ventral saddle, L irregularly trifide, S1 subrectangular, somewhat narrow at the base and slightly bifid at top, S2 as high as S1, irregularly bifid by an oblique secondary lobe, the outer branch higher than the internal one.

Etymology.- As for the subfamily.

Age and occurrence.- Base of the Pimienta Formation. Base of the Upper Tithonian, *Pseudolissoceras zitteli*-*Kossmatia victoris* Zone (Fig. 1).

Discussion.- *Mazatepites* was proposed as a monotypic genus and characterized by a subevolute to evolute shell, with two styles of ribbing, changing from the inner to outer whorls (Cantú-Chapa, 1967). Only the holotype of *M. arredondense* Cantú-Chapa (1967: 7, pl. 1: 4) shows the subevolute coiling and dimorphic pattern of ribbing; it is formed by simple and rectiradiate primary ribs on the inner whorls that become palmate on the outer whorl. By conray, the paratype proposed to this species exhibits only simple, rectiradiate and lamelliform ribs, which are separated by very wide intercostal spaces; it shows a constriction in the outer whorl (Cantú-Chapa, 1967: 7, pl. 1: 1, 1a).

This last type of evolute shell with this sort of simple and very spaced ribbing, even in the last whorl, characterizes the proposed *Cuetzalanites* n. gen.; it differs from *Mazatepites* by its simple and distant ribbing and by its suture line. Umbilical width U/D varies from 0.50 in *Cuetzalanites* to 0.40 in *Mazatepites*. They are here considered as different genera and are separated in different families based on the mentioned morphological patterns, particularly the suture line.

Callomon (*in* Hillebrandt *et al.* 1992) does not indicate which one of the two specimens of *M. arredondense* Cantú-Chapa, 1967, could belong to *Virgatosimoceras*. However, *Cuetzalanites* n. gen. and *Virgatosimoceras* have evolute shells with simple, widely space, and rectiradiate primary ribs, but they differ by their style of lateral and ventral ribbing and by their suture lines.

In the former the primary ribs are sharp, lamelliform and high on the flanks; they are weakened at the ventrolateral part of the shell where trifurcate in fine and weak secondary ribs; all them cross normally the ventral region, even in the internal mould. In the latter, the simple and primary ribs vary from weak to apparently interrupted on middle part of the flanks. This case is observed in representatives of some *Virgatosimoceras* in which ribs are trifurcate from the ventrolateral edges and vanished on the venter (Geysant & Zeiss, 1978).

These genera are also distinguished by their suture lines. *Virgatosimoceras* has S1 strongly rectangular, with large base, slowly bifid at top; S2 and U2 are very shallow, and divided by small elements; E is subrectangular, with a narrow and small saddle; L is somewhat large, superficial and regularly trifurcate.

Cuetzalanites differs from *Virgatosimoceras* by its S1, which is subrectangular with somewhat narrow base and bifid at top; S2 is bifurcate by an inclined accessory lobe; L is rather deep and irregularly trifurcate. The suture line of *Virgatosimoceras rothpletzi virgulifer* Geysant & Zeiss, 1978, is herein illustrated for comparison with that of *Cuetzalanites* (Fig. 2). These genera are homoeomorphic by their evolute shells, and by apparently simple, rectiradiate and well spaced lateral ribbing. Nevertheless, they show significant morphological differences in their suture lines and type of ventral ribbing justifying to be separated in different families.

Age and occurrence.- Base of the Upper Tithonian, Pseudolissoceras zitteli-Kossmatia victoris Zone. Pimienta Formation.

***Cuetzalanites tonatiuhoides* new genus and species**

Figs. 2; 3.1, 4

- 1967 *Mazatepites arredondense* n. sp., Cantú-Chapa: p 7, pl 1, figs. 1, 1a; non pl. 1, fig. 4.
- 1993 *Mazatepites arredondense* Cantú-Chapa, Stinnesbeck *et al.*: p. 69, pl. 3, fig. 3; non pl. 3, figs. 2, 3.

Diagnosis.- As for the genus.

Description.- Evolute and planulate, with subrounded flanks and wide umbilicus; ventral region subrounded. Ornamentation formed by 23 rectiradiate, fine, lamelliform, and very widely spaced primary ribs on the last whorl; they are trifurcate on the external flanks in weak secondaries which cross transversely the venter in the internal mould and the external shell; a single constriction occurs on the last whorl corresponding to the bodychamber.

Etymology.- By its radial ribbing; Tonatiuh aludes the Aztec sun god in mythology; from the Latin, -ooides, having the form.

Type.- Holotype (Ac-89) (Cantú-Chapa 1969: Figs. 1, 1a), refigured herein in Fig. 2 (suture line), and Fig. 3.1, 4.

Discussion.- Most of the main features were already mentioned in the description of the genus. However, another specimen with the morphological characters as the holotype was illustrated as *M. arredondense* by Steinnsback *et al.* (1993: pl. 3: 3). This specimen must be related to *Cuetzalanites tonatiuhoides* n. sp. by its similar coiling and lateral ribbing; it consists of 26 fine primary ribs on the outer whorl, contrary to the holotype above described, which has only 23 ribs. There is no indication of the repository of the material published by Stinnesbeck *et al.* (1993); it is only known that it was collected by these authors in the same outcrop in Mazatepec as the holotype of *C. tonatiuhoides* n. sp.

Age and occurrence.- Base of the Upper Tithonian, Pseudolissoceras zitteli-Kossmatia victoris Zone. Base of the Pimienta Formation. Mazatepec, Puebla, eastern Mexico.

Family Berriasellidae Spath, 1922

Subfamily Richterellinae Sapunov, 1977 (Cantú-Chapa, 2006, emended).

Discussion.- The family Berriasellidae is characterized by its evolute to subevolute shell with subrounded venter and primary

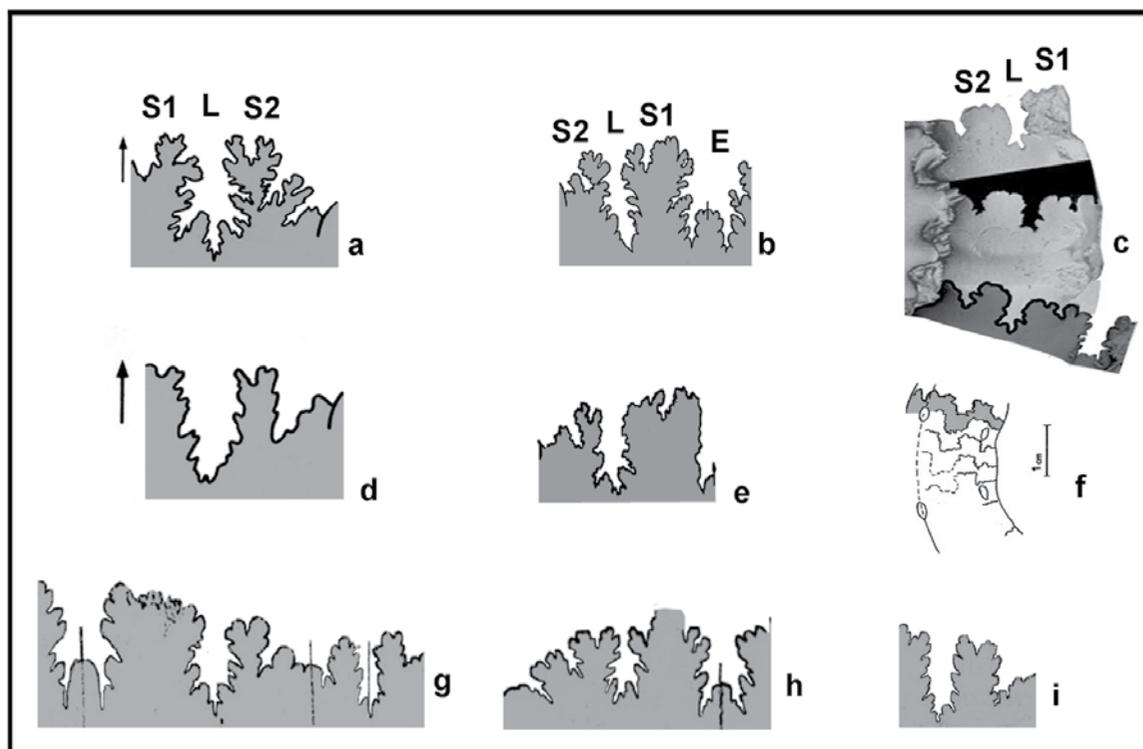


Figure 4. Suture lines of some representatives of the families Simoceratinae and Chignahuapinae showing differences in S1, S2 and L; the latter varies from trifurcate (a, b, d, e, g-i) to bifurcate (c, f); a, *Simoceras volanense* (Santantonio, 1986), S1 is incomplete, b, *Volanoceras (V) volanense volanense* (Fösy, 1988), c, *Chignahuapites chignahuapense* (Cantú-Chapa, 1990), d, *S. aesinense* (Santantonio, 1986), S1 is incomplete, e, *S. (S.) volanense* (Oloriz, 1978), f, *Ch. fozyi* n. gen. and sp. [= *V. (V.) aesinense* (Fösy, 1988)], g, *V. volanense* (Zittel, 1870), h, *S. biruncinatum* Quenst. (in Zittel, 1870), i. *V. aesinense* (Meneghini, 1885). Without scale.

ribs which bifurcate on the upper part of the flank. It is commonly subdivided into two subfamilies based on the ventral ribbing pattern:

- 1) interrupted or crossing perpendicularly, subfamily Berriasellinae, and
- 2) forming chevrons in *Lemencia* Donze and Enay, 1961 (= *Richterella* Avram, 1964), *Kossmatia*, and *Fierrites* Cantú-Chapa, 1993, subfamily Richterellinae (Cantú-Chapa, 2006).

The subfamily Richterellinae was emended after the particular characteristics of its suture line and the ribs which bifurcate on the flanks and are projected forward on the venter (Cantú-Chapa, 2006). It is restricted to the Tithonian, and was distinguished from the subfamilies Sublithacoceratinae and Ataxioceratinae on the basis of their suture line which includes S1 with a wide base, that differs from the narrow base of S1 in the two later subfamilies, and also by its ventral ribbing that cross normally.

However, *Lemencia* was not analysed by Cantú-Chapa (2006). This Lower Tithonian genus based on material from France was characterized by its prorsiradial, regularly

bifurcate or rarely fasciculate ribbing, which are interrupted by a groove or a smooth band on the ventral region. No mention was made about the ribs pattern forming a chevron on the ventral region, excepting in *L. rigida* and *L. parvicostata* (Donze & Enay, 1961).

Avram (1972) modified the original description of *Lemencia*, adding the concept about of the ventral ribbing that forms an important chevron; by the way, it was proposed some new species that were subdivided into two subgenera, *L. (Lemencia)* and *L. (Richterella)*, based on theoretical sexual dimorphism: the former or macroconchs from the Lower Tithonian, and the latter or microconchs from the Upper Tithonian; this strange subdivision is based on inaccurate concepts.

The representatives of *Lemencia* were collected with *Pseudolissoceras planiusculum* (Zittel) and *Subplanites* aff. *pseudocontiguus* Donze & Enay, 1961, from eastern Carpathian Mountains (Avram, 1972). However, nothing was said about the age from the specimens that were collected with *Richterella*. A comparison between *Kossmatia* Uhlig, 1907, and *Richterella* was not provided by Avram (1972). Some specimens of *Richterella* were also determined by Cecca (1986) and Cecca



& Enay (1991) of the Lower Tithonian from France. They were studied after the same dimorphic concepts, but not in comparison with *Kossmatia*.

However, Burckhardt (1912) and Imlay (1943) had made important contributions for the definition of *Kossmatia*, adding considerable information concerning its ontogeny. Imlay (1943) concluded that most significant differences between the American and Alpine-Mediterranean species of this genus are related with the different styles of ribbing, especially on the ventral region. Some of these cases were later analyzed in base of new material studied from Chinameca, eastern Mexico (Cantú-Chapa, 2006; see also 1993); it was pointed out that the differences between these two genera are mostly in S1 of the suture line. The pattern of the ribbing, which forms chevrons on the venter, and the suture line are the most important morphological features which characterize *Kossmatia*. This genus has priority over *Lemencia* and *Richterella*; even if they occur in successive horizons of the Tithonian.

Genus *Kossmatia* Uhlig, 1907

Type species.- *Ammonites tenuistriatus* Gray, 1832; by SD (Roman 1938).

***Kossmatia victoris* Burckhardt, 1906**

- 1906 *Perisphinctes victoris* n. sp.- Burckhardt: p. 131, pl. 36, figs. 1-6.
1912 *Kossmatia victoris* (Burckhardt).- Burckhardt: p. 131.
1930 *Kossmatia victoris* (Burckhardt).- Burckhardt: p. 70.
1967 *Kossmatia victoris* (Burckhardt).- Cantú-Chapa: p. 5, pl. 2, fig. 5, pl. 6, fig. 4.
1980 *Kossmatia victoris* (Burckhardt).- Imlay: pp. 24, 35, 45.
1992 *Kossmatia victoris* (Burckhardt).- Callomon (*in* Hillebrandt *et al.*): p. 268.
1993 *Kossmatia victoris* (Burckhardt).- Steinnesbeck *et al.*: p. 69.
2007 *Kossmatia victoris* (Burckhardt).- López *et al.*: p. 247.

Remarks.- A fragmented specimen from Mazatepec was assigned to this species. It

was collected in association with *Mazatepites* and *Pseudolissoceras zitteli* (Cantú-Chapa 1967: 5, pl. 2: 5, pl. 6: 4) in Mazatepec, and was then compared with *P. victoris* Burckhardt, of the Tithonian (= Portlandian of Burckhardt, 1906) from Mazapil, central Mexico.

K. victoris was studied by Burckhardt (1906) from the so called "Calcaire phos- phoritique grisatres", it was underlying *Substeueroceras* and *Parodontoceras* aff. *calistoides* in the above mentioned locality. The specimen from Mazatepec was assigned to *K. victoris* by its prorsiradiate, fine and regularly bifurcate ribbing forming a chevron on the subrounded and somewhat wide venter; it was dated by its association with *Pseudolissoceras zitteli*. Its age was later considered as the base of the Late Tithonian, as it was already mentioned (Cantú-Chapa, 2001).

Family Simoceratidae Spath, 1924

Subfamily Simoceratinae Spath, 1924

Genus *Volanoceras* Geysant, 1985

Type species.- *Ammonites volanensis* Opeel, 1863; by OD.

Discussion.- *Volanoceras* was proposed as a different genus from *Simoceras* by Geysant (1985), based on the main features of ribbing, position of ventral nodes or tubercles, and suture line. *Volanoceras* was rejected by Cecca (1999 :11) without foundation; neither Oloriz *et al.* (1999) nor Villaseñor *et al.* (2000) accepted the genus.

However, some taxonomic and systematic informations on *Volanoceras* were given by Santantonio (1986), Fözy (1987, 1988), Geysant (1988), Cantú-Chapa (1990) and Schweigert *et al.* (2002).

An important morphological feature was stressed by Cantú-Chapa (1990) in support for the separation of *Simoceras* from *Volanoceras*, it is the alternating position of the two rows of ventro-lateral tubercles in the former, contrary to the symmetrical position in the same place in the latter.

Additionally, Cecca (1999) considered the paleobiogeographic distribution of *Simoceras* as the way to define it. The sexual

dimorphic concept is invoked in some papers, particularly by the mentioned author for establish the systematical classification of these genera; this inaccurate concept is not here accepted.

Volanoceras species are differentiated by the following morphological characters:

(1) The periumbilical ribbing is weak in *V. volanense* (Santantonio, 1986; Fözy, 1988) and *V. chignahuapense* Cantú-Chapa, 1990; or shows tubercles or nodes in *V. aesinense* (Santantonio 1986, Fözy 1988, Schweigert *et al.* 2002). The ribbing varies in specimens from the same sizes, from fine and separated by spaces as wide as the primary ribs in *V. chignahuapense*, to sharp with narrower intercostal spaces in *S. aesinense* (Santantonio, 1986; Schweigert *et al.* 2002).

(2) The suture line of these two genera was described and illustrated by Zittel (1870), Oloriz (1978), Santantonio (1986), Geysant (1988), Fözy (1988), and Cantú-Chapa (1990); the variety of forms of this structure is shown as following:

- L is trifurcate and somewhat wide at the base in *Simoceras volanense* (Oppel, *in* Santantonio, 1986), and *Volanoceras volanense* (Zittel, 1870) (Figs. 4a, g); it is long and narrow in *V. (V.) volanense volanense* (Fözy, 1988), *S. (S.) volanense* (Oloriz, 1978) and *V. aesinense* (Meneghini, 1885) (Figs. 4b, e, i, respectively).

- L is long, somewhat wide and weakly divided at the base in *S. aesinense* (Santantonio, 1986) (Fig. 4d), or is trifurcate and short in *S. biruncinatum* Quenst. (*in* Zittel, 1870) (Fig. 4h).

- L is bifurcate, rectangular and narrow in *V. chignahuapense* (Cantú-Chapa, 1990) (Fig. 4c), and it is also rectangular and wide with undefined division at the base in *V. (V.) aesinense* (Fözy, 1988) (Fig. 4f).

- S1 is very wide, rectangular and weakly bifurcate at top in *V. chignahuapense* (Cantú-Chapa, 1990); *V. (V.) aesinense* (Fözy, 1988), and *V. volanense* (Zittel, 1870) (Figs. 4c, f, g, respectively) This structure is not illustrated

in some specimens or is incomplete in *S. volanense* (Santantonio, 1988), and *S. aesinense* (Santantonio, 1986) (Figs. 4a, d, respectively),

- S2 changes from subrectangular, narrow and long in *S. aesinense* (Meneghini, 1885, *in* Santantonio, 1986), and in *V. aesinense* (Meneghini, 1885) (Figs. 4d, i, respectively), to rectangular and massive in *V. chignahuapense* and *V. (V.) aesinense* (Fözy, 1988)] (Cantú-Chapa, 1990; Fözy, 1988) (Fig. 4c, f, respectively).

- S2 is long, strangled at the base, bifurcate and wide at the top in *S. volanense* (Oppel, *in* Santantonio, 1986) (Fig. 4a), or is very small, narrow, and bifurcate at the top in *S. S. volanense* (*in* Oloriz, 1978) (Fig. 4e).

- Some species of *Volanoceras* are not here discussed because their suture line is unknown. However, the differences previously observed in this structure from some specimens of *Volanoceras* justify their separation in a new taxa.

- By these differences that are in the suture line of the mentioned species here is proposed the following systematic unity.

Subfamily Chignahuapinae new subfamily

Type genus.- *Chignahuapites* new genus

Diagnosis.- Evolute, serpenticonic, wide umbilicus, subquadrate whorl section; simple and prorsiradial or radial primary ribs; two rows of ventro-lateral tubercles with symmetrical position; rare constrictions. Suture line with S1 and S2 rectangular and massive, E narrow; L narrow, rectangular and bifurcate at the base.

Discussion.- The differences of the suture line are manifested in some species of *Volanoceras* that are discussed later, as following:

a) L is narrow, rectangular and bifurcate, and in S2 is rectangular and wide; or

b) L is trifurcate and S2 is subrectangular and long. The unusual L that is bifurcate justify to group some specimens of *Volanoceras* in Chignahuapinae new subfamily, that is here proposed to characterize them (Fig. 4c, f).

Etymology.- Derived from the Chignahuapan village, State of Puebla, Eastern México.

Age.- Tithonian.

Genus *Chignahuapites* new genus

Typespecies.- *Volanoceras chignahuapense* (Cantú-Chapa, 1990, p. 41, fig.2A - D).

Included species.- *Volanoceras (Volanoceras) aesinense* (Meneghini, in Fözy, 1988, p 73-74, pl. X, fig. 2, fig. 17).

Diagnosis.- Evolute and serpenticonic, with subquadrate whorl section and wide umbilicus; flanks subparallel, venter narrow; simple, slowly prorsiradiate or radial ribs; weak and dense or wide and spaced on the flanks, with elongate and symmetric ventrolateral nodes or spines. Suture line with S1 placed on the ventrolateral edge, very large, rectangular, with wide base and small incisions, asymmetrically divided at the top by a secondary lobe. S2 small, rectangular and massive with a small incision at the top. E narrow and deep; L narrow, deep and rectangular with parallel sides, bifurcate by a small and subrounded protuberance at the base.

Etymology.- As for the subfamily.

Age and occurrence.- Base of the Upper Tithonian, *Pseudolissoceras zitteli-Kossmatia victoris* Zone (Fig. 1). It is also present in the Tithonian from Hungary (Fözy, 1988, see below).

Discussion.-The proposed *Chignahuapites* n.gen. differs from *Simoceras* and *Volanoceras* by its suture line with L rectangular, narrow and bifurcate by a small protuberance at the base (Figs. 4c, f). The same structure is trifurcate in some representatives of the latter two genera (Figs. 4a, e, g).

The suture lines of some specimens of *Volanoceras* or *Simoceras* from Argentina, Spain, and other countries were not illustrated, so it is not possible to consider them in this study.

Therefore, some representatives of these three genera show differences and resemblances in their suture lines, as following:

S2 is rectangular, massive and similar in form to S1 in *Chignahuapites* (Cantú Chapa, 1990; Fözy, 1988) (Figs. 4c, f).

However, S2 is very variable in the following cases:

- 1) narrow and strangled in the base and large at the top in *S. volanense* Santantonio (1988) (Fig. 4a).
- 2) rectangular, long and narrow in *S. aesinense* by Santantonio (1986) (Fig. 4d)
- 3) small and narrow in *S. (S.) volanense* (Oloriz, 1978) (Fig. e). In these cases, nothing shows that S2 is similar to *Chignahuapites*.

It should be noted that under the name of *Volanoceras aesinense* were illustrated two types of suture line in specimens from Europe (Santantonio 1986; Fözy, 1988) (Figs. 4d, f). In these cases, the separation into two different taxa are justified, based on the differences of S2 and L.

One of this group is here considered as characteristics of *Chignahuapites* n. gen., by its common style of S2 and L; the former structure is rectangular and massive and the latter is bifurcate in the Mexican specimen already mentioned and other one from Hungary (Cantú-Chapa, 1990; Fözy, 1988, Figs. 4c, f).

By contrary, L is trifurcate in some representatives of *Volanoceras* and *Simoceras* from Europe, and S2 has a great variety of forms; both elements will be discussed later (Figs. 4a, b, d, e, g).

Chignahuapites n. gen. has some morphological characteristics in common with *Volanoceras* and *Simoceras*; they have evolute and serpenticonic shell, with subparallel flanks, narrow venter, and suture line with S1 large, rectangular and asymmetrically divided by a superficial secondary lobe.

However, the former is distinguished from the two latter genera by its ribbing, without periumbilical nodes in some species; contrary to them that have periumbilical ribs with nodes.

Chignahuapites n. gen. differs from them by its L, which is rectangular, narrow, deep and bifurcate by a small and subrounded protuberance at the base. It differs also by its S2 is rectangular, small, massive and similar in form to S1 this genus (Figs. 4c, f). By contrary, S2 is rectangular, long and narrow in specimens described as *Volanoceras aesinense* by Santantonio (1986) (see Fig. 4d); other cases were already mentioned.

Age and occurrence.- Base of the Upper Tithonian in eastern Mexico; it is also present in Hungary.

***Chignahuapites chignahuapense* (Cantú-Chapa, 1990)**

Figs. 3.2, 3; 4c

1990 *Volanoceras chignahuapense* n. sp., Cantú-Chapa, p. 41, fig. 2A-D [figured herein in Figs. 3.2, 3; 4c].

1999 *Simoceras aesinense* Meneghini, Cecca: p. 26.

2002 *Volanoceras aesinense* Meneghini, Schweigert *et al.*, p. 8.

Description.- The original description of *V. chignahuapense* (Cantú-Chapa, 1990) was based on a small and well preserved specimen that exhibits its suture line. It is an evolute and serpenticonic shell with rectiradiate to prorsiradiate simple ribs, borned freely from the umbilical edge and ending in long ventrolateral tubercles with inconstant constrictions.

The suture line is characterized by S1 large, rectangular and placed at the ventrolateral edge; S2 is also rectangular and large; L narrow, rectangular and bifurcate. This specimen was collected from Chignahuapan, a neighbor village of Mazatepec, Eastern Mexico (Fig. 1).

Discussion. Cecca (1999) considered *Ch. chignahuapense* as synonym of *S. aesinense*, but without giving any explanation; it was followed by Schweigert *et al.* (2002). However, considering its ornamentation and suture line the former must be separated as a different taxa from the latter.

It is important to compare *Ch. chignahuapense* with European specimens

assigned to *V. aesinense* (in Santantonio, 1986: pl. 1: 1, 4, pl. 2; and Schweigert *et al.*, 2002: pl. 1:1-4). These specimens exhibit slightly curved to rectiradiate and sharp ribs, the intercostal spaces are narrower than ribs with very broad umbilical tubercles; this sort of ornamentation is not present in *Ch. chignahuapense*. Moreover, the number of primary ribs per whorl is 28 in *Ch. chignahuapense* against 23 in *V. aesinense*, at similar umbilical diameter (U/D = 0.6) (see Santantonio, 1986: pl. 1: 1).

Simoceras aesinense Meneghini (in Santantonio, 1986) differs also from *Ch. chignahuapense* by its suture line, that S2 is narrow, elongated and bifurcate at top (Fig. 4d), contrary to that from the Mexican species which is wide and rectangular (Figs. 4c). Other morphologic differences that occur in the suture line from these taxa were already mentioned; they are sufficient to integrate *chignahuapense* into *Chignahuapites* n. gen.

The specimen described and illustrated by Fözy (1988) as *Volanoceras (Volanoceras) volanense* (Meneghini) (Fözy, 1988, p 73-74, fig. 17, pl. X, fig. 2), is here proposed as the holotype of *Chignahuapites fozyi* n. gen. and sp. Named in honor of István Fözy, in recognition of his studies on Jurassic and Cretaceous ammonites from Hungary.

This Hungarian simoceratid differs from *Ch. chignahuapense* n. sp. by its large and spaced ribs, with elongated umbilical tubercles; in the Mexican specimen ribs born freely from the umbilical edge. However, both specimens are similar U/D ratio (0.6) and suture lines style, with S1, S2 and L large and rectangular (Figs. 4c, f).

All these features are characteristic of *Ch. chignahuapense* supporting the separation from European species as *V. aesinense*.

Age and occurrence.- As the genus.

Conclusion

The study of the suture line has been neglected in previous works, it is necessary to include it in systematic studies of ammonites.



TABLE 1. Shell measurements (in mm) and proportions of Upper Tithonian (Jurassic) ammonites from Mazatepec and Chignahuapan, State of Puebla, eastern Mexico.

Specimens:	D	U	H	W	U/D	H/D	H/W
Mazatepites arredondense holotype Ac-89 paratype Ac-130	145 66	58 28	54 20	18 16	0.4 0.4	0.37 0.30	3 1.25
Cuetzalanites tonatiuhoides n. gen and sp. holotype Ac-90	77	38	20	17	0.5	0.26	1.17
Chignahuapites chignahuapense, holotype Ac-1001	41	26	75	71	0.6	0.18	1.00
Simoceras aesinensis (in Santantonio, 1986, 19 NS3Col 11) Idem (in Santantonio, 1986, NS3Col 20)	51 46	31 28	10.5 9	9.6	0.6 0.6	0.20 0.20	9.1
Chignahuapites fozyi new gen. and sp. holotype, J-10951 [= Volanoceras (Volanoceras) aesinense Fözy, 1988]	106	67			0.6		

The stratigraphic study of the Tithonian-Berriasian sequences of Mazatepec was the basis to characterize the Jurassic-Cretaceous boundary (ammonites and calpionellids) at this particular locality (Cantu-Chapa, 1967).

The results allowed the establish of this boundary in oil-wells throughout the Gulf of Mexico coastal region, and even in the Campeche shelf, the most important petroleum province in Mexico (Cantu-Chapa, 1976, 1982, 2008a-b).

No other locality in the North American continent has been studied and discredited so much.

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Cretaceous boundary in Mazatepec (Remane *et al.* 1999).

After 40 years, Mazatepec still generates theoretical controversy (Oloriz, *in* López-Caballero *et al.* 2007). It is a pleasure to continue studying its ammonites and preserve it as the type locality of the Jurassic-Cretaceous boundary.

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