

## THE SUTURE LINE PATTERNS IN OLCOSTEPHANIDAE AND SPITICERATIDAE, AMMONITES OF THE UPPER JURASSIC-LOWER CRETACEOUS: SYSTEMATIC CONSIDERATIONS

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### Abstract

The systematic classification of the ammonites in the family Olcostephanidae here proposed is in according to different sutural line patterns. The saddle S1 is bifurcated in the Family Spiticeratidae Spath, 1924, and trifurcated in the Family Olcostephanidae Haug, 1910.

New taxa are proposed based on the suture line and their ornamentation, Groebericeratinae n. subfam., Saynoceratinae n. subfam., Garcitinae n. subfam., *Kurdistanites* n. gen., *Peruvites* n. gen., *Spiticeras* (*Djanelidzeites*) n. subgen. Taraisitinae Cantú-Chapa, 1966. All of them are from the Upper Tithonian-Lower Hauterivian.

*Key words:* Ammonites, Spiticeratidae, Olcostephanidae, Upper Tithonian-Lower Hauterivian.

### Resumen

Se propone la clasificación sistemática de las amonitas en la familia Olcostephanidae de acuerdo a los diferentes estilos de su línea de sutura. La silla S1 es bifurcada en la familia Spiticeratidae Spath, 1924, o trifurcada en la familia Olcostephanidae Haug, 1910.

Nuevos taxa son propuestos según la línea de sutura y la ornamentación; subfamilias Groebericeratinae n. subfam., Saynoceratinae n. subfam., Garcitinae n. subfam. Géneros y subgénero *Kurdistanites* n. gen., *Peruvites* n. gen. y *Spiticeras* (*Djanelidzeites*) n. subgen. Taraisitinae Cantú-Chapa, 1966. Todos estos taxa son del Titoniano Superior-Hauteriviano Inferior.

Palabras clave: Amonitas, Spiticeratidae, Olcostephanidae, Titoniano Superior-Hauteriviano Inferior.

### Introduction

The suture line comparison of the subfamilies Spiticeratinae and Olcostephaninae shows that belong to different taxa, rather to be integrated in the same Family Olcostephanidae (Wright *et al.*, 1996).

Through the mid-1970's, these ammonites were studied based in subjective criteria; the most common of them is considerate a supposed sexual dimorphism that would be recognized in base of different sizes of the shells and the presence of peristomal structures or lappets. Therefore, small specimens would be represented by microconch in opposite to large forms which could be correspond to macroconch.

Propositions based only in the ornamentation were accepted with restrictions at species level, but upper categories are descarted in recently studies on the Family Olcostephanidae. The suture lines are not compared between different genera, it is just referring to the lateral lobe (L) or to the ontogenetic development of the suspensive lobe (U), which starts in the protoconch and is developed in the early

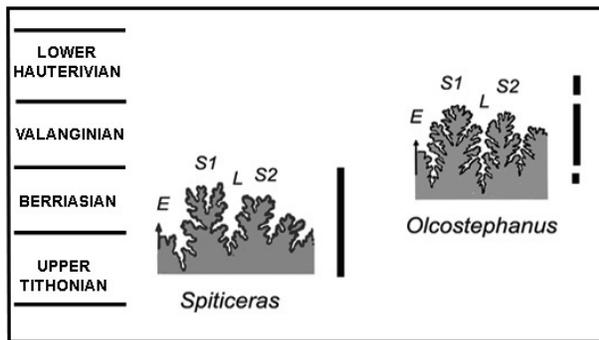
stages of the shell; nothing is indicated about the saddles S1 and S2 (Cooper, 1981; Kvantaliani, *et al.*, 1999). The suture line of Olcostephanidae genera was described and illustrated in its entirety by Burckhardt (1912), Djanelidze (1922), and Imlay (1938), among others.

The type of coiling shell and ornamentation were also considered in recent classifications of this family. Rows of tubercles and their position on the flanks and ventrolateral region, direction, density, thickness, subdivisions of the ribs on these areas, constrictions, flares and lappets are features than dominates over the suture line in descriptions (Riccardi *et al.*, 1971; Copper, 1981; Bulot, 1990; Alvarez & Rawson, 1999).

The purpose of this study is to determine the systematic position of Olcostephanidae genera, according to their suture line in S1 and S2. Both structures are the most persistent elements to characterize taxa such as family and subfamily; by contrary, L is always trifurcated and varies in size and relationships with the ventral lobe (E). By the way, the comparative analysis of S1 and S2 confirms the systematic units already known and serves also to propose here new classifications.

Two types of different suture lines dominate the so-called Olcostephanidae family, *Proniceras-Spiticeras* and *Olcostephanus*, each one define taxa of similar systematic level; they are here considered as representatives of the families Spiticeratidae and Olcostephanidae, with S1 bifurcated or trifurcated, respectively.

S2 is also an important structure, it excels in variable shapes and sizes with respect to S1. These taxa have not phylogenetic relationships between them according to particular features of S1. They are Upper Tithonian-Berriasian, and Valanginian-Lower Hauterivian, respectively (see Roman, 1938; Wright *et al.*, 1996, p. 42) (Fig. 1).



**Figure 1.** Suture lines from genera of the families Spiticeratidae and Olcostephanidae; after Roman, 1938; without scale.

### Technical study of the suture line

The original drawings of this structure are filed in gray in this paper, to emphasize their shape; they are illustrated in the same direction and scale, to make objective their comparisons. With this technique of graphic confrontation, differences and similarities are best manifested in this structure at genus level.

In addition, for analysis and illustrations, copies of the suture lines are transferred to the same side, to make comparisons objectives; it is here implicitly considered that there is symmetry between both sides of the shell.

However, Djanélidzé (1922) observed asymmetry in the suture line of some spiticeratids from France, one side did not correspond fully to the opposite one

The comparative sizes and shapes of S1, S2, L, E, the direction of the suture line from the venter to the umbilicus area, and subdivisions of the same element in different genera are used here to propose systematic classifications of the Families Olcostephanidae and Spiticeratidae.

The suspensive lobe (U) and its ontogenetic evolution is not taken into account in this study, considering that only the adult stage of specimens shows sufficient evidence to classify genera into different groups, based in the suture line.

### SYSTEMATIC PALEONTOLOGY

Order AMMONOIDEA Zittel, 1884

Suborder AMMONITINA Hyatt, 1889

Superfamily PERISPINCTOIDEA Steinmann, 1890

**Discussion.** This superfamily is represented by the families Olcostephanidae, and Neocomitidae, which stratigraphic distribution is the interval corresponding to the Upper Tithonian-Lower Hauterivian. These families have been characterized by concepts of climate and latitudinal distribution, and a supposed sexual dimorphism which is manifested by different sizes of the shell from the same species (Donovan *et al.*, 1980). This same systematic approach is taken by the Treatise (in Wright *et al.*, 1996).

Kvantaliani *et al.* (1999) proposed a systematic classification of the ammonites, based in the development of the suspensive lobe (U), as seen in some Jurassic and Cretaceous taxa. One of them is the Suborder Olcostephanina, which is based on the Superfamily Olcostephanoida Pavlov, 1892.

However, the diagnosis of this suborder would be characterized by *Olcostephanus*, which should be represented by its particular suture line and evolution of the suspensive lobe. The illustration of the suture line, provided by Kvantaliani *et al.* (*op. cit.*), shows S1 broad from the base and bifurcated at the top; S2 is also wide and massive. Therefore, this type of suture line differs from the corresponding genus *Olcostephanus*, which is characterized by S1 trifurcated and thin at the top, and by S2 narrow and irregularly divided at the top. The systematic approach from Kvantaliani *et al.* (1999) is not here considered (Fig. 2).

Family **SPITICERATIDAE** Spath, 1924.

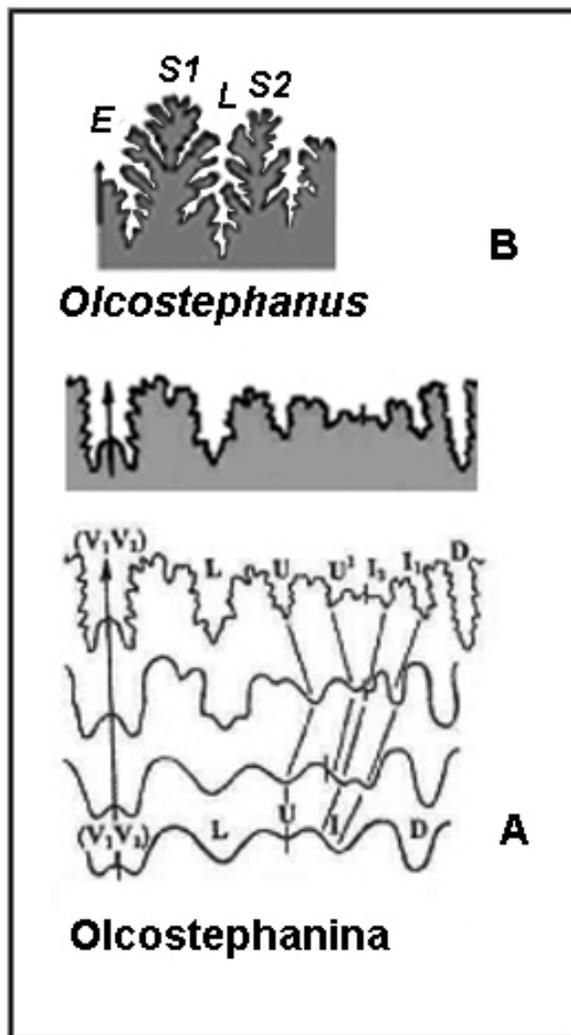
**Type genus.** *Spiticeras* Uhlig, 1903.

**Age.** Upper Tithonian – base Valanginian.

**Ocurrence.** Worldwide biogeographical distribution.

**Diagnosis.** Shell evolute to subevolute, whorl section subrounded to subquadrate; primary ribs bearing periumbilical or lateral inner tubercles that originate some secondary ribs; some bituberculated stage; constrictions and ribs projected forward the peristomal area on the ventral region. Outer whorl smooth in some large specimens. S1 subrectangular and bifurcated at the top, with base narrow or large. S2 narrow, irregularly bifurcated at the top. Ventral lobe E wide and shallow, L trifurcated and shallow.

**Discussion.** The Family Spiticeratidae characterizes genera with suture line formed by S1 and S2 bifurcated at the top, exceptly *Kilianiceras* with S2 irregularly



**Figure 2.** Comparison of the suture lines from *Olcostephanus* (A) and the evolution of *Olcostephanina* (B) (Kvantaliani *et al.*, 1999; this work); without scale.

trifurcated in some specimens (Uhlig, 1905). This family differs from the Family *Olcostephanidae* by having S1 trifurcated; with these suture line patterns hereby is established a clear systematic division between the two mentioned taxa.

Some representatives of the Family *Spiticeratidae* have same type of shell coiling and ornamentation, whereas the suture line shows significant differences between them, these cases will be discussed below. The Family *Spiticeratidae* is divided here in two subfamilies, based in ornamentation and suture line, namely:

1. - Primary ribs thin and divided from a periumbilical or lateral tubercle, that produces fine secondary ribs, which are projected towards the peristome in the ventral area. Suture line with S1 subrectangular, somewhat narrow, with deep lateral incisions, and thin and strangled base. S2 narrow and irregularly divided at the top, L trifurcated: Subfamily *Spiticeratinae* Spath, 1924.

2. - Primary ribs wide, flat, separated by secondary ribs, very weak on the flanks; S1 rectangular and robust, wide base with an additional ventro-basal structure in the ventral side. S2 subrectangular, slightly elongated and projected toward the umbilical area, it is divided irregularly at the top; some specimens posses numerous incisions in the ventral side of S2. L trifurcated, narrow and short: Subfamily *Groebericeratinae* n. subfam. (Fig. 3).

Subfamily *SPITICERATINAE* Spath, 1924 emend.

**Genus type:** *Spiticerus* Uhlig, 1903.

**Included genera:** *Pronicerus* Burckhardt, 1919-21; *Bihenduloceras* Spath, 1925; *Umiaites*, Spath, 1931; *Kilianicerus* Djanélidzé, 1922; *Negrelicerus* Djanélidzé, 1922; *Somalicerus* Spath, 1925; *Kurdistanites* n. gen.

**Genera with unknown suture line.** *Praenegrelicerus* Collignon, 1960; *Cantianicerus* Faraoni *et al.*, 1997.

**Age.** Upper Tithonian– Berriasian (probably Lower Valanginian).

**Ocurrence.** Worldwide biogeographical distribution.

**Diagnosis.** Shell evolute, suboval whorl section, narrow and subrounded venter, periumbilical tubercles originate thin and prorsiradial secondary ribs, inclined ventrally forward; inconstante constrictions. Bituberculated state and last whorl smooth in some genera. Suture line with S1 subrectangular, slightly twisted forward in the umbilical area, with narrow base, forked at the top, with lateral incisions. S2 trifurcate at the top in some specimens U decreases towards the umbilical wall, L trifurcated. E wide and deep with ventrolateral incisions, divided by the low and subrectangular ventral saddle.

**Discussion.** The Subfamily *Spiticeratinae* differs from the Subfamily *Groebericeratinae* n. subfam. that is proposed below, by its suture line with S1 and S2 relatively thin and long, while the latter posses the same elements subrectangular, robust, with wide base (Fig. 3).

The Subfamily *Spiticeratinae* includes some genera that require be analysed, as *Umiaites* and *Pronicerus*, of the Upper Tithonian. Both are apparently similars, the former of Iraq and the latter from Mexico, France, Iraq, Madagascar, Pakistan, Salt Range, Nepal, Bulgaria, Italy, and Cuba (?) (see Wright *et al.*, 1996).

The dimorphic appearance of the last whorl would be the only difference between the these two genera (Shome & Bardhan; 2009; Enay, 2009). However, they differ by their suture lines, where E and the ventral saddle with its ventro-lateral incisions are more superficial than L in *Umiaites*.

In contrast, E and L have similar size, the mentioned incisions are deeper than L in *Proniceras*. In addition, S1 and S2 are high in *Umiaites*. On the contrary, the former is higher than the latter in *Proniceras*, S2 is narrow and become broad at the top in *Umiaites*; the same element is subrectangular in all its structure in *Proniceras*. Therefore, they represent two distinct genera, based in their different suture lines (Fig. 3).

*Cantianiceras* Faraoni *et al.*, 1997, of the Lower Valanginian from Italy could belong to the subfamily Spiticeratinae, by its evolute shell with some constrictions and wide ribs; they are spaced, bituberculated and alternating with thin secondary ribs. All ribs are projected towards in the ventral area. Unfortunately, the suture line is unknown, so it is not possible to define its systematic position within the Family Spiticeratidae.

*Aspidostephanus* Spath, 1925, was considered as belonging to the Subfamily Simoceratinae instead of the Subfamily Spiticeratinae, by its suture line with S1 rectangular, large base and superficial subdivisions (Cantú-Chapa, 2009b, p 282, fig. 2a, b).

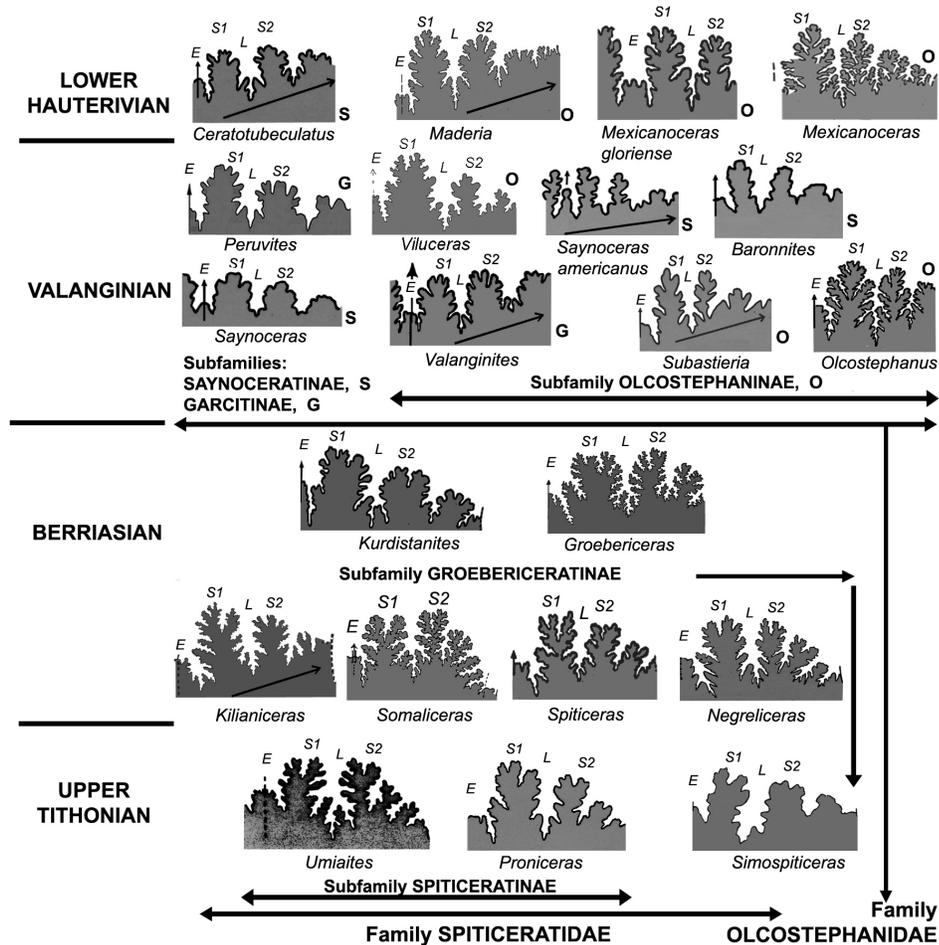
*Spiticeras mojsvari* (Uhlig, 1903, p. 110, pl. XVII, fig. 1a-d) was illustrated and integrated into the Subfamily Spiticeratinae by Djanélidzé, 1922, (p.139, pl. XIV, 1b), as a probably Berriasian species from France. It differs from *Spiticeras* s. str. by having suture line with S1 and S2 wide from the base, the former is divided by two small lobes at the top (see Uhlig, 1903). These elements bear considerable resemblance to *Groebericeras* from Iraq (Fig. 4).

In *S. mojsvari* come together patterns of ornamentation and subevolute coiling of *Spiticeras*, as well as those of the suture line of *Groebericeras*. It could be placed here provisionally in the subfamily Spiticeratinae and to separate it at subgenus level which is described below.

Subgenus **DJANELIDZEITES** n. subgen.

Figs. 4A, B, D

**Type species:** *Spiticeras mojsvari* (Uhlig, 1903) in Djanélidzé, 1922, p 139, pl XIV, 1 = Kilian, 1910, pl. 1, fig. 1a, 1b).



**Figure 3.** Suture lines from selected genera of Spiticeratidae and Olcostephanidae (Upper Tithonian- Lower Hauterivian). (Roman, 1938; Imlay, 1938; Howarth, 1992, Aguirre-Urreta & Rawson, 1999; Bulot *et al.* 1990); without scale.

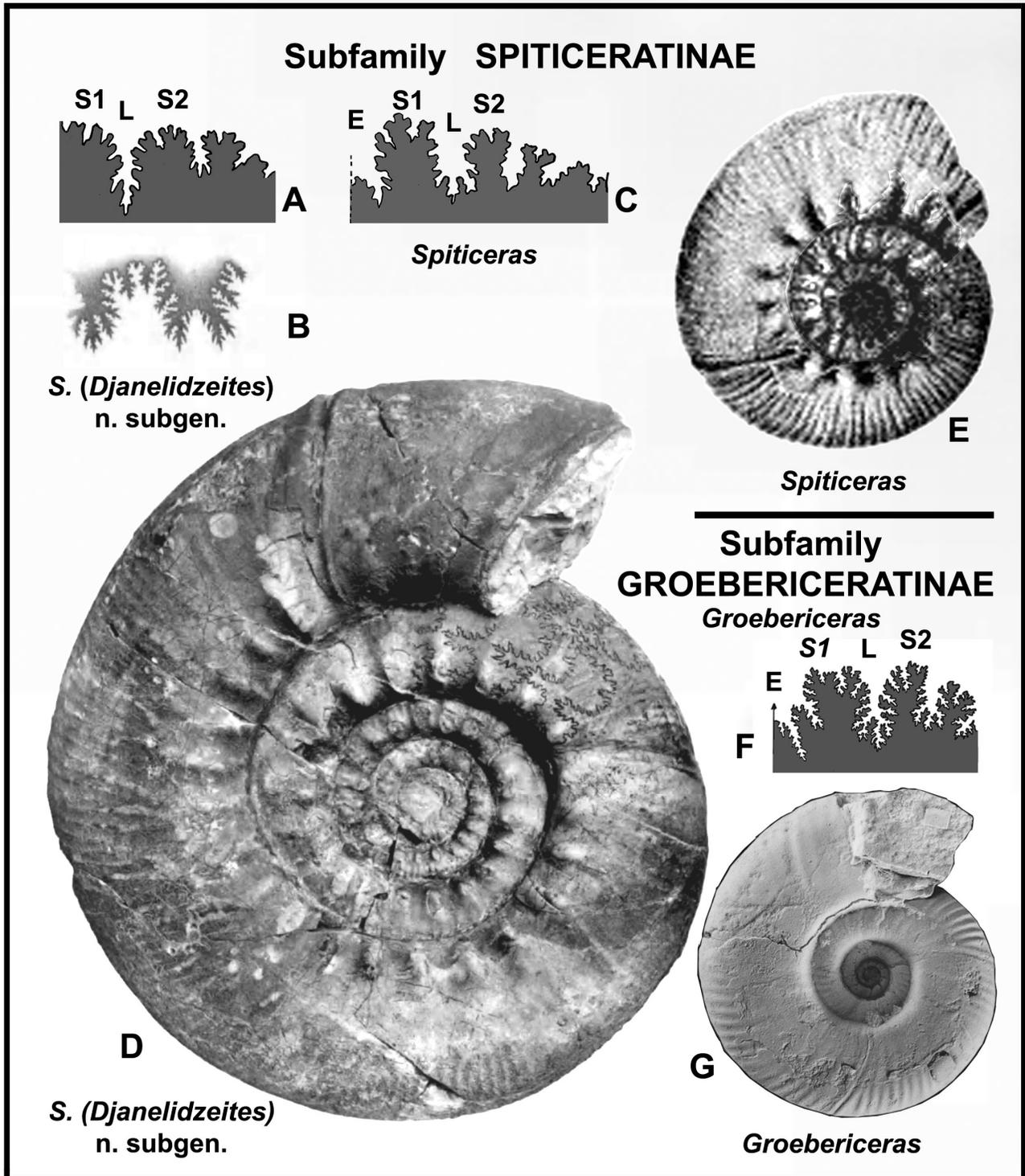
**Included species.** Probably *S. correardi* (Kilian, in Djanélidzé, 1922, pl 160, fig. 37, pl. XVIII, 3ab).

**Etymology.** In honor to J. Djanélidzé, who studied this important group of ammonites from France.

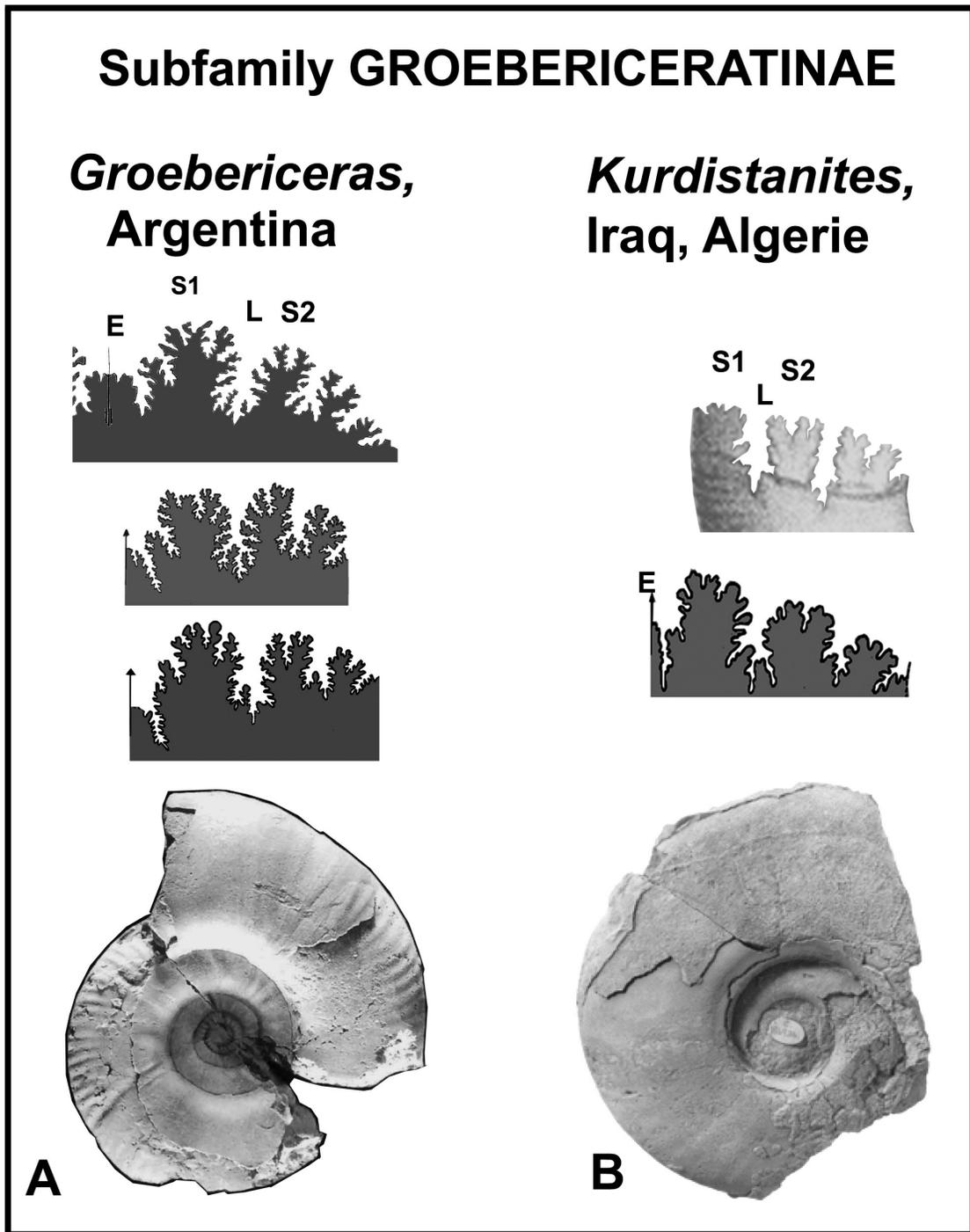
**Age.** Probably Berriasian.

**Geographical distribution.** France.

**Diagnosis.** Shell subevolute, similar to *Spiticeras* by its form; the peri-umbilical tubercles origine thin ribs in the outer flank. Suture line with S1 and S2 wide, rectangular from the base; both are irregularly bifurcated at their top;



**Figure 4.** Comparison of suture line and shells from *Spiticeras* (*Djanelidzeites*) and *Groebericeras*. Age: Berriasian (Aguirre-Urreta & Alvarez, 1999; Djanélidzé, 1922). Scale x1.



**Figure 5.** Comparison of genera *Groebericeras* and *Kurdistanites* n. gen., based on shells and suture line patterns (Aguirre-Urreta & Rawson, 1999; Howarth, 1992). Age: Berriasian; without scale.

latter lower than former. L trifurcated, narrow and deep with small incisions.

**Discussion.** *Djanélidzeites* n. subgen. is here proposed based in its S1 and S2 wide from the base; this sort of suture line differs from other representatives of Spiticeratinae, that have the same elements, where S1 is subrectangular and narrow, with deep lateral incisions and strangled

in its thin base; S2 is narrow and irregularly divided at the top. The specimen described as *Spiticeras mojsvari* (Uhlig, 1903) in Djanélidzé (1922) characterizes this new subgenus based in its suture line (Fig. 4A, B, D).

*S. mojsvari* shows the suture line incomplete in two specimens (Uhlig, 1903, pl. XVII, fig. 1, and Djanélidzé, 1922, pl. XIV, fig. 1). However, these fragmented structures

are massive from their bases, S1 is trifurcated at the top in a bizarre form, that differs from *Spiticeras* s. str. (Fig. 4C). The most representatives of the two specimens of *S. mojsvari* was provided by the latter author, that shows S2 complete; it is here chosen to characterize this genus (Fig. 4A, B, D).

*S. correardi* (Kilian in Djanélidzé, 1922, pl 160, fig. 37, pl. XVIII, 3ab) is from the same locality and probably same age than the specimen already described as *S. mojsvari*; the former shows also S1 wide and robust from the base, and divided regularly at the top. This specimen could be

assigned to *Djanelidzeites* n. subgen.

Subfamily **GROEBERICERATINAE** n. subfam.

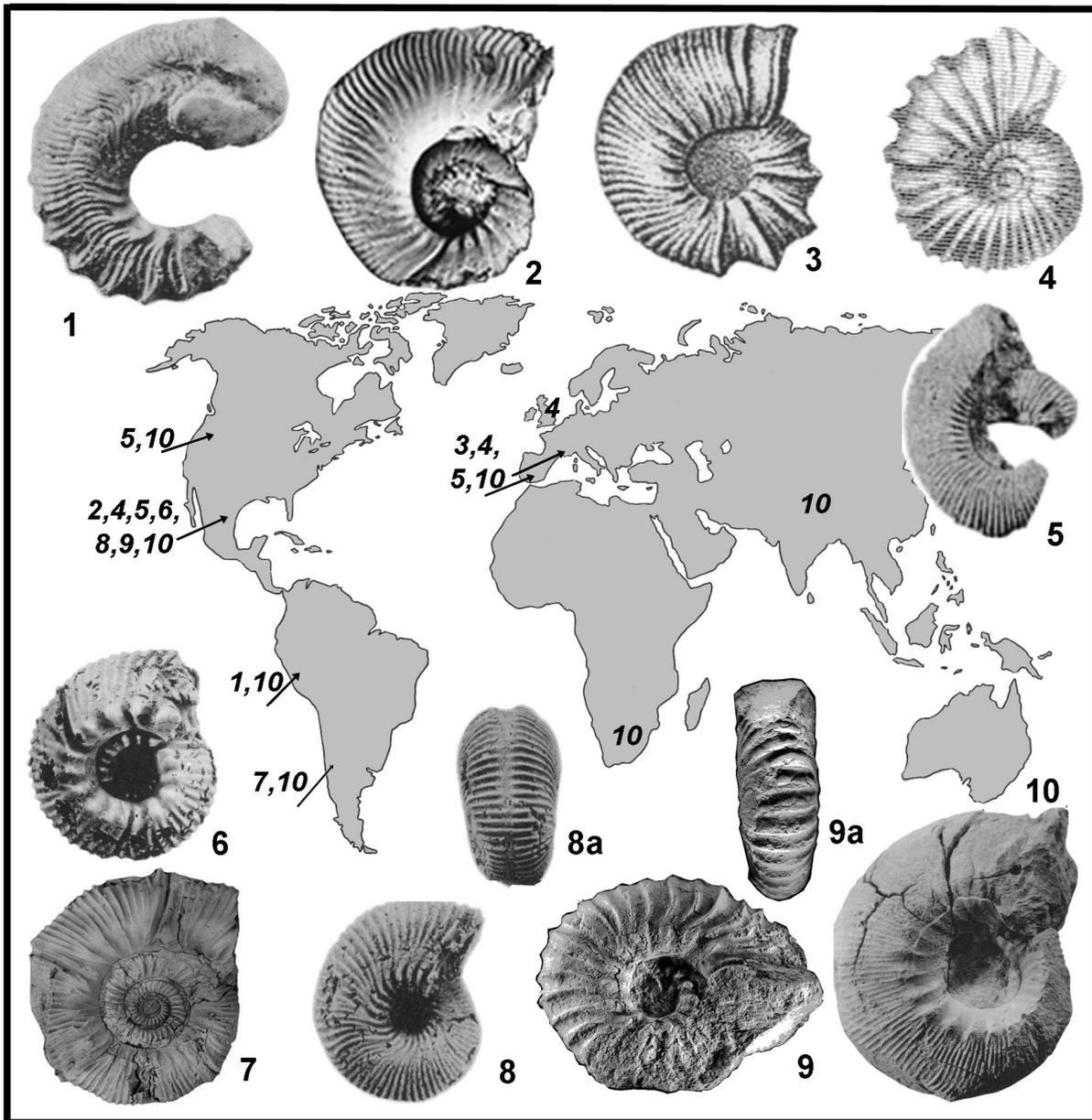
**Type genus.** *Groebericeras* A. Lanza, 1945.

**Included genera:** *Simospiticeras* Oloriz & Tavera, 1979; *Kurdistanites* n. gen.

**Age.** Upper Tithonian - Lower Berriasian.

**Etymology.** Derived from *Groebericeras*.

**Geographic distribution.** Argentina, Algeria, México, France, Iraq.



**Figure 6.** Biogeographic distribution of the following subfamilies: *Capeloitinae* (*Capeloites*, 1-3, *Parastieria*, 4), *Taraisitinae* (*Jean-noticeras*, 5; *Taraisites*, 9, 9a), *Olcostephaninae* (*Maderia*, 6; *Viluceras*, 7; *Mexicanoceras*, 8, 8a; *Olcostephanus*, 10). Age: Valanginian-Lower Hauterivian (Cantú-Chapa, 2001; 2009a; Howarth, 1992; Kemper *et al.*, 1981; Lisson, 1937; Pavlow, 1892; Thieuloy, 1969; Wilke, 1988); without scale.

**Diagnosis.** Shell moderately evolute to subevolute, compressed or inflated whorl section with narrow and subrounded venter. Primary ribs alternating with some secondary ribs, both weaken in midflank, even in outer flank, and projected forward in outer flanks. Inconstant and narrow constrictions. Small tubercles in different position on the flanks, which disappear in large and smooth specimens. S1 wide from the base, subquadrate, even robust and divided irregularly at the top, sporadically with a ventro-basal structure. S2 narrow, irregularly branched at the top, with narrow base and numerous ventro-lateral incisions, or massive from the base with weak lateral incisions and divided at the top. L trifurcated, narrow and shallow. E wide with a small ventral saddle.

**Discussion.** *Groebericeratinae* n. subfam. differs from *Spiticeratinae* by its weak ornamentation that is even smooth in larger specimens. It differs also by the shape of S1 which is subrectangular, robust, weakly divided at the top, sometime with a strong and ventro-basal structure. In contrast, S1 is rectangular, rather thin, clearly divided at the top in *Spiticeratinae*, except in *Proniceras* which has a small and ventro-lateral structure in S1 as *Groebericeras*.

*Groebericeratinae* n. subfam. differs also from *Spiticeratinae* in its saddle S2 which is wide from the base and larger at the top, or rectangular with a narrow base, and irregularly divided at the top, with many incisions in the ventral area (Fig. 3).

Some specimens from Iraq were studied as *Groebericeras* by Howarth (1992); two of them differ from this genus by their suture lines and ornamentation, they represent a different taxa, *Kurdistanites* n. gen. which is described below (Figs. 3, 5).

On the basis of its suture line, *Simospiticeras* Oloriz & Tavera, 1979, of the Upper Tithonian from Spain could be the oldest *Groebericeratinae* n. subfam. It has S1 and S2 wide and rectangular from the base, both are divided at the top (Fig. 3).

*Groebericeras* poblanense Cantú-Chapa (1967) was described from the base of the Lower Tamaulipas Formation (Berriasian) in Mazatepec, Eastern Mexico (Cantú-Chapa, 1967); its suture line is unknown, it can not be integrated into *Groebericeras* or *Kurdistanites*.

Genus **KURDISTANITES** n. gen.

Fig. 5B

**Type species:** *Kurdistanites rocardi* (Pomel, 1889, in Howarth, 1992, p. 626, pl 5, figs. 5, 6, text-fig. 6, E).

**Other specimen:** *Ammonites rocardi* Pomel (1889, p 65, pl VIII, figs. 3-6).

**Etymology.** Derived from Kurdistan.

**Age.** Berriasian.

**Geographic distribution.** Iraq, Algeria.

**Diagnosis.** Shell moderately involute to evolute in large specimens, whorl section compressed to subrounded, narrow and subrounded venter. Principal ribs in internal part of the side alternating with weak secondaries, all disappear in larger specimens; inconstante constrictions. Suture line with S1 and S2 rectangular and robust from the base, divided at the top; S1 with a latero-basal structure in its ventral side. S2 strong and wide at the top. E wide, superficial, and divided by the high ventral saddle. L irregularly trifurcated, wide and superficial.

**Discussion.** *Kurdistanites* n. gen. is proposed to characterize specimens with S1 and S2 rectangular, robust from the base and divided at the top, showing small and superficial incisions on the sides.

S2 has a massive aspect from the base that become wider at the top, with weakly incisions on the sides; It contrasts with the same structure of *Groebericeras*, which is narrow at the base, twisted toward the umbilical area; it is also irregularly forked at the top, and with many deep incisions in the ventral side (Fig. 5).

*G. rocardi* (Pomel) (in Howarth, 1992, p. 626, pl. 6, figs. 1, 4, text-fig. 6, D) is here assigned as the type species of *Kurdistanites* n. gen. rather than *Groebericeras* by its S2, which is broad and massive from the base. Specimens from Iraq show the same sort of robust structure. It should be included in *Kurdistanites* n. gen., rather in *Groebericeras* (see Howarth, 1992).

Moreover, there are several specimens which were illustrated from Kurdistan and Argentina, of which the suture line is unknown. It is not possible to assign them in one of these two genera, *Groebericeras* or *Kurdistanites* n. gen. On the contrary, when the suture line is illustrated, S2 shows some differences between specimens of South America and those of the Tethyan region. In the former this structure is twisted from the narrow base, while in the latter is robust, broad, and straight with a wide base (A. Leanza, 1945; Howarth, 1992). This sort of difference between them could be considered as biogeographic segregation at genus-group level (Fig. 5).

Family **OLCOSTEPHANIDAE** Haug, 1910 emend.

**Type genus.** *Olcostephanus* Neumayr, 1875.

**Age.** Valanginian-Lower Hauterivian.

**Ocurrence.** Worldwide biogeographical distribution.

**Diagnosis.** Shell moderately involute, subglobular or more compressed, subrounded or tabulated venter; dimorphic

or uniforme ornamentation in the last whorl. Sharp and separated primary ribs with one or two rows of tubercles in different position on the flanks. Fine secondary ribs and inconstant constrictions cross transversely or are slightly thin on the mid-ventral line. S1 and S2 long and narrow or wide and subrectangular, both irregularly trifurcated at the top. L trifurcated, superficial or deep.

**Discussion.** Representatives of the Family Olcostephanidae have been studied under dimorphic patterns, based on different size of the shell and presence of peristomal lappets, when are preserved. The comparison with nearby taxa has been realised without considering the suture line patterns (Cooper, 1981; Wright *et al.* 1996).

However, this structure is here considered as the most important morphologic feature in the Olcostephanidae, that allows propose consistent systematic subdivisions. S1 and S2 are trifurcated in this family and differ from the same structures of the Family Spiticeratidae which are bifurcated.

The Family Olcostephanidae is here divided into two subfamilies based on different ornamentation in the last whorl of the shell:

- Dimorphic, Subfamily Capelotinae Cantú-Chapa, 2009a.
- Uniforme in all whorls, Subfamily Olcostephaninae Haug, 1910.
- Both subfamilies have similar S1 and S2 trifurcated.

The Olcostephanidae are also divided considering the tubercle number and position on the sides and on the venter:

1) One row of periumbilical tubercles origine:

a) Bundles of thin and denses secondary ribs, Subfamily Olcostephaninae; or only two or three sharp or fine secondary ribs, Subfamily Taraisitinae Cantú-Chapa, 1966;

b) Lateral or ventrolateral tubercles, or periumbilical bullae that produce thin and together or sharp and separated primary ribs, that cross transversally the rounded venter, Subfamily Garcitinae n. subfam.

2) Two rows of tubercles, Subfamily Sayoceratinae n. subfam.

Subfamily **CAPELOITINAE** Cantú-Chapa, 2009a.

**Type genus.** *Capelotes* Lissón, 1937.

**Included genus.** *Parastieria* Spath, 1925.

**Diagnosis & Discussion.** See Cantú-Chapa, 2009a.

**Age.** Valanginian.

**Geographical distribution.** England, France, Mexico, Peru, Spain (Cantú-Chapa, 2001, 2009a; Howarth, 1992, Kemper *et al.*, 1981; Lisson, 1937; Pavlov, 1892; Thieuloy, 1969; Wilke, 1988) (Fig. 6.1-4).

Subfamily **OLCOSTEPHANINAE** Haug, 1910 emend.

**Type genus.** *Olcostephanus* Neumayr, 1875.

**Included genera.** *Mexianoceras* Imlay, 1938; *Maderia* Imlay, 1938; *Subasteria* Spath, 1923, *Satoites* Cantú-Chapa, 1966; *Viluceras* Aguirre-Urreta & Rawson, 1999.

**Age.** Valanginian-Lower Hauterivian.

**Ocurrence.** Worldwide biogeographical distribution

**Diagnosis.** Shell subevolute, subcircular whorl section, flanks and ventral region subrounded. Uniforme ornamentation in all whorls. Umbilical wall with primary ribs, ending in periumbilical tubercles; from them born bundles of thin and denses secondary ribs, divided at different part of the sides, crossing normally or interrupted at the mid part of the venter; rare constrictions. S1 long and narrow, or with large base. Trifurcated at the top.

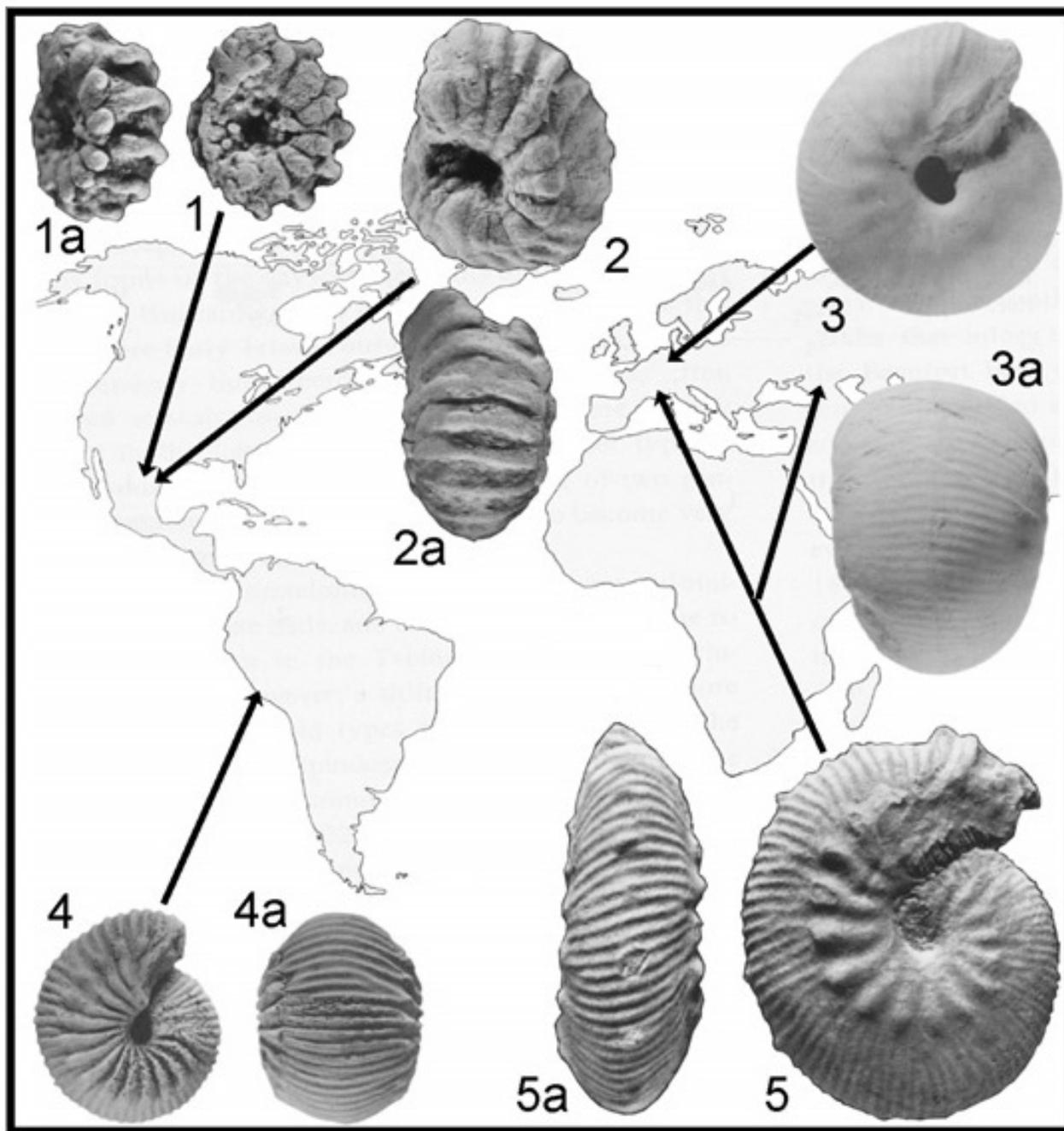
**Discussion.** The subfamily Olcostephaninae differs from the subfamily Capelotinae by its uniforme ornamentation in all whorls, contrary to the latter with dimorphic ornamentation in the last whorl. Differences between the subfamilies Olcostephaninae, Garcitinae n. subfam., and Sayoceratinae n. subfam., will be mentioned in their descriptions.

The systematic position of *Olcostephanus* is controversial, it was based on presumed dimorphism which involved the arbitrary separation of specimens into microconchs and macroconchs, on the base of various subjective criteria: size of the shells and presence or not of peristomal structures or lappets. This strange proposal was questioned by several authors, there was no response from their promoters (see Cantú-Chapa, 2001, p 360).

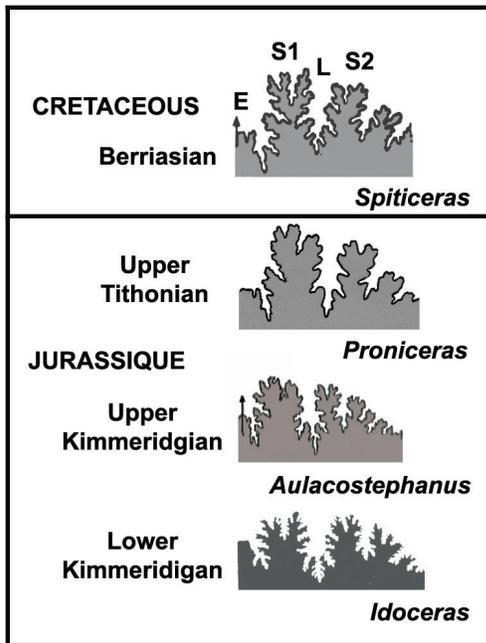
However, some genera of the subfamily Olcostephaninae represent systematic cases, which are characterized by their particular style of the ribbing or the suture line, as follows.

- *Mexianoceras* Imlay, 1938, of the Lower Hauterivian from Mexico, with secondary fine ribs which are interrupted at the midventral line; they cross normally in *Olcostephanus*.

- *Viluceras* Aguirre-Urreta & Rawson, 1999, of the Valanginian from Argentina differs from *Olcostephanus* by its suture line with S1 very wide from the base and divided at the top. In the latter this structure is narrow and long (Figs. 3, 6.7, 10).
- *Satoites* Cantú-Chapa, 1966, was erected to characterize a possible Berriasian *Olcostephanidae* from Japan, with bidichotomic, fine and dense ribs
- This genus was rejected by Cooper (1981) based on comparisons with the Lower Hauterivian *Mexicanoceras* Imlay (1938), and according with the ribbing pattern on the ventral area: crossing normally in *Satoites* or interrupted in



**Figure 7.** Biogeographic distribution of *Garcites* (1,2), *Valanginites* (3), *Peruvites* n. gen. (4), and *Dobrodgeiceras* (5). Age: Valanginian. (Aguirre-Urreta & Rawson, 1999; Howarth, 1992; integrated by Cantú-Chapa, 2001); without scale.



**Figure 8.** Phylogenetic sequence of suture lines of selected Perisphinctoidea genera, from Upper Jurassic-Lower Cretaceous showing similarity in S1 and S2 (Cantú-Chapa, 1992, and this work); without scale.

*Mexicanoceras*. The presence of constrictions in the former or the absence in the latter was not considered in this comparison.

- *Satoites* was considered as a junior form from *Mexicanoceras* by Cooper (1981). This strange way to propose a systematic change was taken by some workers without checking it (Bulot, 1990; Wright *et al.*, 1996). It is here considered inaccurate and misleading.

Subfamily **GARCITINAE** n. subfam.

**Genus type:** *Garcites* Cantú-Chapa, 2001.

**Included genera:** *Dobrodgeicerias* Nikolov, 1963; *Valanginites* Kilian, 1910; *Peruvites* n. gen.

**Age.** Valanginian.

**Etymology:** Derived from *Garcites*.

**Geographical distribution:** Argentine, Mexico, Peru, France, Germany, Bulgaria, Swiserland, Crimea region (Riccardi & Westermann, 1970; Cantú-Chapa, 2001; Nikolov, 1965; Thieuloy & Gazay, 1967; Kemper *et al.*, 1981). (Fig. 7).

**Diagnosis.** Shell small, involute, sphaerocone, compressed to coronate whorl section; deep umbilicus; fine or strong, rectiradiate, slightly sigmoidal, or cuneiform primary ribs, ending in midlateral, outer lateral or ventrolateral tubercles. Simple or bundles of two to four ribs arising from them, crossing transversally the broad and subrounded venter; inconstant ventral

tubercles. Suture line unknown in the genus type, but in *Peruvites* n. gen. with S1 and S2 rectangular, wide base, irregularly trifurcated at the top; L shallow, narrower than saddles.

**Discussion.** The proposed *Garcitinae* n. subfam. differs from the subfamily *Olcostephanidae* by its primary ribs that end in midlateral or ventro-lateral tubercles, which produce simple or sharp secondary ribs in two or four number. By contrary, the *Olcostephanidae* are ornamented with periumbilical primary ribs that terminate in tubercles in the internal part of the sides; from the tubercles radiate bundles of secondary ribs.

*Garcitinae* n. subfam differs from the subfamily *Capeloitinae* by its uniforme ornamentation in the last whorl, contrary to the latter with dimorphic ribbing in the same part of the shell (Cantú-Chapa, 2009a). Therefore, *Garcitinae* n. subfam. differs also from the subfamilies *Olcostephaninae* and *Capeloitinae* by its massive and subrectangular S1 and S2; these structures are fine in representatives of two latter subfamilies.

Species included in *Dobrodgeicerias* are separated by the tubercle position on the flanks: midlateral in the European specimens or outer on the flanks in the Peruvian forms. The former has sporadic tubercles on some midventral ribs, by contrary these structures are absent in this part of the shell, in specimens from Peru (Riccardi & Westermann, 1970).

Therefore, these morphologic features in the *Dobrodgeicerias* species are different, the Peruvian specimens have a broader venter than the European ones. These distinctive features allow to separate them and propose *Peruvites* n. gen. which will be described below. Some morphological patterns from *Dobrodgeicerias*, *Garcites* and *Valanginites* were previously analysed by Cantú-Chapa (2001) (Fig. 7).

Genus **PERUVITES** n. gen.

Figs. 3, 7.4, 4a

**Type species.** *Sphaeroceras* Broggianus of Lisson, 1937, p. 153, pl. 1, figs. 1, 2 [= *Dobrodgeicerias broggianum* (Lisson) in Riccardi & Westermann, 1970, p. 888-889, pl. 127, figs. 1a-d, text-fig. 1)].

**Age.** Valanginian.

**Etymology.** Derived from Peru.

**Geographical distribution.** Peru.

**Diagnosis.** Shell small, sphaerocone and involute, wide whorl section; fine primary ribs at the periumbilical area, slightly sigmoidal and strongly cuneiforme on mid flank

in flabelliforme attitude, ending in outer lateral tubercles, branching two or three sharp secondary ribs, crossing the venter transversely in divergent pattern without weakening, and joined them irregularly with the corresponding tubercle. Suture line with S1 and S2 rectangular, with wide base, irregularly trifurcated at the top (Fig. 3).

**Discussion.** *Peruvites* n. gen. is proposed to characterize small, involute and sphaerocone shell, with sigmoidal and cuneiforme primary ribs that end in outer lateral tubercles; from them origine two or three secondary ribs that cross transversally the subrounded venter, where are joined irregularly in the corresponding outer lateral tubercles, even in zigzag attitude.

*Peruvites* n. gen. differs from the European *Dobrodegeiceras* Nikolov (1963) by the absence of siphonal tubercles on the ribs and by the outer side position of the tubercles, contrary to the latter that has ventral and mid lateral tubercles (Fig. 7.4, 4a).

*Peruvites* n. gen. has major features differences with *Garcites* Cantú-Chapa (2001) from Mexico; the former with fine primary ribs ending in outer side tubercles that origine two or three fine and close together secondary ribs, the latter with wide, close together primary ribs that end in ventrolateral tubercles; they produce a simple, wide and separated rib (Fig. 7, 1, 1a, 2, 2a; 4, 4a).

Subfamily **TARASITINAE** Cantú-Chapa, 1966 emend.

**Type genus.** *Taraisites* Cantú-Chapa, 1966, by original designation.

Other genus. *Jeannoticeras* Thieuloy, 1965.

**Age.** Valanginian-Lower Hauterivian.

**Geographic distribution.** Mexico, France, Tanzania, USA.

**Diagnosis.** Coiling shell subevolute, scaphitoide, sides subrounded, venter narrow and subrounded. Primary ribs in the periumbilical area origine tubercles or bullae producing two or three secondary, sharp or fine ribs, separated by spaces as wide as them; all cross the venter. Suture line unknown.

**Discussion.** The Subfamily Tarasitinae was proposed by Cantú Chapa (1966), to characterize Olcostephaninae specimens with scaphitoide coiling shell and with two or three secondaries ribs borning from periumbilical tubercles, against a dense ribbing in the latter.

The Subfamily Tarasitinae and its type genus *Taraisites* were rejected by Riccardi *et al.* (1971) based on suppose sexual dimorphism, which could be represented by different sizes of the shells, preservation of lappets or peristomal structures and hypothetical concepts about ontogenetic development, or supposed morphological variation.

To these authors, *Taraisites* and *Olcostephanus* could represent the microconch and macroconch, respectively. This proposal was taken by Cooper (1981), Bulot (1990), and Wright *et al.* (1996); these bizarre arguments were already analyzed by Cantú-Chapa (2001, p 360).

Bulot (1990) rejected *Taraisites* by its bifurcated or trifurcated ribbing that born from an periumbilical tubercle, but accepts *Jeannoticeras* which has two or three fine ribs that born from an umbilical bullae. This sort of contradictory arguments are insubstantial and incoherent.

The mythical concept of sexual dimorphism in ammonites was questioned by several authors, none of these arguments contrary to this strange theory has been refused (see Cantú-Chapa, 2001, p 360). *Taraisites* was accepted by Klein (2005) as a different genus from *Olcostephanus*.

Subfamily **SAYNOCERATINAE** n. subfam.

**Type genus:** *Saynoceras* Munier & Chalmas, 1894.

**Included genera:** *Ceratotuberculus* Imlay, 1938; *Baronnites* Bulot, Company & Thieuloy, 1990.

**Age.** Valanginian-Lower Hauterivian.

**Geographic distribution.** France, Spain, Germany, Mexico (see Wright *et al.*, 1996).

**Diagnosis.** Dwarf, involute, inflated to trapezoidal whorl section, ventral band smooth. Lateral and ventrolateral sharp tubercles. Ribbing sharp, sometime looped. Suture line with S1 and S2 robust, large from the base, or narrow, long and rectangulaire, parallel or divergente, and trifurcated at the top. E and L same high. L narrow.

**Discussion.** The Subfamily Saynoceratinae here proposed is classified in the Olcostephanidae by its S1 and S2 which are trifurcate; it is distinguished from other subfamilies already described by its double row of lateral and ventrolateral tubercles, by its trapezoidal section with tabulated venter, and by its ribbing sharp and even looped pattern.

Saynoceratinae n. subfam. differs from the subfamily Olcostephaninae by its suture line with S1 and S2 massive or narrow with weak incisions, except in *Baronnites* and *Saynoceras americanus* Imlay, 1938, which structures are narrow, long and parallel or divergente, respectively.

Incorporating these elements, the definition of the Subfamily Saynoceratinae become complete. Both taxa differ from *Saynoceras* and *Ceratotuberculus* by the same elements stablishing a clear separation. Otherwise, S1 is long and narrow with strong and lateral incisions in Olcostephanidae.

The subfamily Saynoceratinae n. subfam. differs from the subfamily Capelotinae by its uniforme ornamentation

in the last whorl and by their two rows of tubercles. Saynoceratinae differs from Garcitinae n. subfam. and Taraisitinae by the mentioned ornamentation, consisting in the presence of two rows of tubercles.

### Conclusions

New data are here added to the systematic paleontology of the families Spiticeratidae and Olcostephanidae based on the two principal elements from the suture line, S1 and S2, which are bifurcate or trifurcate, respectively. In the same order, they are from different ages: Upper Tithonian-Berriasian, and Valanginian-Lower Hauterivian.

The Spiticeratidae are here related with the Lower Kimmeridgian Idoceratidae by having similar evolute or subevolute shell, ribs inclined forward on the ventral region, and by its suture line with S1 and S2 bifurcate. However, S2 is higher than S1 in *Idoceras* (Cantú-Chapa, 1992) (Fig. 8).

By contrary, the phylogenetic relationship from Olcostephanidae with S1 and S2 trifurcate and with one or two rows of tubercles is not easy to establish with other taxa. This family is here subdivided in the five subfamilies, Olcostephaninae, Capelotinae, Garcitinae n. subfam., Taraisitinae and Saynoceratinae n. subfam., according to different coiling shell, ornamentation and position lateral or ventral of the tubercles.

The subfamily Saynoceratinae with double row of tubercles is also olcostephanidae by its similar suture line. This proliferation of forms occurs in the Valanginian-Lower Hauterivian.

This work shows tools to establish the systematic classification of the ammonites here studied. In contrast, concepts disqualified without providing evidences were used in some studies about this subject, as the following:

*Taraisites* and *Satoites* represent synonymous subjectives; or they correspond to a morphological convergence without phylogenetic relationships (!); both cases are here considered inaccurate and misleading (see Riccardi *et al.*, 1971; Cooper, 1981; and Bulot, 1990).

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