## THE TITHONIAN-LOWER VALANGINIAN STRATIGRAPHY AND AMMONITE FAUNA OF THE VACA MUERTA FORMATION IN PAMPA TRIL, NEUQUÉN BASIN, ARGENTINA

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Abstract.- The sedimentary succession corresponding to the Vaca Muerta Fm (Tithonian-Lower Valanginian) at Pampa Tril (Neuquén Basin, Argentina) is described in detail. In this framework, the ammonite succession, sampled bed-by-bed, is described for first time. The Vaca Muerta Fm reaches 421.6 m in thickness in the study area, consisting of a succession of shales (strongly bituminous in the lower part) with several relatively thin intercalations of calcareous shales and fine-grained sandstones; it overlies the Tordillo Fm (Kimmeridgian continental sandstones) and underlies the Quintuco Fm (Lower Valanginian greenish gray claystones). The scope and definition of the Quintuco Fm are shortly reviewed.

Four lithofacies are differentiated in the Vaca Muerta Fm: (1) *bituminous shale*: gray to black, fine-grained clastic deposits with high organic matter contents, calcareous concretions, and abundant fossils, (2) *sandy shale*: moderate contents of organic matter, lighter in colour, with tuffaceous sandstone levels intercalated, and few fossils, (3) *calcareous shale*: carbonate material with varying proportions of fine-grained epiclastics and organic matter, forming thick-massive beds of marly aspect and conchoidal fracture, with moderately abundant fossils (ammonites and marine reptiles), and (4) *fine-grained sandstone*: psamitic components (quartz grains) with total absence of pelitic components and minimal contents of organic matter, scarcely fossiliferous. Volcanic ash evidences the activity of the western magmatic arc. Storm event records are frequent and recurrent all throughout the succession. The sequence reflects an upward-shallowing marine environment with euxinic-anoxic passing to dysoxic conditions, and increasing input of terrigenous epiclastics along an outer ramp.

The fauna of the succession is composed mainly of ammonites, followed by bivalves, gastropods, reptiles, fishes, and nautiloids. Ammonites occur in abundance throughout the sequence, mainly in the calcareous and sandstone levels. Nine ammonite families are represented in the fauna, including 35 genera, of which one is new: Lytoceratidae (*Lytoceras*), Ataxioceratidae (*Lithacoceras*, *Choicensisphinctes*, *Krantziceras*, *Catutosphinctes*, *Mazatepites*, *Paraboliceras*), Neocomitidae (*Parodontoceras*, *Pseudoparodontoceras* gen. nov., *Substeueroceras*, *Blanfordiceras*, *Neocosmoceras*, *Raimondiceras*, *Cuyaniceras*, *Subthurmannia*, *Thurmanniceras*, *Pseudoblanfordia*, *Lissonia*, *Pseudofavrella*), Olcostephanidae (*Groebericeras*, *Spiticeras*, *Aspidostephanus*), Himalayitidae (*Windhauseniceras*, *Corongoceras*, *Himalayites*), Aspidoceratidae (*Pseudolissoceras*), and Oppeliidae (*Metahaploceras*, *Pasotiia*, *Parastreblites*, *Cieneguiticeras*). The fauna (especially the perisphinctoids) is dominated by adult and juvenile macroconchs whereas adult microconchs are very scarce. *Lithacoceras picunleufuense* is very well represented by adult macroconchs which show clearly the aspect of the successive transients from the very base of the Andean Tithonian sequence. The genera *Choicensiphinctes* and *Catutosphinctes* are also well represented throughout the Tithonian, exhibiting the main evolutionary changes of the lineages.

The well controlled stratigraphic distribution of the 55 species described allows, considering the succession of their assemblages, a rather confident chronostratigraphic subdivision of the column at zonal level. Furthermore, the recognition of fourteen ammonite biohorizons (four of them tentatively) increases notably the resolution of the cronostratigraphic subdivision, enabling much more precise time-correlations. Three of these biohorizons are new: *internispinosum* alfa Hz. (base of a standard Internispinosum Zone), *azulense* Hz. (Alternans Zone), and *koeneni* Hz. (Koeneni Zone). The Internispinosum (Tithonian) as well as the Noduliferum and Damesi zones (Berriasian) are standarized by fixation of their bases by means of biohorizons. The rich succession studied allows to time-correlate some few Andean horizons with the Tethyan Primary Standard Scale through the Tithonian and Berriasian. For first time the tipically Tethyan Berriasian *Subthurmannia boissieri* is documented confidently from horizoned samples (well preserved macroconchs) in the upper Noduliferum-Damesi zones interval.

Keywords: Neuquén Basin • Vaca Muerta Formation • Tithonian-Valanginian • Stratigraphy • Ammonite fauna • Chronostratigraphy.

Resumen.- Estratigrafía y fauna de amonites de la Formación Vaca Muerta (Tithoniano-Valanginiano Inferior) en Pampa Tril, Cuenca Neuquina, Argentina. La sucesión sedimentaria correspondiente a la Fm Vaca Muerta (Tithoniano-Valanginiano Inferior) en Pampa Tril se describe detalladamente. En este contexto, la sucesión de amonites, muestreada estrato por estrato, se describe por primera vez. La Fm Vaca Muerta presenta un espesor de 421.6 m, y consiste en una sucesión de lutitas (fuertemente bituminosas en la parte inferior) con numerosos intercalaciones de pizarras calcáreas y areniscas finas. La Fm Vaca Muerta yace sobre la Fm Tordillo (areniscas continentales kimmeridgianas) y subyace a la Fm Quintuco (arcillitas verde-grisáceas del Valanginiano Inferior). El alcance y la definición de la Fm Quintuco son revisados aprovechando la información obtenida en el presente relevamiento.

Cuatro litofacies son diferenciadas en la Fm Vaca Muerta: (1) *lutita bituminosa*: depósitos clásticos finos, grises a negros, con alto contenido de materia orgánica, abundantes concreciones calcáreas y abundantes fósiles, (2) *lutita arenosa*: color mas claro, contenido de material orgánica moderado, niveles de arenisca tobácea intercalados, pocos fósiles, (3) *lutita calcárea*: material calcáreo con proporciones variadas de material epiclástico finamente granulado y materia orgánica, formando capas gruesas masivas con aspecto margoso y fractura concoidal, fósiles moderadamente abundantes (amonites y reptiles marinos), y (4) *arenisca fina*: componentes psamíticos (granos de cuarzo) con total ausencia de componentes pelíticos y mínimo de materia orgánica, fósiles escasos. La presencia de ceniza volcánica evidencia la actividad volcánica del arco magmático occidental. A través de toda la sucesión hay frecuentes y recurrentes registros de eventos de tormentas. La sucesión refleja un ambiente marino de somerización progresiva con condiciones anóxico-euxínicas pasando a disóxicas, y un incremento del

ingreso de epiclásticos terrigenos a lo largo de una rampa distal.

La fauna de la sucesión está compuesta principalmente por amonites. seguidos por bivalvos, gastrópodos, reptiles, peces y nautiloideos. Amonites se presentan en abundancia a través de toda la secuencia, principalmente en los niveles calcáreos y areniscas. Nueve familias de amonites están representadas en la fauna, incluyendo 35 géneros de los cuales uno es nuevo: Lytoceratidae (Lytoceras), Ataxioceratidae (Lithacoceras, Choicensisphinctes, Krantziceras, Catutosphinctes, Mazatepites, Paraboliceras), Neocomitidae (Parodontoceras, Pseudoparodontoceras gen. nov., Substeueroceras, Blanfordiceras, Neocosmoceras, Argentiniceras, Raimondiceras, Cuyaniceras, Subthurmannia, Thurmanniceras, Pseudoblanfordia, Lissonia, Pseudofavrella), Olcostephanidae (Groebericeras, Spiticeras, Aspidostephanus), Himalayitidae (Windhauseniceras, Corongoceras, Himalayites), Aspidoceratidae (Physodoceras, Pseudhimalayites, Toulisphinctes), Haploceratidae (Haploceras), Lissoceratidae (Pseudolissoceras), y Oppeliidae (Metahaploceras, Pasottia, Parastreblites, Cieneguiticeras). La fauna (especialmente los perisphinctoideos) está dominada por macroconchas adultas y juveniles mientras que las microconchas son muy escasas. Lithacoceras picunleufuense está muy bien representada por macroconchas adultas que muestran claramente el aspecto de los sucesivos transients a partir de base de la secuencia del Tithoniano andino.

La detallada distribución estratigráfica de las 55 especies de amonites permite, considerando la sucesión de asociaciones, establecer una consistente subdivisión cronoestratigráfica de la columna a nivel zonal. Además, el reconocimiento de catorce bio-horizontes de amonites (cuatro de ellos tentativamente) incrementa sustancialmente la resolución en la subdivision cronoestratigráfica, lo cual posibilita correlaciones temporales mucho mas precisas, e.i. alta resolución. Tres de estos biohorizontes son nuevos: el Hz. internispinosum alfa (base de una Zona Internispinosum estándar), el Hz. azulense (Zona Alternans), y el Hz. koeneni (Zona Koeneni). La Z. Internispinosum (Tithoniano andino) así como las zonas Noduliferum y Damesi (Berriasiano andino) son estandarizadas mediante la fijación de sus bases por un biohorizonte de amonites. La rica sucesión estudiada pemite correlacionar temporalmente algunos horizontes andinos con partes del Tithoniano y Berriasiano de la Escala Primaria Estándar del Tethys. Por primera vez el berriasélido tethysiano Subthurmannia boissieri (macroconchas bien preservadas) se documenta a partir de muestras posicionadas exactamente en niveles de un intervalo determinado por las zonas Noduliferum (parte superior)-Damesi.

Palabras clave: Cuenca Neuquén • Formación Vaca Muerta • Tithoniano-Valanginiano • Estratigrafía • Fauna de amonites • Cronoestratigrafía.

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#### INTRODUCTION

The Pampa Tril area, located in northern Neuquén Province (Fig. 1A), is characterized by extensive outcrops of Upper Jurassic-Lower Cretaceous rocks, represented by the Auquilco (Oxfordian), Tordillo (Kimmerdigian), Vaca Muerta (Tithonian-Lower Valanginian), Mulichinco (Lower Valanginian), and Agrio (Valanginian-Lower Barremian) formations (Fig. 1B). The regional geology and the stratigraphy of the Vaca Muerta Formation in this area have been differently studied by several authors (e.g. Groeber 1946, Weaver 1931, Leanza & Hugo 1977, Spalletti et al. 1999, and references below).

The ammonite fauna of the Vaca Muerta Fm in the study area had not been monographed till today, there exist only citations in brief biostratigraphic reports. Weaver (1931) described the general rock succession in the area of Puerta Curacó (Curacó Canyon) including our study area; main occurrences of ammonites were depicted in the Section 3 of his Plate 1. A section of Pampa Tril (as Pampa Tril-La Yesera) has been studied by Leanza & Hugo (1977), reporting the occurrence of some few ammonites which could be compatible with the results of the present study.

The purpose of this report is to describe the local stratigraphy, the ammonite fauna sampled bed-by-bed, and the chronostratigraphic classification derived from its biostratigraphy. Some species and some genera needed revision of different aspects of their typology, biostratigraphy, and/or taxonomy. The obtained results allow to discuss some important chronostratigraphic issues of the Andean Tithonian-Berriasian zonation, and the differentiation of new ammonite biohorizons. Since the succession is thick and the involved time interval is long, the number of ammonites collected is huge and hard to present in a single report. Nevertheless, we have decided to concentrate all the information and interpretations in this single report for this succession, which is especially important in palaeontologic and stratigraphic terms for several reasons which are discussed below. Among them, stands the dense occurrence of moderately well-preserved ammonites which allow to recognize all the zones of the Tithonian and Berriasian, as well as part of the Lower Valanginian. On the other hand, the lithologic monotony all along the succession suggests a rather stable environment, few changing in its relative position within the depositional setting of the basin. These conditions reduce much of the variation in the composition of the local ammonite assemblages produced by differential preservation and/or migrations that usually hamper or make difficult to piece together the successive fragments of the lineages.

We distinguish: (a) biozone as a body of rock characterized by its fossil content; (b) chronostratigraphic zone as a sheet of rock (one or more strata) bounded by two time-planes and recognized by its fossil content; and (c) standard chronostratigraphic zone as a chronostratigraphic zone defined only by an ammonite biohorizon at its base, then conforming a succession of standard zones without gaps or overlaps. These definitions and the corresponding and more convenient nomenclature are widely discussed by Callomon (1985, 1995).

Abbreviations are used throughout the text for Biozone (Bz.) and chronostratigraphic Zone (Zone or Z.). The biostratigraphic unit denominated ammonite biohorizon -or horizon for short (Hz.)- is used in its typical form, as explained by Callomon (1985, 1995). The regional subdivision of the Tithonian adopted is the tripartite, with a middle part differentiated. All the localities mentioned in the text are positioned in Fig. 1, where in addition the abbreviations used throughout the text are indicated.

For shortening the manuscript, the following references are abbreviated: Parent, Garrido et al. 2011 (PGSS 2011), Parent et al. 2011 (PSS 2011), Parent, Garrido et al. 2013a (PGSS 2013a), Parent, Garrido et al. 2013b (PGSS 2013b), Parent, Myczinski et al. 2010 (PMSS 2010), Parent, Schweigert et al. 2008 (PSSE 2008).

#### STRATIGRAPHY

The Vaca Muerta Fm is part of a transgressive-regressive sedimentary cycle of Kimmeridgian to Valanginian age, denominated Lower Mendoza Group by some authors (Vergani et al. 1995, Leanza 2009, Arregui et al. 2011, Leanza et al. 2011). Several lithostratigraphic units conform this sedimentary cycle, in which the distribution, lithology and thickness of each formation are conditioned by the palaeogeographical features of the basin and their corresponding environments of deposition. In this sense, along the basin the Vaca Muerta Fm shows strong variations of thickness and age. Close to the cratonic passive margin the succession is 129 m (or less) in thickness, restricted in age to the interval early to middle Andean Tithonian, while in the depocentre it can reach 1250 m with Tithonian to early Andean Valanginian age (Leanza 1973, Leanza & Hugo 1977). In general, this unit exhibits a continuous shallowing-upwards cycle of sedimentation (Leanza 1993, Leanza & Hugo 1977), where the palaeogeographic features of the basin determined a marine sedimentation under generalized anoxic conditions (Howell et al. 2005).

In the study area, the deposits of the Vaca Muerta Fm were originated on a basinal to outer ramp setting, with predominant deposition of black shales intercalated with intervals of major carbonate sedimentation (Spalletti et al. 1999; see Figs. 2, 3A-B). Although the outcrops of the Vaca Muerta Fm at Pampa Tril-Yesera del Tromen area (Fig. 1B) are very extensive, the partial coverage thereof (especially in its middle section) makes difficult to carry out a complete lithostratigraphic profile of this unit from a single transect. Due to it, a combined profile was elaborated from three different sections (Fig. 1B), which were laterally correlated to each other through guide levels. As result, the total thickness measured for the Vaca Muerta Fm at Pampa Tril-Yesera del Tromen area is 421.6 m (Fig. 2).

It is generally agreed that within the study area, the Vaca Muerta Fm deposits lay through a regional net contact on sedimentites of the Kimmeridgian Tordillo Fm (Holmberg 1976, Gulisano & Gutiérrez-Pleimling 1995, Spalletti et al. 1999; see Fig. 3C). This contact can be traced through a notable surface of stratigraphic discontinuity, often accompanied and highlighted by a thin and continuous horizon rich in iron oxide (limonite; see Fig. 3D). Respect to the upper boundary some authors indicate a direct contact of the Vaca Muerta Fm with the sandstones and carbonatic sandstones of the Mulichinco Fm (Holmberg 1976, Spalletti et al. 1999), defined through the Huncalican unconformity (Leanza 2009). However, Gulisano & Gutiérrez-Pleimling (1995) recognized the presence of the Quintuco Fm in this area, developed between the Vaca Muerta and Mulichinco formations. According to these latter workers, the Quintuco Fm is represented by a 100 m-thick succession of inner to outer shelf claystones and sandstones with skeletal limestones.

The scope of the definition of the Quintuco Fm has been widely debated, mainly due to the different concepts introduced by Weaver (1931) in the original description. The confusion regarding the identity of this unit arise because this author included several sedimentary successions within its definition, distributed through the basin and characterized by



Figure 1. A: Neuquén (or Neuquén-Mendoza) Basin (gray area), west-central Argentina, with indication of the Pampa Tril (PT) and other localities mentioned in text: CH: Charahuilla, PL: Picún Leufú, CL: Cerro Lotena, CG: Cerro Granito, LC: Los Catutos, PC: Portada Covunco, CA: Cañadón de los Alazanes, MQ: Mallín Quemado, SVM: Sierra de Vaca Muerta, CDA: Cajón de Almanza, PQ: Puerta Quintuco, CM: Chacay Melehué, MR: Mallín Redondo, AY: Arroyo del Yeso, BB: Bardas Blancas, MC: Molinos Colgados, PM: Paso del Montañés, AL: Arroyo Loncopué, CP: Casa Pincheira, AD: Arroyo Durazno, RV: Rodeo Viejo, AC: Arroyo Cieneguita, BDF: Baños del Flaco, AA: Arroyo Alberjillo, AP: Arroyo Paraguay, CB: Cajón del Burro-Río Choicas, AM: Arroyo de la Manga, RD: Río Diamante, ACP: Arroyo Cruz de Piedra, PLB: Paso Los Bayos. Dotted line indicating the transect of localities considered in Fig. 86. B: Geologic map of the Pampa Tril area composed from results of the present study with indication of the studied section (segments 1-3).

different lithologies and of different ages (see Leanza 1973). Recently, Leanza et al. (2011) redefined the Quintuco Fm as nearshore siliciclastics deposited during de Andean late Berriasian-early Valanginian, between the Vaca Muerta and Mulichinco formations. According to these authors this unit shows a wide distribution between Sierra de la Vaca Muerta (Fig. 1A: SVM) and Puerta Quintuco (PQ, the type locality; see Fig. 1A), decreasing in thickness from south to north, from 350 m (at SVM area) to less than 30 m (at PQ area).

In the original description Weaver (1931) indicated that in the northern Neuquén Province the deposits of the Quintuco Fm are composed predominantly by dark gray to black clay shales, clarifying that "The black shales of the Quintuco Formation pass downward into similar shales of the upper Tithonien beds and usually upon a lithologic basis it is impossible to determine the line of demarcation. There are,



Figure 2. Lithostratigraphic profile of the Vaca Muerta Formation in the Pampa Tril area. The upper right inset shows the stratigraphic relationships of the studied section. The stratigraphic levels 1-120 are indicated as PT-1 to PT-120 (PT: Pampa Tril) throughout the text and figures. *Sections* I-III explained in the text.

however, well defined faunal distinctions which can be utilized in establishing the contact relations. These transitional beds are widely spread, and involve all of the northern two-thirds of Neuquen." (Weaver 1931: 55).

From those definitions and our field observations, we consider the Quintuco Fm in the Pampa Tril-Yesera del Tromen area as a 20 m-thick succession, consisting of greenish gray pelites (claystones), devoid of fossils, located in sharp contact over sandy shales of the Vaca Muerta Fm and covered in erosive contact by the sandy beds of the Mulichinco Fm (Fig. 3E-F).

The reasons to exclude such deposits from the Vaca Muerta Fm are: (a) a sharp lithologic change occurs, passing abruptly from a thick, dominantly shaly succession with high content of organic matter, to a succession of massive, greenish gray claystone with low organic matter content, clearly delimited by a regional sharp contact, and (b) the mentioned changes imply a significant modification in the environment towards shallower sedimentation conditions. The thinness of the Quintuco Fm in the study area is coincident with the observations of Leanza et al. (2011), who noted a significant thinning of this unit from south to north through the basin, indicating for Puerta Quintuco site (100 km south the study area) a thickness of only 30 m.

#### Lithofacies

Bituminous shale: This lithofacies constitutes the dominant deposits of the first 46.7 m of the unit (Fig. 2, levels PT-1-20). It corresponds to fine to very-fine grained clastic deposits, conformed by shales and sandy shales very rich in organic matter, characterized by dark gray to black colour, and the development of a very-fine lamination (Fig. 4A). Fetid odour and presence of small veins of kerogen material are frequent, mainly in the basal levels. Small pyrite cubes, sometimes altered to limonite, also occur with high frequency in these deposits. Occasionally, thin (3 to 10 mm-thick) tuffaceous sandstone horizons are interstratified. Less frequently, 10-15 cm-thick massive sandstone tabular beds are also interbedded in the bituminous shale succession (Fig. 4B). These latter levels usually show plastic deformation and load cast structures, and in some sectors they may exhibit a dense bioturbation represented by the ichnogenus Palaeophycus Hall, 1847. Spherical carbonate concretions are distributed along this section, showing an increase in the size and frequency upwards. The concretional bodies can internally have small crystals of pyrite and chalcopyrite (Fig. 4C), and preserve the original horizontal lamination of the shale deposits. Around them, the host sediment exhibits a deformation of the lamination according with the geometry of the concretion (Fig. 4D). Well preserved fossils occur in these concretions.

Interpretation: The domain of very fine laminated, pelitic-type deposits, denotes subaqueous sedimentation under low-energy conditions, where decantation has been the main deposition process. No perturbation of the primary lamination indicates no activity of benthonic organisms and minimal to null action of subaqueous currents, suggesting in this latter case sedimentation under the storm wave base (offshore zone) (Walker & Plint 1992). The high content of organic matter and the development of pyrite and chalcopyrite are attributed to conditions of severe oxygen deficiency of the water mass, indicating anoxic to euxinic conditions (Kauffman 1986, Potter et al. 2005). The occasional occurrence of thin tuffaceous sandstone horizons, suggests a sporadic source of pyroclastic material derived from the western magmatic arc. Tabular beds of massive sandstone with load casts indicate a fast clastic influx, possibly related to storm events and deposited in the

form of distal tempestites (Einsele 1992). Deformation of the lamination around the fossiliferous concretions suggests these carbonate structures originated during an early diagenetic stage, prior to the compaction process of the sediments (Richardson 1921, Marshall & Pirrie 2013).

**Sandy shale**: This lithofacies exhibits similar features to those described for bituminous shales, but having a lower contents of organic matter, what becomes more evident upwards the stratigraphic column. Its colour ranges from medium gray and dark green matte (Fig. 4E), with loss of the fetid odour and no visible kerogenic material. Tuffaceous sandstone levels also occur sporadically intercalated, being in this case slightly thicker, about 15 cm (Fig. 4F). Thin bedding-parallel veins of fibrous calcite ("beef") are a common feature in these deposits. Just as mentioned by Rodrigues et al. (2009), imprints of monotoid bivalves occur in these calcite veins. No spherical carbonate concretions were developed in this facies.

*Interpretation*: The domain of finely laminated, fine-grained epiclastic deposits, allows to infer a subaqueous low-energy environment, where the sedimentation was mainly regulated by decantation in sectors located under storm wave base. The absence of benthic activity and the presence of organic matter, suggest an oxygen-deficient water mass with development of anoxic to dysoxic conditions (Savdra & Botjer 1986, Potter et al. 2005). The veins of fibrous calcite correspond to post-depositional features, originated by precipitation from supersaturated aqueous solutions under overpressure conditions (Rodrigues et al. 2009).

**Calcareous shale**: This lithofacies is formed by carbonate material predominantly, with varying proportions of finegrained epiclastic fractions and organic matter. In the outcrops these deposits form 20 to 80 cm-thick tabular beds with marly appearance, with massive aspect and conchoidal fracture (Fig. 4G). In the exposed surface the rock colour varies from very light gray to buff cream. The rock surface in fresh (unweathered) is medium to dark gray in colour and shows the development of faint lamination. The calcareous shale facies is mainly present in the middle part of the succession, subordinate to the sandy shale deposits (Fig. 2). Well preserved ammonites and articulated marine reptiles occur (see Spalletti et al. 1999, Pol & Gasparini 2009).

*Interpretation*: The lamination and the organic matter contents suggest a low-oxygen environment, under dysoxic to anoxic conditions (Savdra & Botjer 1986, Potter et al. 2005). The occurrence of well-preserved, complete and articulate marine reptiles is consistent with a subaqueous environment characterized by low-energy mass waters and low to null activity of predators or big scavengers. The carbonate fraction may have been derived from the supply and accumulation of skeletal remains of phytoplankton during stages of greater population expansion and activity (Einsele 1992). However, a redistribution and enrichment of calcium carbonate in the shaly sediments by effect of differential diagenesis processes should not be dismissed (Wetsphal et al. 2008).

**Fine-grained sandstone**: This lithofacies shows similar characteristics to those of the sandy shale deposits, but showing in this case a total absence of pelitic components and minimal contents of organic matter (Fig. 4H). Scarce fossils occur in this facies. The psamitic components are dominated by quartz grains, presenting well textural maturity. Their deposits are characterized by light colours and little contents of carbonate cement. Horizontal lamination is well developed, often



**Figure 3. A**: General view of the outcrops of the Vaca Muerta Fm at Pampa Tril - Yesera del Tromen area. **B**: Detail of the black shale deposits of the Vaca Muerta Fm at the study area. **C**: General view of the basal contact of the Vaca Muerta Fm with the underlying Tordillo Fm at Yesera del Tromen area. **D**: Detail of the contact between Vaca Muerta and Tordillo formations. Note the ferric oxide (limonite) band which delimits the contact. **E**: General view of the top contact of the Vaca Muerta Fm with the Quintuco Fm. **F**: Detail of the greenish-gray, massive claystone of the Quintuco Fm overlain by calcareous sandstones (Mulichinco Fm). – The hammer is 260 mm in length.

intercalated with faint wave-ripple cross-lamination. Occasionally, hummocky structures are also present in these levels. In general, these deposits are predominant towards the upper third of the succession (Fig. 2), subordinated to the sandy shale facies.

*Interpretation*: These deposits represent episodes of major clastic influx, whereas the associate structures indicate relationship with sporadic occurrence of high and mediumenergy currents, under the effect of combined flows and waning oscillatory flows (Hunter & Clifton 1982, Dott & Bourgeois 1982, Cheel & Leckie 1993).

In summary, the studied sedimentary succession

corresponding to the Vaca Muerta Fm (Fig. 2) is dominated by shale to sandy shale deposits. The *section*-I (Fig. 2: levels PT-1 to PT-20) shows high content of organic matter evidenced by the marked black colour of the deposits, the fetid odour, and the presence of small veins of kerogen. The occurrence of small crystals of pyrite and chalcopyrite and spherical carbonate concretion is also typical of these levels. This interval evidences a low-energy subaqueous environment, developed under euxinic to anoxic conditions. In levels PT-21 to PT-120 the sandy shales facies conform the dominant deposits, showing gradual decreasing in the organic matter content upwards in the sequence. The sporadic recurrence of the calcareous shale facies typify the *section*-II (levels PT-21 to PT-82, Fig. 2), while the irruption and recurrence of the fine-



**Figure 4. A**: Bituminous shale facies of the lower part of the succession (common in levels PT-1 to PT-20). **B**: Bed of massive sandstone intercalated in bituminous shales (frequent in levels PT-11 to PT-18). **C**: Calcareous concretion with chalcopyrite crystals (frequent in levels PT-13 to PT-20). **D**: Fossiliferous calcareous concretion within sandy shale deposits (common in levels PT-21 to PT-32). **E**: Sandy shale facies (common in levels PT-21 to PT-120). **F**: Tuffaceous sandstone bed intercalated within sandy shale deposits (occasionally present between levels PT-27 and PT-35). **G**: Calcareous shale facies (marly type; frequent from level PT-82). **H**: Laminate fine-grained sandstone facies (commonly intercalated between levels PT-83 to PT-120). – The hammer is 260 mm in length.



**Figure 5**. Distribution of the ammonite fauna in the studied section of Pampa Tril through levels PT-1 to PT-106 as numbered in Fig. 2. Solid bars indicate normal in-situ record; gray bars virtual recorded range; arrowheaded lines indicate estimated position of loose specimen(s). Chronostratigraphic classification and ammonite bio-horizons (horizon for short) explained in text. Horizons firmly recognized indicated by gray boxes, tentatively by blank boxes. Broken lines indicate non-standard zones. Abbreviations: Mendoz. (Mendozanus), Proxim. (Proximus), Nodulif. (Noduliferum).



**Figure 6.** A: *Lithacoceras picunleufuense* Parent, Garrido, Schweigert & Scherzinger, transient alpha [M], complete adult (unumbered specimen), level PT-4, *picunleufuense* alpha Hz., Picunleufuense Z. [ $L_{BC}$  = 330°,  $D_p$  = 203 mm]. A<sub>2</sub>: transverse section (bodychamber gray) at D = 146 mm (indicated with a line in A<sub>1</sub>), A<sub>3</sub>-A<sub>4</sub>: innermost whorls (x2). B: *Lytoceras montanum* (Oppel), phragmocone (MOZ-PI 8494), level PT-42, Alternans Z. B<sub>3</sub>: enlarged (x2) view showing the delicate plain ribs with smooth interspaces. – The asterisk indicates the last septum. The bar represents 10 mm for natural size views (A<sub>1</sub>-A<sub>2</sub>, B<sub>1</sub>-B<sub>2</sub>), and 5 mm for double size views (A<sub>3</sub>-A<sub>4</sub>, B<sub>3</sub>).

grained sandstone facies characterizes the *section*-III (levels PT-83 to PT-120, Fig. 2). Along the *sections*-II and III, prevail oxygen-deficient environments; however, a gradual change from anoxic to dysoxic conditions is developed. It is worth to note that the youngest record of fossil herpetofauna occurs in the *section*-II (Fig. 2: level PT-56), within the Andean Upper Tithonian Koeneni Zone (see Figs. 2, 5 and discussion of age in the Chapter Biostratigraphy and time-correlation). The activity of the western magmatic arc is evidenced by the occasional

ocurrence of volcanic ash through the *sections*-I and II, while storm event records are frequent and recurrent all through the succession. In general, the Vaca Muerta Fm in the study area reflects an upward-shallowing marine environment, thus a transition from euxinic-anoxic to dysoxic conditions and increasing input of terrigenous epiclastic sediments towards the basin. According with the model proposed by Spalletti et al. (1999) these deposits take place along an outer ramp environment with recurrence of storm episodes.



Figure 7. Lithacoceras picunleufuense Parent, Garrido, Schweigert & Scherzinger, transient alpha [M], almost complete adult (MOZ-PI 7868), level PT-6, picunleufuense alpha Hz., Picunleufuense Z. – The asterisk indicates the last septum. All natural size (x1).

#### Distribution of the ammonite fauna

The distribution of the ammonites recorded in the studied section is shown in Fig. 5, referred to the levels of our succession in Fig. 2. The pattern of occurrence throughout the succession is one of rather dense and continuous records, mainly a rather regular alternation of a level with ammonites with a level with no ammonites. This pattern is especially regular in the interval of levels PT-1-14, Picunleufuense-Zitteli ["Mendozanus"] zones, where ammonites are the most abundant. There are apparent breaks (see Fig. 5) which mean nothing but no-collection from covered beds (e.g. levels PT-15-18, PT-23-31, Internispinosum Zone), and short transects with ammonites more or less abundant but crushed and poorly preserved, thus not considered. These transects are in the upper Alternans Z. (levels PT-42-48), Wichmanni Z. (levels PT-77-85) and Riveroi Z. (levels PT-89-103). The chronostratigraphic classification adopted and the ammonite biohorizons (horizons hereafter for short) recognized are discussed in the chapter Biostratigraphy and time-correlation. The "Mendozanus" Zone is considered to be included into the Zitteli Zone by the overlapping of the guide-assemblages as discussed below in the same chapter. Therefore, pending a solution, it is noted as Zitteli ["Mendozanus"] Zone throughout the text.

## SYSTEMATIC PALAEONTOLOGY

**Conventions.**- The material described is housed at the Museo Prof. Olsacher, Zapala (MOZ-PI) and casts at the Laboratorio de Paleontología y Biocronologia, Universidad Nacional de Rosario (LPB-M). Bodychamber is abbreviated with Bc and phragmocone with Ph; macroconch (female): [M], microconch (male): [m]. Measurements are indicated as follows: diameter (*D*), diameter at the last adult septum ( $D_{\rm ls}$ ) and diameter at adult peristome ( $D_{\rm p}$ ), all given in millimeters [mm]; umbilical width (*U*), whorl width (*W*), whorl height ( $H_{\rm l}$ ), and whorl ventral (or apertural) height ( $H_2$ ), all given as dimensionless proportions of *D*; length of bodychamber ( $L_{\rm BC}$ ) in degrees [°]. The numbers of primary (*P*) and ventral (*V*) ribs are per half whorl; the numbers of umbilical ( $T_{\rm U}$ ), lateral ( $T_{\rm L}$ ) and ventrolateral ( $T_{\rm vL}$ ) tubercles are per half whorl. Levels of occurrence of the



**Figure 8.** *Lithacoceras picunleufuense* Parent, Garrido, Schweigert & Scherzinger [M], Picunleufuense Z. A-B: Adult [M] phragmocones (MOZ-PI 7870/1, MOZ-PI 7870/2, respectively) of transient alpha, level PT-6, *picunleufuense* alpha Hz.; B<sub>3</sub>: innermost whorls (x2). C: Apertural view (last part of bodychamber removed) of the complete adult [M] (MOZ-PI 8376/2) from level PT-8; lateral view in Fig. 9. – The asterisk indicates the last septum. The bar represents 10 mm for natural size views, except for  $B_3(x2)$ .



**Figure 9.** *Lithacoceras picunleufuense* Parent, Garrido, Schweigert & Scherzinger [M], complete adult with peristome (MOZ-PI 8376/2), level PT-8, Picunleufuense Z. [ $L_{BC} = 270^\circ$ ,  $D_p = 265$  mm]. Apertural view in Fig. 8C.  $A_1$ : lateral view (x1) of the complete ammonite with last half of the bodychamer removed and shown as  $A_2$  (reduced x0.5). – The asterisk indicates the last septum. The bar represents 10 mm for  $A_1$ , and 20 mm for  $A_2$ .

specimens denoted by the level number and the prefix PT (Pampa Tril) and referred to Fig. 2. Bio- and chronostratigraphic units cited in this chapter are discussed below, in the next chapter. Open nomenclature as suggested by Bengtson (1988). Interpretation and nomenclature of species,

as usually widely variable assemblages (transients) forming lineages (genera), follow the criteria and conventions discussed at some extent by Dietze et al. (2005), PSS (2011) and Parent & Garrido (2015). Lists of synonyms are mainly referred to lists already published.



**Figure 10.** *Lithacoceras picunleufuense* Parent, Garrido, Schweigert & Scherzinger [M], complete adult with peristome (MOZ-PI 8376/1), level PT-8, Picunleufuense Z.  $[L_{BC}=280^{\circ}, D_{p}=294 \text{ mm}]$ .  $A_{1}$ : natural size (x1) view;  $A_{2}$ : reduced view (x0.5). – The asterisk indicates the last septum. The bar represents 10 mm for  $A_{1}$ , and 20 mm for  $A_{2}$ .



Figure 11. *Lithacoceras picunleufuense* Parent, Garrido, Schweigert & Scherzinger [M], transient beta, complete adult with peristome (unnumbered), level PT-10a, *picunleufuense* beta Hz., Picunleufuense Z. [ $L_{BC}$  = 310°,  $D_p$  = 205 mm]. – The asterisk indicates the last septum. Natural size (x1).

Order Ammonitida Fischer, 1882 Suborder Lytoceratina Hyatt, 1889 Superfamily Lytoceratoidea Neumayr, 1875 Family Lytoceratidae Neumayr, 1875 Subfamily Lytoceratinae Neumary, 1875

Genus Lytoceras Suess, 1865 Type species: Ammonites fimbriatus J. Sowerby, 1817 (ICZN Opinion 130)

## Lytoceras montanum (Oppel, 1865) Fig. 6B

**Material**.- An incomplete phragmocone with test (MOZ-PI 8494), level PT-42.

**Description and remarks.** The specimen is small (max preserved D = 35 mm) and wholly septated, very evolute with compressed (higher than wide) oval whorl section. The sculpture consists of thin, irregularly spaced, plain primary ribs



Figure 12. A: Choicensisphinctes cf. platyconus Parent, Garrido, Schweigert & Scherzinger, inner whorls (MOZ-PI 8439/2), level PT-1. B-D: Choicensisphinctes platyconus, picunleufuense alpha Hz., Picunleufuense Z. B: Adult phragmocone (MOZ-PI 7554), level PT-2. C: Inner whorls (unumbered), level PT-4. D: Incomplete adult [M] (MOZ-PI 7865), level PT-4. – The asterisk indicates the last septum. All natural size (x1).

which born on the umbilical seam, covering the flanks and venter; between the ribs the shell is smooth.

*L. montanum* is characterized by the crinkled ribs on outer whorls, but in the inner whorls they are plain (cf. Zittel 1870: pl. 26: 3-4, Fischer 1994: pl. 86: 3, Főzy & Scherzinger 2013b: pl. 3) as in the present specimen. The chronostratigraphic range of this species seems to be Tithonian-lower Berriasian.

Occurrence and distribution.- Level PT-42. Alternans Zone. The species has been recorded mainly from the Mediterranean Province and probably Mombasa and Kenya (Főzy & Scherzinger 2013b). The present specimen represents one of the scarce records of lytoceratids in the Tithonian of the Neuquén Basin (see Steuer 1897 transl. 1921, Krantz 1926, 1928). The palaeoecological or palaeobiogeographical significance is hard to be evaluate from poor material. The Neuquén Basin was connected with the Pacific Ocean through a volcanic arc during most of the Jurassic (Spalletti et al. 2000, Parent 2006), with marine conditions different to those of open and deep waters (oceanic) usually assumed as typical for lytoceratids and phylloceratids (Westermann 1996). There are records of lytoceratids in the Neuquén Basin from at least the Toarcian (Spalletti et al. 2012) and throughout most of the Jurassic (e.g. Westermann & Riccardi 1982, Hillebrandt, Westermann et al. in Westermann 1992, Joly 2012). Due to the scarcity and/or fragmentary preservation of the known material, these records seem to represent brief incursions into the basin, or drifting shells transported by currents from the Pacific Ocean through the platforms of the volcanic arc. The similarly oceanic phylloceratids may be much more abundant at least in the Aalenian and upper Bathonian-lower Callovian including very large specimens (Parent 1998).

## Suborder Ammonitina Fischer, 1882 Superfamily Perisphinctoidea Steinmann, 1890 Family Ataxioceratidae Buckman, 1921 Subfamily Lithacoceratinae Zeiss, 1968

Genus *Lithacoceras* Hyatt, 1900 Type species: *Ammonites ulmensis* Oppel, 1858; by original designation.

**Remarks.-** The use of this genus seems safe in morphologic terms as discussed in Parent et al. (2006), PGSS (2011) and PSS (2011) but remains to be established the level of genetic relationships between the Andean and Tethyan groups which could belong to two different, but closely related lineages. The establishment of these relationships depends mainly on a more accurate time-correlation than that currently available. The



Figure 13. Choicensisphinctes platyconus Parent, Garrido, Schweigert & Scherzinger, picunleufuense alpha Hz., Picunleufuense Z., incomplete adult [M] (MOZ-PI 7873), level PT-6. – The asterisk indicates the last septum. Natural size (x1).

succession of Andean species attributed to this genus seem to belong to a single, few variable lineage. From the older:

(1) Lithacoceras picunleufuense [M & m], Picunleufuense Z.: at least two transients have been distinguished (see below). This species occurs in abundance all throughout the basal levels of the Tithonian in the Neuquén Basin.

(2) *Lithacoceras malarguense* (Spath, 1925), *malarguense* Hz., lowermost Zitteli ["Mendozanus"] Z. Material to be published elsewhere has been recently collected from the Zitteli ["Mendozanus"] Z. of Cerro Granito.

(3) *L*. n. sp. aff. *picunleufuense* (in PSS 2011), *falculatum* Hz., Proximus Z. of Arroyo Cieneguita.

This latter species has been proposed (PSS 2011) as the root of the Andean Lithacoceratinae genus *Zapalia* Leanza & Zeiss, 1990 (type species: *Z. fascipartita* Leanza & Zeiss, 1992), which is known to occur in abundance in the Internispinosum *Z.* at Los Catutos (Leanza & Zeiss 1990, Zeiss & Leanza 2010). *Lithacoceras* is abundant only in the Picunleufuense *Z.*, the records in the Zitteli ["Mendozanus"] and Proximus zones are scarce.

*Lithacoceras picunleufuense* Parent, Garrido, Schweigert & Scherzinger, 2011 Figs. 6A, 7-11

**Synonymy.**- See PGSS (2011: 53).

**Material.**- 10 complete adult [M] from levels PT-4, 6, 8 and 10a. 35 incomplete or fragmentary specimens from levels PT-2, 4, 6, 8, and 10a.

**Description.**- Macroconchs evolute from the innermost whorls, suboval to rounded subtrapezoidal in whorl section. Ribbing on inner whorls moderately dense, prosocline, narrowly biplicate. Through the end of the adult phragmocone or beginning of the adult bodychamber occurs the typical short stage of primaries regularly trifurcated in a virgatotome style. Bodychamber with primaries coarser and divided in several secondaries, sometimes in sheaves; coarse and undivided near peristome.

**Remarks.-** The species occurs at several levels of the lowermost part of the section in the form of different morphotypes, differing to some extent from the holotype. From the variation of adult size and strength and density of ribbing, can be recognized the two transients already distinguished in PGSS (2011), and a third morph occurring between the horizons of these transients. The distribution is as follows, from below:

(a) Transient alpha (Figs. 6A, 7, 8A-B), levels PT-2, 4, 6: typical specimens matching the holotype in size, shell shape and sculpture ( $D_p = 160-200$  mm).

(b) A large morphotype (Figs. 8C, 9-10), level PT-8: large



Figure 14. Choicensisphinctes platyconus Parent, Garrido, Schweigert & Scherzinger, picunleufuense alpha Hz., Picunleufuense Z., nearly complete adult [M] (MOZ-PI 7898), level PT-6. The last whorl is bodychamber. – Natural size (x1).

specimens ( $D_p = 260-350$  mm) which differ from those of transient alpha in reaching a larger adult size with bodychambers covered by strong undivided primaries and smooth venter. Within the type material of Picún Leufú (transient alpha) there is a fragment of adult bodychamber (PGSS 2011: fig. 8A) which shows similar features at comparable size, larger than the holotype.

(c) Transient beta (Fig. 11), level PT-10a: compressed specimens, more finely and densely ribbed in the phragmocone than the large morphotype and the transient alpha. Adult size  $D_p = 195-215$  mm. These ammonites can be distinguished from those of lower levels by being more compressed with finer and denser ribbing on the juvenile phragmocone. In this sense, *Lithacoceras malarguense* (Spath, 1931) of the *malarguense* Hz. shows a very similar ribbing at comparable diameters.

**Occurrence and distribution.**- The stratigraphic range of *L*. picunleufuense, in the present section, is from level PT-2 to level PT-10a. This species is the index and part of the guideassemblage of the Picunleufuense Standard Chronostratigraphic Zone, the base of the Andean Lower Tithonian, typically the base of the Vaca Muerta Fm or less frequently the top of the Tordillo Fm (e.g. Casa Pincheira, Fig. 1A). It has been recorded all along the basin, from Arroyo Cieneguita (PSS 2011) and C. Pincheira (Parent 2003a) in the North up to the southern end of the Neuquén Basin in Picún Leufú (PGSS 2011) and Estancia M. Juana (PGSS 2013b), also including Portada Covunco (PGSS 2013a), C. Alazanes (Parent 2001), Cerro Lotena-Cerro Granito and Mallín Quemado (to be published elsewhere) and other localities (material under study from Arroyo Durazno, Río Diamante, and Chacay Melehué).



Figure 15. *Choicensisphinctes platyconus* Parent, Garrido, Schweigert & Scherzinger, Picunleufuense Z. A: Nearly complete adult [M] (MOZ-PI 7912), level PT-8. B: Phragmocone (MOZ-PI 7924), level PT-8. C: Adult [M] phragmocone (MOZ-PI 6113), level PT-6;  $C_1$ : innermost whorls (x2),  $C_4$ - $C_5$ : inner whorls, last whorl removed. – The asterisk indicates the last septum. All natural size (x1), except  $C_1$  (x2). The bar represents 10 mm except for  $C_1$  (5 mm).

#### Genus Choicensisphinctes Leanza, 1980 Type species: Perisphinctes choicensis Burckhardt, 1903; by original designation.

**Remarks.-** The holotype of the type species was figured by Burckhardt (1903: pl. 6: 10-11) with a hand-drawing. It is a small and incomplete [M?] phragmocone, by which there is no information about the adult phragmocone and the aspect of the bodychamber. This unfortunate situation prevents meaningful comparisons of the holotype of *C. choicensis* with other specimens. However, the holotypes of *Choicensisphinctes* erinoides and *Choicensisphinctes limits* are adult phragmocones with the beginning of the bodychamber preserved at least in this latter one (see PGSS 2011). This part of the shell is almost smooth, suggesting the bodychamber would be smooth.

Choicensisphinctes platyconus Parent, Garrido, Schweigert & Scherzinger, 2011 Figs. 12-16, 17B, 28A

#### **Synonymy.**- See PGSS (2011: 66).

**Material**. - 41 more or less complete specimens from levels PT-2, 4, 6, 8, and 10a; 3 cf.-specimens from levels PT-1-2.

Remarks.- The characteristic features of the macroconch of this species are well represented by the present material. Moderately involute platyconic shell with higher than wide whorl section, the flanks are flat or gently rounded and the venter rounded. The ribbing on the phragmocone is fine and commonly dense; the primary ribs bifurcate on the middle or the upper half of the flank and occur frequent polyschitozomics. In the last whorl of the phragmocone most primaries polyfurcate in three to six secondaries projected forwardly, irregularly in virgatotome style. In the adult bodychamber the primaries become stronger, blade-like and more widely spaced with no furcations, mostly fading-off from the ventro-lateral shoulder leaving the venter smooth. The microconchs are commonly one forth to half the size of the macroconchs; the ribbing is fine and dense, polyfurcated on the adult bodychamber, and the peristome bears a pair of rather short, typically subtriangular lappets (see PGSS 2011).

The species occurs in several levels of the section, from PT-2 to PT-10a, and poorly preserved cf.-specimens in level PT-1 (Fig. 12A). In this range, it shows a wide intraspecific variation through the four main morphotypes A-D described from the type material of Picún Leufú (see PGSS 2011). These morphotypes show an apparent trend to segregation in different levels, but the available material is not enough for statistical evaluation.

The specimen in Fig. 17B from level PT-10a is a well preserved, adult [M] which matches the specimen from the *picunleufuense* beta Hz. of P. Leufú (PGSS 2011: fig. 21A) with very fine and prosocline ribbing in the phragmocone, passing shortly to much more widely spaced and stronger primaries on the bodychamber. This morphotype associated (in the same concretion) with *L. picunleufuense* transient beta (Fig. 11) allows to recognize the *picunleufuense* beta Hz., level PT-10a in the present section.

The fragmentary but conspicuous specimen in Fig. 28A from level PT-12 (Zitteli ["Mendozanus"] Z.) could be assigned to *Choicensisphinctes* for the blade-like primary ribs from the lower flank, trifurcate with polyschizotomics. This ribbing style differentiates *Choicensisphinctes* from *Lithacoceras* and *Catutosphinctes*. Identical fragmentary ammonites have been also recorded in other localities in similar (A. Cieneguita) or lower (Cerro Lotena) stratigraphic position. These specimens could be assigned to *C. platyconus* morph A, in comparison with the specimen form Picún Leufú figured in PGSS (2011: fig. 17A). These specimens suggest that the successive species of the genus would have developed rare extreme variants from the Picunleufuense Z. up to, at least, the Zitteli ["Mendozanus"] Z.

#### Choicensisphinctes cf./aff. platyconus Parent, Garrido, Schweigert & Scherzinger, 2011 Figs. 17A, 18-20

- 2003a Choicensisphinctes choicensis Burckhardt Parent: 154, fig. 8.
- 2011 Choicensisphinctes cf./aff. platyconus n. sp. PGSS: 30, fig. 23B-E.
- ?2011 Choicensisphinctes cf./aff. platyconus Parent et al. PSS: 29, fig. 6C-E.
- ?2013a Choicensisphinctes cf./aff. platyconus Parent et al. PGSS: 11, figs. 5D, 6, 7A-D.



**Figure 16.** *Choicensisphinctes platyconus* Parent, Garrido, Schweigert & Scherzinger, adult [M] with beginning of the bodychamber (MOZ-PI 7931), level PT-8, Picunleufuense Z. – The asterisk indicates the last septum. Natural size (x1).

**Material.-** 4 well preserved [M] from level PT-6; 2 well preserved [M] from level PT-8.

**Description.-** Adult macroconchs. Platyconic to serpenticonic, widely umbilicate, whorl section suboval to rounded subrectangular. Ribbing dense, bi- or trifurcate throughout the phragmocone, becoming stronger and more widely spaced on the end of the phragmocone and the beginning of the bodychamber. Primaries divide in sheaves of several secondaries, which gradually disconnect from the primaries becoming intercalatories towards peristome.

**Remarks.-** The present specimens are very similar in shellshape and style of ribbing to the specimens listed in the synonymy. All of these specimens listed occur in the upper Picunleufuense Z. of Portada Covunco (PGSS 2013a), Casa Pincheira (Parent 2003a), and A. Cieneguita (PSS 2011), but the new material comes from a lower stratigraphic position, below the *picunleufuense* beta Hz. This species is assigned to *Choicensisphinctes* in terms of the sculpture ontogeny, which clearly corresponds to the diagnosis of the genus (Leanza 1980; see discussion in PGSS 2011) and compares closely with *C. platyconus. Choicensisphinctes* is a genus characterized by platyconic to suboxyconic macroconchs, so that in this sense *C.* cf./aff. *platyconus* is the most evolute (or widely umbilicated) species, ranging its *U/D* from 0.40 to 0.50 through D = 50-200mm (juvenile to adult).



Figure 17. A: Choicensisphinctes cf./aff. platyconus Parent, Garrido, Schweigert & Scherzinger, portion of bodychamber (somewhat crushed) of a [M] (MOZ-PI 7911) showing the characteristic structure of the ribbing; level PT-8, Picunleufuense Z. B: Choicensisphinctes platyconus, complete adult [M] (unnumbered), level PT-10a. – The asterisk indicates the last septum. All natural size (x1).

PGSS (2013a) have noted the high resemblance of the material from Portada Covunco with the lectotype of *Virgatosphinctes multifasciatus* Uhlig (1910: pl. 60: 1) from the Tithonian of Jandu, India. This specimen can be clearly assigned to the genus *Malagasites* Enay, 2009 (Type species: *Perisphinctes haydeni* Uhlig, 1910). Interestingly, the specimen of Fig. 18A is identical in every detail of size, shell-shape and sculpture with the Indian specimen. Furthermore, the corresponding microconch of *M. multifasciatus* among the material illustrated by Uhlig could likely be the specimen

shown in the same plate (Uhlig 1910: pl. 60: 2). This latter specimen, although very incomplete, can be closely compared with microconchs of *Choicensisphinctes*, like the lectotype of *Choicensisphinctes mendozanus* figured by Burckhardt (1900: pl. 25: 7).

This high level of similarity could be enough for discarding the possibility of homoeomorphism between the Andean and Indian specimens. If these forms were closely related genetically, it could be expected that the local populations would have been in contact through the Mozambique Corridor,



**Figure 18.** *Choicensisphinctes* cf./aff. *platyconus* Parent, Garrido, Schweigert & Scherzinger, level PT-6, *picunleufuense* alpha Hz., Picunleufuense Z. A: Nearly complete adult [M] (MOZ-PI 7935);  $\mathbf{A}_i$ : inner and innermost whorls (x2) visible from the right side view (frontal apertural position). B: Adult [M] phragmocone (MOZ-PI 7907). – The asterisk indicates the last septum. All natural size (x1).



Figure 19. Choicensisphinctes cf./aff. platyconus Parent, Garrido, Schweigert & Scherzinger, level PT-6, picunleufuense alpha Hz., Picunleufuense Z. A: Complete adult [M] (MOZ-PI 7885). B: Nearly complete adult [M] (MOZ-PI 7887). – The asterisk indicates the last septum. All natural size (x1).

and thus they should be recorded in intermediate palaeogeographic positions. Evidence for this latter condition could be the very similar, although fragmentary specimen figured from the Tithonian of Antarctica by Thomson (1979: pl. 5: fig. e), indistinguishable from the present form, especially from the specimens of Portada Covunco (PGSS 2013a). These relationships would concur with the hypothesis of Enay & Cariou (1997: 5) about a possible derivation of *Virgatosphinctes* Uhlig, 1910 (as well as *Malagasites*) from *Choicensisphinctes*.

**Occurrence.-** Levels PT-6 and PT-8, lower Picunleufuense Z. The material from Portada Covunco, Casa Pincheira, and Arroyo Cieneguita occurs in a somewhat higher stratigraphic position, between the *picunleufuense* beta and *malarguense* horizons (middle to upper Picunleufuense Z.).

## Choicensisphinctes cf. burckhardti (Douvillé, 1910) Fig. 21

**Material**.- 1 well-preserved, complete adult [M] phragmocone (MOZ-PI 7933), PT-8; 1 well-preserved phragmocone (MOZ-PI 7555), PT-10b; 1 fragmentary [m?] phragmocone (MOZ-PI 8455), PT-12-14 (loose).

**Description.**- Phragmocone platyconic, involute with moderately narrow umbilicus tending to enlarge through ontogeny. Whorl section compressed subrectangular to suboval, with high flanks and narrow, rounded venter. Ribbing dense and fine, composed by fine prosocline primaries, which divide in three to six secondaries around the mid-flank. Two weak and narrow, but conspicuous constrictions per whorl, followed by a polyschizotomic rib. Intercalatory ribs are not clearly developed. Seconday ribs cross the venter unchanged and evenly spaced.

The largest specimen (Fig. 21B) shows the last preserved whorl incipiently uncoiled, with primary ribs more widely spaced and coarser. The smallest specimen (Fig. 21C) seems to be a microconch comparable with that of *C. platyconus*.



Figure 20. Choicensisphinctes cf./aff. platyconus Parent, Garrido, Schweigert & Scherzinger, level PT-8, Picunleufuense Z. Adult [M] phragmocone with beginning of the bodychamber (MOZ-PI 7909). – The asterisk indicates the last septum. Natural size (x1).

**Remarks.-** The present specimens have similar ribbing ontogeny and involution with the holotype of *C. burckhardti* (see revision in PGSS 2011). The whorl section of the holotype (Burckhardt 1903: pl. 6: 4) is more inflate, but considering the wide variation in whorl section and involution observed frequently in the species of *Choicensisphinctes*, this difference could represent merely intraspecific variation.

**Occurrence and distribution.**- The specimens come from levels PT-8 and PT-10b, one loose from PT-12-14. The stratigraphic position of the holotype is in the *malarguense* Hz. (PGSS 2011: 95) of Casa Pincheira, between the *picunleufuense* beta Hz. and the *perlaevis* Hz. (Zitteli ["Mendozanus"]Z.), apparently equivalent to level PT-10b.

## Choicensisphinctes erinoides (Burckhardt, 1903) Figs. 22-27, 28B, 29A

- \* 1900 *Perisphinctes* aff. *erinus* d'Orbigny. –Burckhardt: 42, pls. 25: 1 [holotype].
- 1900 *Perisphinctes* aff. *lothari* Oppel. Burckhardt: 41, pl. 25: 6-8.
- 1903 *Perisphinctes* cf. *nikitini* Michalski. Burckhardt: 49, pl. 6: 8.

- 1903 *Virgatites scythicus* Vischniakoff. Burckhardt: 45, pl. 7: 1-8.
- \* 1903 *Perisphinctes erinoides* n. sp. Burckhardt: 51, pl. 8: 1-3 [holotype].
- 1903 Perisphinctes aff. erinus d'Orbigny. Burckhardt: 52, pl. 9: 1-2.
- 1911 Virgatites mendozanus n. sp. Burckhardt: 482.
- 1930 Craspedites limits nov. nom. Burckhardt: 110.
- 1931 *Virgatosphinctes andesensis* (R. Douvillé). Weaver: 422, pl. 47: 313-314, pl. 48: 318-320.
- 1959 Virgatosphinctes lenaensis n. sp. Corvalán: 22, pl. 4: 14-15.
- 1959 *Perisphinctes* aff. *erinus* D'Orbigny. Corvalán: 26, pl. 3: 12.
- ?1959 Virgatosphinctes andesensis (Douvillé). Corvalán: 23, pl. 5:19.
- ?1979 *Virgatosphinctes mendozanus.* Leanza & Leanza: 24-25, pl. 4: 2.
- ?1979 Virgatosphinctes sp. Blasco et al.: 287, pl. 1: 5-6.
- 1980 *Choicensisphinctes erinoides* (Burckhardt). Leanza: 34, pl. 4: 1.
- 1980 Choicensisphinctes limits (Burckhardt). Leanza: 33.
- 1992 *Pseudinvoluticeras douvillei* Spath. Westermann: pl. 80: 1.



**Figure 21**. *Choicensisphinctes* cf. *burchhardti* (Douvillé). A: phragmocone (MOZ-PI 7912), level PT-8, Picunleufuense Z. B: complete? adult [M] phrgmocone (MOZ-PI 7555), level PT-10b, lower Zitteli ["Mendozanus"] Z. C: fragmentary [m?] (MOZ-PI 8455), level PT-12, Zitteli ["Mendozanus"] Z. - All natural size (x1).

- 2011 *Choicensisphinctes erinoides* (Burckhardt). PGSS: 75, fig. 22B.
- 2011 Choicensisphinctes cf. mendozanus (Burckhardt). PGSS: 77, fig. 24.
- 2011 *Choicensisphinctes* cf. *erinoides* (Burckhardt). PSS: 33, figs. 9, 10A.
- 2011 Choicensisphinctes cf. limits (Burckhardt). PSS: 33, figs. 10B-C, 11-12, 13A.
- 2013a *Choicensisphinctes* cf. *erinoides* (Burckhardt). Parent et al.: 16, fig. 9A, App. 1.
- 2013a *Choicensisphinctes* cf. *limits* (Burckhardt). Parent et al.: 33, fig. 9B.
- 2013 *Choicensisphinctes choicensis* (Burckhardt). Kietzmann & Vennari: fig. 9a.
- 2013 *Choicensisphinctes erinoides* (Burckhardt). Kietzmann & Vennari: fig. 9b.
- 2015 *Virgatosphinctes scythicus* (Vischniakoff). Salazar & Stinnesbeck: 5, fig. 4C-E, fig. 6A-C.
- 2015 *Lithacoceras malarguense* (Spath). Salazar & Stinnesbeck: 11, fig. 8, fig. 9D.

**Material.**- Abundant material (phragmocones, and adult macro- and microconchs) from levels PT-10c, 12 and 14.

**Remarks.**- The species has been described and figured in detail by Burckhardt (1900, 1903), Leanza (1980), and more recently by PGSS (2011, 2013a) and PSS (2011). The [M] is mainly known from phragmocones; the bodychamber is known partially in some few specimens; the [m] is better known from adult specimens with lappets (see references in the synonymy above).

The present specimens are entirely comparable with those from equivalent biostratigraphic horizons in Arroyo Cieneguita, including macroconchs, which intergrade from evolute (Figs. 22-23, 25A-B) to involute (Figs. 24, 26A, 28) but with identical inner whorls and sculpture ontogeny up to, at least, the beginning of the adult bodychamber. These two morphotypes have been described from samples of Arroyo Cieneguita as C. cf. erinoides and C. cf. limits. Nevertheless, the new material makes clear that the extremes of the spectrum of variation can be matched with the holotype of C. erinoides (evolute) and the holotype of C. limits (involute). The large [M] phragmocone with beginning of its bodychamber from level PT-14 (Fig. 27D, 28) perfectly matches the holotype of C. *limits*, and its inner whorls show an abrupt variocostation from about D = 80-90 mm in the same form that the holotype of C. erinoides (see Burckhardt, 1900: pl. 25: 1). The adult [M] specimen in Fig. 22 (level PT-10c) is closely comparable with



**Figure 22.** *Choicensisphinctes erinoides* (Burckhardt, 1903) [M] morph erinoides, adult phragmocone (MOZ-PI 7945), level PT-10c, lower Zitteli ["Mendozanus"] Z. **A**<sub>2</sub>: whorl section at about the maximum size. – Natural size (x1).



**Figure 23.** Choicensisphinctes erinoides (Burckhardt, 1903) [M] morph erinoides, complete adult (MOZ-PI 7950), level PT-10c, lower Zitteli ["Mendozanus"] Z. – The asterisk indicates the last septum. Natural size (x1).



Figure 24. Choicensisphinctes erinoides (Burckhardt, 1903) [M] morph limits, nearly complete adult phragmocone (MOZ-PI 7945), level PT-10c, lower Zitteli ["Mendozanus"] Z. – Natural size (x1).

the holotype of *C. erinoides* at comparable size (adult phragmocone), showing the adult aspect of an evolute morphotype of the species, with the adult phragmocone heavily ribbed periumbilically. The complete [M] in Fig. 23 is a rather small adult showing the bodychamber is smooth following the heavily ribbed adult phragmocone. The involute and evolute macroconch variants have been recorded from levels PT-10c-14 within the Zitteli ["Mendozanus"] Zone.

The corresponding microconch of the species is represented by *C. mendozanus* (Burckhardt, 1911). The sexual dimorphic correspondence is well represented by the identity between the lectotype (an almost complete microconch) of *C. mendozanus* (Burckhardt 1900: pl. 25: 7) and the inner whorls of the larger macroconch of *C. erinoides* figured in PSS (2011: fig. 10A) as *C.* cf. *erinoides*. Two additional adult microconchs from level PT-12 are shown in Figs. 27C and 29A.

The new material from the studied section confirms that *C. erinoides* and *C. limits* differ only in the degree of involution associated with a somewhat higher density of ribbing in the involute specimens. The sculpture ontogeny is the same in all the specimens, described as three morpho-sculptural stages in PSS (2011: 33): *perisphinctoid, mendozanus* and *bullate* stages. The whorl section is suboval in the inner whorls and suboval to subtrapezoidal, even suboxyconic, in the adult phragmocone and beginning of the bodychamber. Thus, *C.* 

*erinoides* and *C. limits* must be considered synonyms as they merely represent intraspecific variants of a single species. Unfortunately, as pointed out above, *C. choicensis* cannot be compared, since it consists of only the inner whorls of a probable macroconch.

For denoting the main morphological aspect of the macroconch specimens at hand, the different morphotypes could be labelled as *C. erinoides* morph erinoides and *C. erinoides* morph limits.

**Occurrence and distribution.**- Levels PT-10c to PT-14 associated with *Pseudolissoceras zitteli* among other species (see Fig. 5), indicating the Zitteli ["Mendozanus"] Zone. The specimens figured by Kietzmann & Vennari (2013) are said to occur in the Zitteli ["Mendozanus"] Z., what could be correct considering the already well established stratigraphic position of the species based on figured material (Parent 2003a, PSS 2011, PGSS 2011 and PGSS 2013a).

*C. erinoides* is distributed all throughout the Neuquén Basin, from the region of Río Leñas in Central Chile (Corvalán 1959) and Baños del Flaco (Salazar & Stinnesbeck 2015, see synonymy) to the southernmost localities in southern Neuquén Province (e.g. Picún Leufú). It probably also occurs in the Austral Basin (Blasco et al. 1979, Kraemer & Riccardi 1997). Some forms of *Choicensisphinctes* (usually assigned to



**Figure 25.** *Choicensisphinctes erinoides* (Burckhardt, 1903) [M], level PT-12, *erinoides* Hz., Zitteli ["Mendozanus"] Z. Evolute variant. A: Small adult [M] with beginning of bodychamber (MOZ-PI 8449), morph erinoides. B: Adult [M] phragmocone (MOZ-PI 7961), morph erinoides. C: inner whorls (MOZ-PI 8443) showing sculptural details from D=30 to D=70 mm. – The asterisk indicates the last septum. All natural size (x1).

*Virgatosphinctes*) from Antarctica could belong to the present species (e.g. Howlett 1989: pl. 3: 2-3). In Perú are known some specimens which could belong to the present species (Welter 1913, Knetchel et al. 1947: pl. 13: 1-6, pl. 14: 1-3).

## Choicensisphinctes sp. A (in PSS 2011) Fig. 29B

Material.- A well preserved phragmocone (MOZ-PI 7568), PT-19.

**Remarks.-** The present specimen is characterized by being moderately evolute with suboval whorl section and sharp, dense ribbing. Virtually identical specimens from very similar stratigraphic position have been collected in Arroyo Cieneguita (PSS 2011: fig. 13B) and, especially, in Cerro Lotena (still



Figure 26. Choicensisphinctes erinoides (Burckhardt, 1903) [M] morph limits, level PT-12, erinoides Hz., Zitteli ["Mendozanus"] Z. Involute variant. A: Complete? adult [M] phragmocone (MOZ-PI 7947) lateral view; ventral view in Fig. 27A. B: inner whorls (MOZ-PI 7954);  $B_2$ : innermost whorls (x2). – All natural size (x1), except  $B_2$ . The bar represents 10 mm for A,  $B_1$ , and  $B_3$ , but 20 mm for  $B_2$ .

unpublished). The specimen from A. Cieneguita is a complete adult [m] identical to the present specimen at comparable diameter. These specimens belong to an undescribed species of the Proximus Z.

## Choicensisphinctes striolatus (Steuer, 1897) Figs. 29C-D, 30-32

Synonymy.- See Parent (2003a).

Material.- Three adult [M] with incomplete bodychamber from levels PT-40 (MOZ-PI 8917), PT-51 (MOZ-PI 8130) and

PT-52 (MOZ-PI 8131/1). Two cf.-specimens, phragmocones (MOZ-PI 7573, 7575), from levels PT-32-38.

**Description**.- Inner whorls moderately compressed, platyconic, finely and densely ribbed. Adult phragmocone and first half whorl of bodychamber stouter and evolute, with subrectangular to suboval whorl section. Ribbing composed of densely spaced sharp primaries, which bifurcate on the upper half of the flanks; ventral ribbing strong crossing the venter unchanged.

Remarks.- The lectotype of the species (Steuer 1897: pl. 14: 8-



**Figure 27.** *Choicensisphinctes erinoides* (Burckhardt, 1903) [M], Zitteli ["Mendozanus"] Z. A: Adult [M] phragmocone (MOZ-PI 7947), level PT-12, *erinoides* Hz., ventral view; lateral view in Fig. 26A. **B**: Beginning of bodychamber of a junvenil [M] (MOZ-PI 7952), level PT-12, *erinoides* Hz. **C**: Adult [m] with beginning of bodychamber (MOZ-PI 7967), level PT-12, *erinoides* Hz. **D**: Adult [M] phragmocone (MOZ-PI 6656), level PT-14, ventral view; the lateral view in Fig. 28B. – All natural size (x1). The asterisk indicates the last septum.



**Figure 28.** A: *Choicensisphinctes* cf. *platyconus*, fragmentary bodychamber (MOZ-PI 7961), level PT-12, *erinoides* Hz, Zitteli ["Mendozanus"] Z. **B**: *Choicensisphinctes erinoides* (Burckhardt, 1903) [M] morph limits, level PT-14, Zitteli ["Mendozanus"] Z., adult phragmocone (MOZ-PI 6656), lateral view; ventral view in Fig. 27D. – All natural size (x1).



**Figure 29.** A: *Choicensisphinctes erinoides* (Burckhardt, 1903) [M], nearly complete adult [m] (MOZ-PI 8453), level PT-12, *erinoides* Hz., Zitteli ["Mendozanus"] Z.. B: *Choicensisphinctes* sp. A (in PSS 2011), phragmocone (MOZ-PI 7568), level PT-19, *internispinosum* alpha Hz. (new), Internispinosum Z. C-D: *Choicensisphinctes* cf. *striolatus* (Steuer), phragmocones (MOZ-PI 7573 and 7575), loose from levels PT-32-38, Alternans Z. – All natural size (x1). The asterisk indicates the last septum.

9; refigured in Parent 2003a: fig. 9A-B) is a small phragmocone, as well as the more finely ribbed variant *Reineckeia striolatissima* (Steuer 1897: pl. 14: 5-6; refigured in Parent 2003a: fig. 9C-D) and the material described by Leanza (1945: pl. 2: 2, 5, 7-9 12-13) and PSS (2011: fig. 14A-D; not fig. 11). Thus, attribution of our large macroconchs with part of bodychamber (Figs. 30-32) to the present species is based on the identity of the inner whorls, whereas the adult whorls preserve the shell-shape and style of ribbing. Furthermore, all these specimens occur in a stratigraphic position comparable to that indicated by Leanza (1945) and PSS (2011) in the Alternans-lower Koeneni zones, where no other similar ammonites are known.

Two cf.-specimens shown in Fig. 29C-D were found loose in the field, coming from the interval of levels PT-32-38 (lower part of the Alternans Z.). The specimen in Fig. 29D is almost identical to specimens from the Alternans Z. of Arroyo del Yeso (Leanza 1945: pl. 2: 2, 12, 7, 9) and Casa Pincheira (Parent 2003a: fig. 11). All these specimens are compressed and finely ribbed with marked prosocline constrictions, resembling the much older specimen described below under *Choicensisphinctes*? n. sp. A. The specimen in Fig. 29C is more inflated, somewhat similar to *Choicensisphinctes* sp. A (Fig. 29B) but with stronger primary ribs. These intermediate forms give strong support to the assignation of *Reineckeia striolata* to *Choicensisphinctes* as proposed in PSS (2011) on the basis of shell morphology, sculpture and form of the sexual dimorphism.

**Occurrence and distribution**.- Levels PT-40 (Alternans Z.) and PT-50-51 (basal levels of the Koeneni Z.). In Arroyo del Yeso Leanza (1945) has recorded the occurrence in a similar range; in Arroyo Cieneguita the species is mostly restricted to the *striolatus* Hz. at the base of the Koeneni Z. From a well age-controlled succession in Arroyo Durazno, Gerth (1925b: 125-126) has recorded *C. striolatus* (as *Substeueroceras steueri* 



Figure 30. Choicensisphinctes striolatus (Steuer), nearly complete adult [M] (MOZ-PI 8917), level PT-40, azulense Hz. (new), Alternans Z. A<sub>3</sub>: ventral view of the phragmocone (x1). – Natural size (x1). The asterisk indicates the last septum.

Gerth, 1925; see discussion in PSS 2011) associated with the first local occurrence of *S. koeneni* in the level overlying an Alternans Z. assemblage, which match the type assemblage of the *bardense* Hz. (PSS 2011: 84). Gerth (1925b: 87) considered *Steueroceras steueri* as a geographic variant of *Steueroceras striolatissimum* (= *Choicensisphinctes striolatus*), which occurs in the same stratigrahic horizon in several other localities.

## Choicensisphinctes? n. sp. A Fig. 33A-D

**Material**.- 4 phragmocones from levels PT-1 (MOZ-PI 8439/3), PT-2 (MOZ-PI 6112), PT-4 (MOZ-PI 7867), and PT-6 (MOZ-PI 7899).

**Description**.- Stout serpenticones with subrectangular whorls, slightly wider than high. Finely and densely ribbed by primaries curved forwardly, most bifurcated on the upper third of the flank; ventral ribbing evenly spaced, crossing the venter unchanged; three to five prosocline constrictions per whorl, marked on the flanks and venter. **Remarks.**- The combination of subrectangular whorls covered by fine and dense prosocline ribs curved forwardly with mild constrictions makes this ammonite a conspicuous element among the Lower Tithonian fauna. The genus *Choicensisphinctes* includes some similarly evolute and densely ribbed morphotypes, but the characteristic combination of features of the present species has not been observed in the range of variation of the known species. *Perisphinctes densistriatus* Steuer, 1897 was assigned to *Choicensisphinctes* by Parent (2003a). The holotype is superficially similar to the present specimens, but more rounded in whorl section; the density and strength of ribbing is comparable to the specimen from level PT-6 (Fig. 33A). A closer comparison must await for complete adult specimens.

Present specimens are closely comparable with the inner whorls of the holotype of *Kawhiasphinctes antipodus* Stevens (1997: pls. 29: 1-2, 30: 1) from the lower half of the Puti Siltstone (Middle? Tithonian) of New Zealand. Our incomplete material prevents comparison of the adult whorls what could shed light about possible relationships.

There are other poorly known ammonites, which show similar morphology and ribbing. The holotype of



Figure 31. Choicensisphinctes striolatus (Steuer), nearly complete adult [M] (MOZ-PI 8130), level PT-51, Koeneni Z. – Natural size (x1). The asterisk indicates the last septum.

Virgatosphinctes haughtoni Spath (1931: pl. 77: 6) from the Lower? Tithonian of an undefined locality of Madagascar is very similar. A similar ammonite, which could be significant for time-correlation between the Neuquén Basin and Mexico is the holotype of Perisphinctes aguilari Burckhardt (1906: pl. 27: 6-9). The specimen is poorly preserved, but shows the same fine prosocline ribbing and subrectangular whorls observed in the present species. This specimen of *P. aguilari* was collected from a 1-2 m thick horizon of phosphoritic limestones in the East of Vereda del Quemado, Mazapil, Mexico. From this same horizon Burckhardt (1906: pls. 30: 4, 8, 31: 5-9, 32: 1-2) collected the material described as Virgatites mexicanus and other names, a representative of Lithacoceras closely related with L. picunleufuense (see Parent et al. 2006, PGSS 2011). Below this horizon occur H. cf. hybonotum and H. cf. beckeri figured by Burckhardt (1906: pl. 27: figs. 1, 5 and fig. 3, respectively), indicating time-correlation with the Beckeri and/or Hybonotum zones.

**Occurrence and distribution**.- Most specimens come from levels of the lower part of the Picunleufuense Z. (PT-2, 4, 6); a poorly preserved one from a the level PT-1, below the *picunleufuense* alpha Hz., probably uppermost Kimmeridgian.

This specimen from level PT-1, associated with  $\hat{C}$ . cf. *platyconus* (Fig. 12A) and another poorly preserved ammonite, which could not be identified yet, are the first ammonite records in the Neuquén Basin below the *picunleufuense* alpha Hz.

# Genus *Krantziceras* Parent, Scherzinger & Schweigert, 2011

Type species: *Krantziceras compressum* Parent, Scherzinger & Schweigert, 2011; by original designation.

**Remarks.-** The genus was defined from ammonites of the Noduliferum Z. but the material described below extends its stratigraphic range downwards, into the lower Internispinosum Z. Furthermore, *Krantziceras*? n. sp. A could indicate a much older origin of the genus, in the Picunleufuense Z.

#### Krantziceras? n. sp. A Fig. 33E-F

**Material**.- 2 phragmocones: MOZ-PI 7862 from level PT-2 and MOZ-PI 7866 from level PT-4.

**Description**.- The larger specimen (maximum D = 130 mm) is an adult phragmocone possibly complete, showing incipient uncoiling. Compressed, evolute and widely umbilicate (W/D =0.18, U/D = 0.50 at D = 130 mm); whorl section subrectangular higher than wide ( $W/H_1$  c. 0.72), with flat flanks and wellrounded venter.

In the inner whorls the ribbing is rather dense (P = 21-26 for D = 25-80 mm); primary ribs sharp, prosocline, bifurcated on the upper third of the flanks after a slight swelling. In the outermost whorl the ribbing is composed by prosocline to concave primaries (P = 35 at D = 130 mm), bifurcating

regularly in narrowly splayed secondaries which cross the venter evenly spaced and unchanged. There are narrow constrictions well marked on flanks and venter, preceded by a polyfurcate primary rib. After the constrictions, the point of furcation is situated on the mid-flank and gradually moves up to the upper third of the flank.

**Remarks.-** Doubts about the assignation of this species to *Krantziceras* come from the form of the constrictions and the gently projected secondary ribbing, which differ from remaining species of the genus.

**Occurrence**.- Levels PT-2 and PT-4, *picunleufuense* alpha Hz., Picunleufuense Z.

## Krantziceras cf. disputabile (Leanza, 1945) Fig. 34B

**Remarks.**- 1 well-preserved phragmocone (MOZ-PI 8468) from level PT-22 (Internispinosum Z.). The specimen is a phragmocone with an injury on the end of the last whorl. Behind the injury, the shell is platyconic with flat flanks and venter; densely ribbed by prosocline primaries of which most bifurcate on the upper flank; ventral ribbing interrupted by a well-marked smooth groove. It closely resembles the inner whorls of the lectotype of *K. disputabile* (Leanza 1945: pl. 9) in lateral view, but the venter cannot be compared. On the other hand, the lectotype comes from a stratigraphically higher horizon in the Koeneni Z.

#### Krantziceras azulense (Leanza, 1945) Fig. 34A

**Material.**- 1 well-preserved, almost complete adult [M] (MOZ-PI 8493) from level PT-40.

**Description**.- Platycone, moderately evolute and widely umbilicate (U/D = 0.44-0.48), with subrectangular-suboval whorl section ( $W/H_1$  c. 1). Ribbing of inner whorls sharp and dense (P=25 at D=45-55 mm), slightly prosocline. On the last whorl of phragmocone and bodychamber the primaries are stiff, subradial, densely spaced (P=34-37 at D=120-135 mm); most of them bifurcate in narrowly splayed secondaries on the upper half of the flanks; there are some few undivided primaries. Ventral ribbing evenly spaced, irregularly interrupted on mid-venter by a narrow groove. The phragmocone ends at about  $D_{\rm is}=135$  mm.

The bodychamber is poorly preserved, possibly  $L_{\rm BC}$  about 270° at an estimated  $D_{\rm p}$  about 230 mm. Ribbing is unchanged respect to the phragmocone but with several undivided primaries.

**Remarks.**- Our specimen is almost identical at comparable diameter (phragmocone) to the holotype of *Aulacosphinctes azulensis* figured by Leanza (1945: pl. 1: 6-7) from his bed d of Arroyo del Yeso (Fig. 1A). *A. azulensis* was considered as belonging to *Catutosphinctes* by PGSS (2011) but the new material allows to include the species in *Krantziceras* because of the subradial, stiff ribs, some undivided and the secondaries very narrowly splayed. The phragmocone of the present specimen is also very similar in shell-shape and sculpture to the holotype of *Aulacosphinctes wanneri* Krantz, 1926 (refigured in PSS 2011: fig. 14I), but it has more irregular ribbing and the secondaries gently projected forwardly. Although the significance of these differences cannot be definitely evaluated from the scarce material available, the holotypes of *A*.



Figure 32. *Choicensisphinctes striolatus* (Steuer), adult [M] phragmocone (MOZ-PI 8131/1), level PT-52, Koeneni Z. – Natural size (x1).

*azulensis* and *A. wanneri* come from very similar stratigraphic positions within the Alternans Z. suggesting they are closely related.

**Occurrence and distribution**.- Level PT-40, *azulense* Hz. (new), Alternans Z. In Arroyo del Yeso the holotype was collected from the bed d (in Leanza 1945: 89) associated with densely ribbed, inflated phragmocones of *C. striolatus* closely comparable with the phragmocone of the older of our specimens (Fig. 30) from level PT-40.

Krantziceras compressum Parent, Scherzinger & Schweigert, 2011 Figs. 35-36

**Material**.- 47 well-preserved specimens from level PT-60; 2 from level PT-61.

**Remarks.-** The specimens from level PT-60 perfectly match the holotype. The specimen in Fig. 35A is a complete adult [M] with bodychamber, uncoiled and irregularly ribbed by an increasing number of undivided and progressively crowded primaries towards the peristome ( $D_p = 195$  mm). The bodychamber is longer than three quarters of whorl:  $L_{\rm BC} = 320^{\circ}$ . The variability in the present sample is very narrow like in the type series.

In levels PT-56 and PT-58 occur specimens more densely and less evenly ribbed than those of level PT-60. These specimens are indicated as *Krantziceras* cf. *planulatum*


**Figure 33. A-D**: *Choicensisphinctes*? n. sp. A, *picunleufuense* alpha Hz., Picunleufuense Z. A: Phragmocone (MOZ-PI 7899), level PT-6. B: Phragmocone (MOZ-PI 7867), level PT-4. C: Phragmocone with beginning of bodychamber (MOZ-PI 6112), level PT-2; C<sub>3</sub>: whorl section (bodychamber grey) at maximum size. D: Phragmocone (MOZ-PI 8439/3), level PT-1, Upper Kimmeridgian or lowermost Tithonian. E-F: *Krantziceras*? n. sp. A, *picunleufuense* alpha Hz., Picunleufuense Z. E: Inner whorls (MOZ-PI 7866), level PT-4. F: Adult? phragmocone (MOZ-PI 7862), level PT-2. –All natural size (x1).

(Vennari et al. 2012) in Fig. 5 for they compare closely with K. planulatum, which differs from the typical specimens of K. compressum in being more densely and finely ribbed in the inner whorls, more rounded in whorl section and the ventral groove more persistent (see Vennari et al. 2012: figs. 4-5). The type material of this latter species is indicated to come from a horizon located below the first recorded occurrence of Groebericeras bifrons Leanza in Real de las Coloradas, A. Durazno (Vennari et al. 2012: 101-102), a species frequent in the Noduliferum Z. (Leanza 1945, A.-Urreta & Alvarez 1999, PSS 2011; this report, see below). This stratigraphic succession is the same as recorded in the studied section (Fig. 5). K. planulatum could be considered as an early transient of K. compressum, showing small differences, which should not justify a specific differentiation under the criteria of the present study, but the name is retained herein as a separate chronospecies. The type horizon of K. planulatum (the level

wherefrom the holotype was collected, unfortunately not indicated in Vennari et al. 2012) is considered herein as a valuable bio-horizon (*planulatum* Hz., see below) of the uppermost Koeneni Z., below the *compressum* Hz. which is designated below as the standard base of the Noduliferum standard Zone (see discussion below).

*Krantziceras disputabile* (Leanza, 1945) is very similar to *K. compressum*, but its primary ribs become stronger from the end of the adult phragmocone and all through the bodychamber.

**Occurrence and distribution.**- Levels PT-60-61, basal Noduliferum Z. The level PT-60 (*compressum* Hz.) is the source of abundant and well preserved specimens, including adults with bodychamber. Few specimens from levels PT-56 and PT-58 are compared with *K. planulatum*. The species has been recorded in the type locality (A. Cieneguita, PSS 2011)



**Figure 34. A**: *Krantziceras azulense* (Leanza), nearly comple adult [M] (MOZ-PI 8493), level PT-40, *azulense* Hz. (new), Alternans Z.; A<sub>3</sub>: inner whorls as observed from the left side. **B**: *Krantziceras* cf. *disputabile* (Leanza), phragmocone (MOZ-PI 8468), level PT-22, Internispinosum Z. – All natural size (x1). The asterisk indicates the last septum.



**Figure 35**. *Krantziceras compressum* Parent, Scherzinger & Schweigert, level PT-60, *compressum* Hz., Noduliferum Z. A: Cast of a complete adult [M] (LPB-M 150). B: Inner whorls (MOZ-PI 8497/3);  $B_2$ : innermost whorls (x2). C: Inner whorls (MOZ-PI 8497/2). D: Adult? phragmocone (MOZ-PI 8497/1). – All natural size (x1), except  $B_2(x2)$ . The bar represents 10 mm, except for  $B_2$ . The asterisk indicates the last septum.

and P. Tril (this report). The early transient *K. planulatum* (Vennari et al. 2012) occurs in the *planulatum* Hz. at its type locality in Real de las Coloradas (see discussion below) and level PT-58 of the studied section.

Subfamily Torquatisphinctinae Tavera, 1985 Genus Catutosphinctes Leanza & Zeiss, 1992 Type species: Catutosphinctes rafaeli Leanza & Zeiss, 1992; by original designation

Catutosphinctes guenenakenensis Parent, Garrido, Schweigert & Scherzinger, 2011 Figs. 37, 38A Synonymy.- See PGSS (2011), PSS (2011), and PGSS (2013).

Material.- Several specimens from levels PT-2, 6, 8, and 10b.

**Remarks.-** The species is abundant in the studied section, mainly as phragmocones. The collected specimens match the type material from Picún Leufú.

Some specimens from levels PT-6 and PT-10b (Figs. 37C-D, 38A) have the inner whorls very evolute and coarsely ribbed by acute and widely spaced primary ribs, closely resembling the inner whorls of the holotype of *Catutosphinctes windhauseni* (Weaver, 1931; refigured in PGSS 2011: fig. 25A), by which we have doubts in the assignation (*C. cf. windhauseni* could be adequate also). This later species occurs



**Figure 36**. *Krantziceras compressum* Parent, Scherzinger & Schweigert, level PT-60, *compressum* Hz., Noduliferum Z. A: Adult [M] phragmocone with beginning of bodychamber (MOZ-PI 8134);  $\mathbf{A}_i$ : ventral view of the inner whorls showing the groove at D = 50 mm;  $\mathbf{A}_i$ : innermost whorls (x2);  $\mathbf{A}_i$ : whorl section at D = 66 mm (phragmocone). B: Adult? specimen with part of the bodychamber (MOZ-PI 8140). C: Adult [M] with bodychamber crushed (MOZ-PI 8501). D: Adult [M] with incomplete bodychamber (MOZ-PI 8498). – All natural size (x1), except  $\mathbf{A}_i$  (x2). The bar represents 10 mm, except for  $\mathbf{A}_i$ . The asterisk indicates the last septum.

in Cerro Lotena (type locality) and Cerro Granito in a slightly higher stratigraphic position in the lower Zitteli ["Mendozanus"] Z., but it is not yet clear on which horizons. Anyway, these specimens could be considered intermediate forms between both species.

**Occurrence and distribution.**- The occurrence is limited to the Picunleufuense Z. in the studied section as well as in the remaining localities where it has been recorded.

### Catutosphinctes n. sp. aff. guenenakenensis Parent, Garrido, Schweigert & Scherzinger, 2011 Fig. 38B-E

Material.- 2 well-preserved phragmocones (MOZ-PI 7962-7963), 1 fragmentary [M] phragmocone (MOZ-PI 8442), and a

portion an adult [M] bodychamber (MOZ-PI 7932) from level PT-12; 1 cast of an adult [M] phragmocone with part of the bodychamber (LPB-M 151) from level PT-14.

**Remarks.-** The phragmocone of this species differs from that of *C. guenenakenensis* in the inner whorls, and apparently in the larger adult size of the macroconchs. The inner whorls bear strong constrictions after which the shell enlarges 'segmentally' (sensu Arkell 1957: L313). Besides these differences, whose significance must be evaluated from better preserved material, the species occurs in the Zitteli ["Mendozanus"] Z., above *C. windhauseni.* 

Catutosphinctes proximus (Steuer, 1897) Figs. 39-40, 41A-B



**Figure 37.** *Catutosphinctes guenenakenensis* Parent, Garrido, Schweigert & Scherzinger, Picunleufuense Z. A: Adult [M] phragmocone (MOZ-PI 7552), level PT-2, *picunleufuense* alpha Hz.;  $A_3$ : innermost whorls (x2). B: Adult [M] phragmocone (MOZ-PI 7905), level PT-6, *picunleufuense* alpha Hz.;  $B_1$ : innermost whorls (x2). C: Phragmocone (MOZ-PI 7878), level PT-6, *picunleufuense* alpha Hz.;  $C_2$ : innermost whorls (x2). D: Phragmocone (MOZ-PI 7878), level PT-6, *picunleufuense* alpha Hz.;  $C_4$ : innermost whorls (x2). D: Phragmocone (MOZ-PI 7878), level PT-6, *picunleufuense* alpha Hz.;  $C_4$ : innermost whorls (x2). D: Phragmocone (MOZ-PI 7878), level PT-6, *picunleufuense* alpha Hz.;  $C_4$ : innermost whorls (x2). D: Phragmocone (MOZ-PI 7878), level PT-6, *picunleufuense* alpha Hz.;  $C_4$ : innermost whorls (x2). D: Phragmocone (MOZ-PI 7878), level PT-6, *picunleufuense* alpha Hz.;  $C_4$ : innermost whorls (x2). D: Phragmocone (MOZ-PI 7878), level PT-6, *picunleufuense* alpha Hz.;  $C_4$ : innermost whorls (x2). D: Phragmocone (MOZ-PI 7878), level PT-6, *picunleufuense* alpha Hz.;  $C_4$ : innermost whorls (x2). D: Phragmocone (MOZ-PI 7892), level PT-6, *picunleufuense* alpha Hz. E: Adult [M] with incomplete bodychamber (MOZ-PI 7932), slightly crushed, level PT-8. – Natural size (x1), except A\_3, B\_1 and C\_2 (x2). The bar represents 10 mm for natural size (x1) views. The asterisk indicates the last septum.

Synonymy.- See Leanza (1980) pars, Parent (2003a), and PSS (2011).

**Material.** 1 incomplete specimen from level PT-18 and 19 specimens from level PT-19.

**Remarks.-** The macro- and microconchs of the sample from level PT-19 compares closely in whorl section, involution and sculpture ontogeny with the material from the upper part of the Proximus Z. of Arroyo Cieneguita described in PSS (2011: fig. 18). Two transients have been recognized within the species (Parent 2003a), the older transient alpha and the type transient beta to which would belong the specimens of levels PT-18-19.

It has long been suspected that *Windhauseniceras internispinosum* (Krantz, 1926) originated from late representatives of *C. proximus* (Parent 2001, PSS 2011). Confirmation of this phylogenetic hypothesis was in need of abundant and well preserved material from controlled stratigraphic position. This material with exigent conditions is now available from the samples from level PT-19 that



**Figure 38.** A: *Catutosphinctes guenenakenensis* Parent, Garrido, Schweigert & Scherzinger, phragmocone (MOZ-PI 7944), malarguense Hz., lower Zitteli ["Mendozanus"] Z. **B-E**: *Catutosphinctes* n. sp. aff. guenenakenensis, Zitteli ["Mendozanus"] Z. **B**: Inner whorls (MOZ-PI 7962), level PT-12, *erinoides* Hz.; **B**<sub>3</sub>: innermost whorls (x2). **C**: inner whorls (MOZ-PI 7963), level PT-12, *erinoides* Hz. **D**: Cast of a probably complete adult [M] (LPB-M 151), level PT-14. **E**: Portion of an adult [M] bodychamber (MOZ-PI 8441/1), level PT-12, *erinoides* Hz. – All natural size (x1), except B<sub>3</sub> (x2). The bar represents 10 mm for natural size (x1) views, except for B<sub>3</sub> (5 mm). The asterisk indicates the last septum.

illustrates clearly the morphologic transition between these two species as described below (under *W. internispinosum*).

# Catutosphinctes inflatus (Leanza, 1945) Figs. 41C, 42

**Occurrence and distribution.**- The bulk of material comes from level PT-19, *internispinosum* alpha Hz. (new), lower Internispinosum Z., upper Middle Tithonian. See below comparison and relationships with *W. internispinosum*.

**Material**.- 2 fragmentary specimens from level PT-30, 1 adult [M] phragmocone with beginning of bodychamber from level PT-36, and 2 adult [M] phragmocones with incomplete bodychamber from level PT-38.



**Figure 39**. *Catutosphinctes proximus* (Steuer), from level PT-18, upper Proximus Z. (A) and PT-19, *internispinosum* alpha Hz. (new), lowermost Internispinosum Z. (**B-E**). A: Phragmocone (MOZ-PI 7565). **B**: Adult [M] with fragmentary bodychamber (MOZ-PI 8017). **C**: Inner whorls (MOZ-PI 8015); **C**; innermost whorls (x2). **D**: Juvenil? [M] phragmocone with beginning of bodychamber (MOZ-PI 8004). **E**: Adult [M] phragmocone (MOZ-PI 8010). All natural size (x1), except  $C_3(x2)$ . The bar represents 10 mm for natural size (x1) views. The asterisk indicates the last septum.



**Figure 40**. *Catutosphinctes proximus* (Steuer), level PT-19, *internispinosum* alpha Hz. (new), lowermost Internispinosum Z. A: Nearly complete juvenile [M] (MOZ-PI 8040); A<sub>3</sub>: ventral view of the inner whorls. B: Phragmocone (MOZ-PI 8048); B<sub>3</sub>: innermost whorls (x2). C: Juvenile [M] (MOZ-PI 8035/1); C<sub>3</sub>: innermost whorls (x2). D: Adult [M] phragmocone (MOZ-PI 8035/2); shell laterally assymetric with the right side (D<sub>3</sub>) typical of the transient of the species, and left side (D<sub>1</sub>) more finely and densely ribbed. –All natural size (x1), except B<sub>3</sub> and C<sub>3</sub>(x2). The asterisk indicates the last septum.



**Figure 41. A-B**: *Catutosphinctes proximus* (Steuer), level PT-19, *internispinosum* alpha Hz. (new), lowermost Internispinosum Z. **A**: Nearly complete subadult [M] (MOZ-PI 8461); **A**<sub>3</sub>: innermost whorls (x2). **B**: Adult [m?] with almost complete bodychamber (MOZ-PI 8037). **C**: *Catutosphinctes inflatus* (Leanza, 1945), adult? [M] with beginning of bodychamber (MOZ-PI 8081), level PT-36, *vetustum* Hz., Alternans Z. – All natural size (x1), except A<sub>3</sub> (x2). The bar indicates 10 mm, except for A<sub>3</sub> (5 mm). The asterisk indicates the last septum.



**Figure 42**. *Catutosphinctes inflatus* (Leanza, 1945), level PT-38, Alternans Z. A: Adult [M] phragmocone with beginning of bodychamber (MOZ-PI 7578); ventral views showing the weakening of the ventral groove from the end of phragmocone ( $A_1$ ) through the beginning of the bodychamber ( $A_2$ );  $A_4$ : ventral view of the inner whorls;  $A_5$ : innermost whorls (x2); note in A, the ventral spines broken off (arrows). B: Nearly complete adult [M] (MOZ-PI 8110), last portion belongs to the bodychamber;  $B_2$ : innermost whorls (x2). –All natural size (x1), except  $A_5$ ,  $B_2$ (x2). The asterisk indicates the last septum.

**Remarks.-** The species, typical of the Alternans Z., was described in detail in PSS (2011). The lowermost record in the studied section is by poorly preserved specimens from level PT-30. The specimen from the level PT-36 (Fig. 41C) is closely comparable with the macroconch of Arroyo Cieneguita (PSS 2011:fig.21A), occurring in the same horizon, the *vetustum* Hz.

The specimens from level PT-38 (Fig. 42A-B) are also very similar but with less inflated whorls. Fig. 42A<sub>3</sub> shows the basis of two ventral spines broken off. This tendency to form ventral spines is similarly manisfested in *Windhauseniceras internispinosum* proposed to be originated in late *C. proximus* (see discussion below).

The rather wide interval in the present section where the species is recorded, from level PT-30 (upper Internispinosum *Z*.) to PT-38 (Alternans *Z*.), is equivalent to the range of the species in Arroyo Cieneguita.

# Catutosphinctes sp. A

**Remarks.**- Two large incomplete adult [M] bodychambers from level PT-56 indicate the persistence of the genus up to the Koeneni Z. These bodychambers belong to large specimens (D > 230 mm) with suboval to subrectangular whorl section and strong, undivided, subradial widely separated primary ribs. Similar bodychambers are known from large macroconch *Catutosphinctes* of the Proximus, Internispinosum and Alternans zones of Cerro Lotena, as well as fragments from the Alternans Z. of Cañadón de los Alazanes (Parent 2001: fig. 8K-L).

#### Genus Mazatepites Cantú-Chapa, 1967

Type species: *Mazatepites arredondense* Cantú-Chapa, 1967; by monotypy

**Remarks.-** The genus is rather poorly known, especially in regards to its phyletic relationships. Superficial resemblance with some simoceratids was discussed by Scherzinger et al. (2010). Inclusion in the Torquatisphinctinae based on the style of ribbing was discussed in PSS (2011) where an emended diagnosis was proposed.

# Mazatepites arredondense Cantú-Chapa, 1967 Fig. 43

Synonymy.- See PSS (2011).

**Description**.- 1 incomplete, well-preserved microconch (MOZ-PI 7946). Slender, very evolute serpenticone from about 20 mm in diameter, with whorl section suboval passing to compressed subrectangular in the bodychamber ( $W/H_1 = 0.64$  behind the peristome). Inner whorls with strong, radial undivided ribs. On the last whorl of the phragmocone the primaries are blade-like and more widely spaced, each one forming a clavus on the ventro-lateral shoulder. The clavi remain exposed in the umbilical window, in contact with the umbilical seam of the bodychamber. Sculpture of the bodychamber composed by slightly prosocline, strong undivided primaries which cross the venter unchanged or little weakened; there is a constriction well marked on flanks and venter, followed by a flared rib.

The specimen is an adult [m] with complete bodychamber  $(L_{BC} = 140^{\circ})$  ending in a peristome  $(D_{p} \text{ estimated 65 mm})$  composed by a pair of short lappets and a ventral horn.

Remarks.- The species is well represented in the Proximus Z.



**Figure 43.** *Mazatepites arredondense* Cantú-Chapa, adult [m] (MOZ-PI 7946), loose from levels PT-11-12, Zitteli ["Mendozanus"] Z.;  $A_1$ - $A_2$ : ventral views in two positions (x1);  $A_3$ : lateral view (x1);  $A_4$ : detail of the sculpture of the last whorl of the phragmocone (x2). – The bar indicates 10 mm for natural size views. The asterisk indicates the last septum.

in Arroyo Cieneguita (PSS 2011) by macroconchs and a probable microconch which is very similar but more inflate than the present specimen.

**Occurrence and distribution.**- The specimen was collected ex-situ from the interval of levels PT-11-12, Zitteli ["Mendozanus"] Z., expanding the range of the genus in the Neuquén Basin.

Subfamily Ataxioceratinae Buckman, 1921 Genus Paraboliceras Uhlig, 1910 Type species: Ammonites jubar Blanford, 1865; subsequent designation of Roman (1938)

# Paraboliceras? sp. A Fig. 44

**Material.-** 1 poorly preserved specimen (MOZ-PI 8471) from level PT-26 (Internispinosum Zone).

**Description.-** The specimen is less than a half whorl representing the end of the phragmocone and beginnig of the bodychamber. Widely umbilicated. Whorl section subrectangular, higher than wide; umbilical wall rather high and vertical, and venter tabulate. Ribbing irregular, with a conspicuous arrangement of groups of two or three primaries of which one or two bifurcate on the umbilical shoulder and once more bi- or trifurcate at mid-flank. These groups of ribs are separated by narrow spaces resembling a shallow constriction, about ten per half whorl, and confined to the flank. The secondary and the scarce intercalatory ribs raise slightly on the ventro-lateral shoulder, then fade off at the sides of a wide smooth ventral band.

**Remarks.-** The ribbing and especially the ventral sculpture suggest the specimen could be assigned to *Paraboliceras*. The best resemblance seems to be with the specimen of *Paraboliceras mutilis* (Oppel, 1865) figured by Westermann (1992: pl. 87: 3) from the Tithonian of Telefomin, Eastern

Indonesia. Other specimens resembling the present one are those from Nepal described by Enay (2009: pl. 15: 2 and pl. 17: 4) as *Paraboliceras cyrtoptichum* (Uhlig, 1910) and *Paraboliceras* n. sp. D, respectively from the *Paraboliceras* beds (upper? Kimmeridgian). There are not many significant differences, but our poor material preserves only a part of the shell and the *Paraboliceras* from Nepal are said to be Kimmeridgian in age, whereas our specimen comes from beds of the upper Middle Tithonian Internispinosum Z.

#### Family Neocomitidae Salfeld, 1921 Subfamily Berriasellinae Spath, 1922

Genus Parodontoceras Spath, 1923a Type species: Hoplites calistoides Behrendsen, 1891; by original designation.

Parodontoceras calistoides (Behrendsen, 1891) Figs. 45-52

**Synonymy.-** See Leanza (1945), Klein (2005) pars, and Aguirre-Urreta & Vennari (2009).

**Material**.- 65 well-preserved specimens from levels PT-32, 35-40, 42.

**Description.-** All the specimens show the characteristic morphology and ornamentation of the species. The innermost whorls (D = 3-6 mm) are globose and involute, with rounded whorls covered by weak ribs on the flanks, and the venter smooth then weakly ribbed.

Macroconchs (Figs. 45A, C-F, 46-51): From about D = 7-8mm up to the end of the adult phragmcone the shell is involute to moderately involute, platyconic with subrectangular, higher than wide whorl section, gently convex to flatten flanks and tabulate venter. Ribbing fine to very fine, dense and flexuous; primaries born on the umbilical wall, cross the shoulder directed backwards, and run the flanks inflected or subfalcate at mid-flank, where most bifurcate. There are intercalatory ribs irregularly distributed. Ventral ribbing is typically interrupted at the sides of a more or less wide smooth band. The adult bodychamber begins between 95 and 185 mm in diameter in different specimens. It is markedly uncoiled, at least three quarters whorl long in the largest and best preserved specimen. The ribbing becomes somewhat coarser and more widely spaced, bifurcation becomes obscure, and towards the peristome, the primaries are wide and simple with coarse growth lines between them.

*Microconch* (Fig. 45B): one specimen which seems adult at much smaller size, slightly uncoiled at the beginning of the bodychamber. The phragmocone is identical to the remaining specimens and the bodychamber is finely and densely ribbed as the phragmocone. No lappets are preserved preventing a definitive dimorphic assignation.

**Remarks.**- As pointed out by Krantz (1928) this species is very variable in rib strength and density. Our material allows to describe the intraspecific variation in terms of changes in the vertical succession of several transients which characterize the species. There are some differences in the mean morphology and sculpture between the level-assemblages PT-32 to PT-42, showing vertical variations (Fig. 52). These variations are observed in the phragmocones, which is the part of the shell more commonly preserved in our samples. Inflation of the shell, measured as the relative whorl width (W/D), is very



**Figure 44**. *Paraboliceras*? sp. A, beginning of bodychamber (MOZ-PI 8471), level PT-26, Internispinosum Z. – Natural size (x1). The asterisk indicates the last septum.

constant throughout the range. The relative umbilical width (U/D) is the most fluctuating feature, contracted in the transient of level PT-40 and suddenly enlarged in level PT-42. The rib density (measured as P) shows a slight trend to increasing density, but with a notorious reduction in the specimens of level PT-42 (Fig. 51) which are the less densely ribbed. Differently, the transient of level PT-40 includes the most extremely dense and finely ribbed specimens which otherwise have typical shell-shape (Fig. 50C). The adult modifications (uncoiling, contraction of the whorls and variocostation) have no influences in the trends because we have considered only a single measurement of each macroconch phragmocones withint 24 < D < 80 mm. Despite our samples are small (n = 2-4) for a statistical evaluation, the correlated changes of U/D and P in levels PT-40 and PT-42 suggest they are characterizing evolutionary changes of the lineage in the recorded interval.

The adult size of the macroconchs also shows variations: in levels PT-32 (Fig. 45C, F) and PT-36 (Fig. 46A) it is estimated in  $D_p = 150-180$  mm, whereas in level PT-40 (Fig. 48) is  $D_p = 280-290$  mm. This difference in diameter is equivalent to an additional whorl in the larger macroconch in respect to the smaller ones from the deeper levels.

Among the studied material, the specimens from level PT-38 are the most similar to the holotype (refigured by Mazenot 1939: pl. 7: 1), especially that in Fig. 47A with an umbilicus relatively wide and the ventral ribbing weakly interrupted on phragmocone and beginning of bodychamber.

The sample from level PT-36, *vetustum* Hz. (Fig. 46) is, significantly, the most similar to the sample from the same horizon in Arroyo Cieneguita. The macroconch figured by PSS (2011: fig. 23A) is identical to that in Fig. 46A with the same adult size, very evolute and with the distinctive inflation of the ventral ribbing before interrupting besides a wide smooth band.

The specimen figured as *P*. cf. *calistoides* (Fig. 53, level PT-35) lies morphologically close to the range observed in *P*. *calistoides* of levels PT-32-36 (see Fig. 52, black circle). The morphology and sculpture of the inner whorls is in fact identical but in the last whorl the primary ribs are coarser and stiffer, bi- or trifurcate, as well as more evolute. It cannot be



**Figure 45**. *Parodontoceras calistoides* (Behrendsen), level PT-32, Alternans Z. A: phragmocone (MOZ-PI 8064); A<sub>3</sub>: ventral view of the innermost whorls (x2). B: ?Adult [m] with complete bodychamber (MOZ-PI 8063). C: Adult [M] phragmocone (MOZ-PI 8061). D: [M] phragmocone with beginning of bodychamber (MOZ-PI 8074). E: Juvenile [M] with part of bodychamber (MOZ-PI 8079). F: Nearly complete adult [M] (MOZ-PI 8058). –All natural size (x1), except A<sub>3</sub>. The bar indicates 10 mm, except for A<sub>3</sub> (5 mm). The asterisk indicates the last septum.



**Figure 46**. *Parodontoceras calistoides* (Behrendsen), level PT-36, *vetustum* Hz., Alternans Z. A: Nearly complete adult [M] (MOZ-PI 8094);  $A_1$ : ventral view of the bodychamber,  $A_3$ : ventral view of the last whorl of phragmocone,  $A_4$ : lateral view of the beginning of the last whorl of phragmocone, bodychamber removed. **B**: Adult [M] phragmocone (MOZ-PI 8478); lateral ( $B_1$ ) and ventral views ( $B_2$ ) of the inner whorls (x2). **C**: Juvenile with beginning of bodychamber (MOZ-PI 8102). **D**: Phragmocone (MOZ-PI 8577). – All natural size (x1), except  $B_1$ - $B_2$  (x2). The bar indicates 10 mm for natural size views (x1). The asterisk indicates the last septum.

discarded the possibility that this specimen represents a variant of the species in this horizon.

**Occurrence and distribution**.-Our material ranges the interval levels PT-32-42, Alternans Z. The species is typical of this zone all throughout the basin (e.g. Gerth 1925, Krantz 1928, Leanza 1945; see PSS 2011: 54-55 for discussion) and occurs also in the lower Koeneni Z. These later records consist of ammonites matching *Thurmannia discoidalis* Gerth (1925b: pl. 5: 3), considered a late transient of *P. calistoides* (PSS 2011).

#### Genus Pseudoparodontoceras nov.

Type species: Pseudoparodontoceras dezai n. gen. et n. sp.

**Etymology**: After the close resemblance of the outer whorls with those of *Parodontoceras calistoides*.

**Diagnosis:** Inner whorls evolute, suboval in whorl section, densely ribbed, bituberculate. Outer whorls *Parodontoceras*-like, compressed subrectangular with ribbing flexuous, bifurcated and ventrally interrupted.

Species included: Currently only the type species.

**Remarks and comparison**: The close resemblance between the outer whorls of the type species with those of *Parodontoceras calistoides* suggest possible relationship. According to R. Enay (pers. comm. 23/09/2014) this group of ammonites could be assigned to the Himalayitidae, but more likely to the Berriasellinae. We concur with the latter suggestion. Indeed, although the similarity of the innermost whorls is usually a more reliable indication of phylogenetic relationships than the outer ones, it must be considered that the berriasellids (in modern conceptions) have developed tubercles at different times in some of their lineages (see



**Figure 47**. *Parodontoceras calistoides* (Behrendsen), level PT-38, Alternans Z. A: Almost complete juvenile [M] (MOZ-PI 8480). B: Phragmocone (MOZ-PI 8485). C: Phragmocone (MOZ-PI 8485). C: Phragmocone (MOZ-PI 8485). C: Phragmocone (MOZ-PI 8486). – All natural size (x1), except  $C_1$  (x2). The bar indicates 10 mm for natural size views (x1). The asterisk indicates the last septum.

Wright et al. 1996). Furthermore, the virtual identity with the outer (adult) whorls of *Parodontoceras* and, partially, *Berriasella*, may be considered a strong additional criterion for an assignation to the Berriasellinae.

However, the himalayitid affinity could be suggested by the bituberculate inner whorls, resembling especially *Dickersonia sabanillensis* Imlay, 1942 from the upper Tithonian of Cuba. Nevertheless, *Pseudoparodontoceras dezai* n. gen. n. sp. is more involute from the inner whorls and the middle and outer whorls are compressed subrectangular with more distant and stronger primary ribs and a wide ventral smooth band. Futhermore, the adult specimens are much larger than those of *D. sabanillensis*.

### Pseudoparodontoceras dezai n. gen. n. sp. Figs. 54-55

**Etymology**: After Mario Alberto Deza (1958-2002), who made important contributions to the geology of N Neuquén.

**Material.**- Holotype (MOZ-PI 8082), nearly complete [M?] from level PT-36 (Fig. 54B). Additional specimens: 1 from level PT-32, 1 from level PT-38, 2 from level PT-40, 2 cf.-specimens from level PT-50. Alternans Zone, Upper Tithonian.

**Type locality and section**: Pampa Tril, Neuquén Province (Figs. 1-2).

**Type horizon**: Bed and level PT-36, Vaca Muerta Formation, *vetustum* Hz., Alternans Z., Upper Tithonian.

**Description.-** Through D = 5-10 mm: whorl section suboval depressed; primary ribs with a mid-flank tubercle from which divides in two or three secondaries, all fading on the venter at the sides of a smooth band. Through about D = 10-80 mm: whorl section suboval to subrectangular higher than wide; densely ribbed, bituberculated by lateral and ventrolateral spiny tubercles; venter with a wide smooth band. The bodychamber begins at about 40 and 60 mm in diameter in the two complete specimens (Fig. 54B-C), the smaller apparently

subadult (or microconch). It has higher than wide, subrectangular whorl section; the ribbing is strong, flexuous, with some primaries simple, others bifurcated on the upper half of the flank; all ribs fade out on the venter besides a wide smooth ventral band. Peristome and septal suture lines not preserved.

**Remarks.-** The adult whorls of the present species are homoeomorphic with those of the partially coeval *P. calistoides*, but with very different bituberculate inner whorls (compare Fig. 54B, D-E with Figs. 45A, 46B, and 50A). The innermost whorls (Fig. 54E) show superficial resemblance with those of *P. calistoides* but differing significantly by the presence of lateral tubercles.

**Occurrence.-** The available material comes from the Alternans Z. levels PT-32-40. Two specimens (Fig. 55) preliminary included in the species come from level PT-50, upper Alternans Z.

Genus Substeueroceras Spath, 1923a Type species: Odontoceras koeneni Steuer, 1897; by original designation.

> Substeueroceras? sp. A Fig. 56

**Description and remarks.**- A well-preserved phragmocone (MOZ-PI 8477) from level PT-36 (*vetustum* Hz., Alternans Z.) very similar to *S. koeneni*, differing by being more inflate and more evolute from the innermost whorls. This specimen comes from a level of the Alternans Z., co-occurring with *Parodontoceras calistoides*, below the levels of the Koeneni Z. where *S. koeneni* occurs in abundance (PT-53-56). However, the specimen could be assigned to *Substeueroceras* by the style of ribbing with some primaries bifurcating on the umbilical shoulder and some again on the upper flank. This specimen was already discussed in PSS (2011) as a probable early representative of *Substeueroceras*.



Figure 48. Parodontoceras calistoides (Behrendsen), level PT-40, azulense Hz. (new), Alternans Z. Complete adult [M] (MOZ-PI 8115), lateral view. Apertural view in Fig. 49. – Natural size (x1). The asterisk indicates the last septum.



**Figure 49**. *Parodontoceras calistoides* (Behrendsen), level PT-40, Alternans Z. Complete adult [M] (MOZ-PI 8115), apertural view. ventral view in Fig. 48.–Natural size (x1). The asterisk indicates the last septum.

## Substeueroceras koeneni (Steuer, 1897) Fig. 57

Synonymy.- See Klein (2005) pars.

**Material**.- 1 phragmocone from level PT-53, 6 incomplete specimens from level PT-54, and 3 incomplete specimens from level PT-56.

**Remarks.**- The species has been described in detail by Steuer (1897) and Gerth (1925b). PSS (2011: fig. 23F, 24) have figured the first complete adult macroconch, coming from the Koeneni Z. of Mallín Quemado.

The type horizon is the level Cieneguita IV of Steuer (1897, transl. 1921). The specimen in Fig. 57A is identical to the paralectorype (Steuer 1897: pl. 17: 1-2; refigured in PSS 2011: Ap. 2C). This specimen is important for showing the typical inner whorls of the species: involute, compressed platyconic, with the venter narrow and subtabulate. The ventral ribs end with a swelling besides a narrow groove. This morphology could be barely distinguished from some variants of *P. calistoides* from older horizons (e.g. Figs. 46D, 47C, 50B), if not for the ribs divided on the lowermost flank and some trifurcated up flank.

A large fragment of an adult [M] bodychamber (Fig. 57C) from level PT-56 represents a variant with a rather flat and smooth venter at about D = 180 mm.

**Occurrence and distribution.**- The species occurs in abundance in the range of levels PT-53-56, Koeneni Z. The main occurrence is in level PT-54 (a conspicuous bank of calcareous sandy shale) associated with abundant *Himalayites* cf. *treubi* Uhlig, conforming the *koeneni* Hz. (new). The species is widely distributed throughout the Neuquén Basin (Gerth 1925a, 1925b, Leanza 1945, Leanza & Hugo 1977, PSS 2011), apparently confined to the Koeneni Z.

Genus Blanfordiceras Cossmann, 1907 Type species: Ammonites wallichi Gray, 1832; by original designation.

Blanfordiceras vetustum (Steuer, 1897) Fig. 58A-B

Synonymy.- See PSS (2011).

**Material**.- 1 adult [m?] phragmocone (MOZ-PI 8085) from level PT-36 (Alternans Z., *vetustum* Hz.). 3 well preserved macroconch specimens (MOZ-PI 8119) from level PT-46, Alternans Z.

**Remarks.-** The species was revised in detail by PSS (2011) based on abundant material from Arroyo Cieneguita. The macroconchs (see Fig. 58B) from level PT-46 are typical representatives of the species but were collected above the levels where occur the species which characterize the *vetustum* Hz.

From level PT-36 (*vetustum* Hz.) comes the specimen shown in Fig. 58A, which has its inner whorls identical to the macroconchs of Arroyo Cieneguita and that in Fig. 58B, but with a moderate variocostation with apparent incipient uncoling from small size (about D = 30 mm). This variocostation at small, apparently adult size with respect to the macroconchs strongly suggests this specimen is a microconch of the species. It is interesting to note that Enay (2009: pl. 52: 5-6) has figured two specimens (*Blanfordiceras pusillum* Enay,



Figure 50. Parodontoceras calistoides (Behrendsen), level PT-40, azulense Hz. (new), Alternans Z. A: Nearly complete juvenile? [M?] (MOZ-PI 8490);  $A_3-A_4$ : ventral and lateral views (x2) of the innermost whorls. B: Phragmocone (MOZ-PI 8492). C: Phragmocone (MOZ-PI 8116). – All natural size (x1). The bar indicates 10 mm for natural size views (x1). The asterisk indicates the last septum.



Figure 51. Parodontoceras calistoides (Behrendsen), level PT-42, Alternans Z. The latest representatives of the species recorded in the studied section. A: Adult [M] phragmocone (MOZ-PI 8916). B: Phragmocone with beginning of bodychamber (MOZ-PI 8915). – All natural size (x1). The asterisk indicates the last septum.

2009) from Nepal which are very similar to this specimen. Also many of his macroconch *Blanfordiceras* from Nepal are indistinguishable from the macroconchs of *B. vetustum* which occurs in abundance in Madagascar (PSS 2011) according to illustrations by Collignon (1960).

The specimen in Fig. 58C from level PT-38 is similar to *Blanfordiceras bardense* (Krantz, 1926), which differs from *B. vetustum* by the lower position of the point of furcation on the flanks and by the higher rib density in the inner whorls, with several intercalatory ribs on the adult phragmocone.

**Genus** *Neocosmoceras* **Blanchet, 1922** Type species: *Hoplites sayni* Simionescu, 1899; by subsequent designation of Roman (1938). **Remarks.**- The genus seems to be widely distributed in the marine basins of western South America and Antarctica. It was described for the first time by Steuer (1897) as *Hoplites malbosiformis* (from Malargüe); later by Gerth as *Acanthodiscus wichmanni* Gerth, 1925b from Arroyo de La Manga (southern Mendoza); from Mallín Redondo and Río Maipo (northern Neuquén Basin) by Leanza (1945, as *Octagoniceras egregium*) and A.-Urreta & Charrier (1990) respectively; Kietzmann & Vennari (2013: fig. 9e) figured as *Neocosmoceras* aff. *perclarum* (Matheron) a small specimen, which shows resemblance with the lectotype of *N. wichmanni* (discussed below). Based on material from Cantera Tres Lagunas (Chubut), Austral Basin, Olivero (1983) proposed *Neocosmoceras ornatum*, but later it was taken as the type species of *Chacantuceras* A.-Urreta & Raswon, 1998. Some



**Figure 52**. *Parodontoceras calistoides* (Behrendsen). Stratigraphic variation profile of relative umbilical width (U/D), relative whorl width (W/D), and number of primary ribs per half whorl (P) of juvenile macroconch phragmocones (24 < D < 80 mm) of figured specimens from levels PT-32-42 as indicated at left hand; n: number of specimens considered per level. The vertical broken line represents the dimensions of the holotype from an unknown horizon. The triangle indicates the biometric position for D = 65 mm of the complete adult [M] from level PT-40 (Fig. 48), and the black circle *Parodontoceras* cf. *calistoides* (Fig. 53) from level PT-35.

dubious fragments from the Austral Basin were figured by Riccardi (1977: figs. 5d-e). Thomson (1974) described a small tuberculated ammonite from Alexander Island as *Neocosmoceras* aff. *sayni*.

## *Neocosmoceras malbosiforme* (Steuer, 1897) Fig. 59A-B

**Type specimen.**- The holotype (by monotypy) comes from Malargüe, Mendoza (Fig. 1A); type horizon: level Malargüe-III of Steuer (1897). The specimen is completely septate, but remains of the next whorl show the beginning of uncoiling (bodychamber?), suggesting it is an adult phragmocone.

**Material.** 1 almost complete crushed specimen (MOZ-PI 8175) and fragments of bodychamber from level PT-65; 1 phragmocone (MOZ-PI 8148) from level PT-66.

**Description**.- Moderately evolute and compressed throughout the ontogeny with whorl section suboval in the phragmocone, subrectangular to suboval in the bodychamber. The largest specimen (Fig. 59A) has more than a half whorl of bodychamber and a maximum preserved D=320 mm.

The sculpture ontogeny pass through three stages: (I) inner whorls (D < 40-50 mm) with widely spaced, bold primary ribs which bear an umbilical and a ventrolateral tubercle, and small ventral tubercles; (II) in the middle whorls (from about D = 50-80 mm) the umbilical tubercles tend to fade off, the ventrolateral tubercles migrate to the mid-flank and two or three secondary ribs born from them; there are one or two ribs intercalated between the lateral tubercles; and (III) the outer whorls (adult phragmocone and bodychamber from about D = 220 mm) are ornamented only by densely spaced, flexuous primaries, which bifurcate at about mid-flank.

**Remarks.-** The inner whorls of the present specimens are identical to the phragmocone of *Neocosmoceras sayni*, e.g. Mazenot (1939: pl. 28: 9, pl. 29: 1 lectotype). The specimen from level 1771 of Mallín Redondo described by Leanza (1945: pl. 5: 1-2) is identical to our specimens and to the holotype of the species.

The lectotype of *N. sayni* is a lappeted microconch. *N.* aff *sayni* (in Mazenot 1939: pl. 29: 2) has identical phragmocone,

and bears a whorl long bodychamber preserved, although not uncoiled. It is thus juvenile/subadult, and may well be a large microconch or a juvenile macroconch. Accounting for the identical sculptural ontogeny and shell morphology at comparable sizes, and the comparable stratigraphic position, it can be assumed that *N. sayni* is the corresponding microconch of *N. malbosiforme*, thus a junior synonym.

**Occurrence and distribution**.- Our material comes from the levels PT-65 (*transgrediens* Hz.) and PT-66, lower Damesi Z. The known records of the genus are in the Berriasian; Le Hegarat (1973: fig. 133) indicates the stratigraphic range of *N. sayni* through the interval Occitanica-lower Boissieri zones. *Neocosmoceras wichmanni* (Gerth) described below occurs in Lower Valanginian beds (levels PT-71-72) or the Wichmanni Z.

The holotype of *N. malbosiforme* was collected by Bodenbender in the level Malargüe-III of Steuer (1897), as part of an important ammonite assemblage, which under current taxonomy whenever possible, is as follows:



**Figure 53**. Parodontoceras cf. calistoides (Behrendsen) [M?], level PT-35, Alternans Z. Phragmocone (MOZ-PI 8473).  $A_1$ - $A_2$ : lateral and ventral views (x1),  $A_3$ : innermost whorls (x2). – The bar indicates 10 mm for  $A_1$ - $A_2$ but 5 mm for  $A_3$ .



**Figure 54**. *Pseudoparodontoceras dezai* n. gen. n. sp., Alternans Z. A: Nearly complete adult [m?] (MOZ-PI 8077), level PT-32. B: Holotype (MOZ-PI 8082), nearly comlete adult [M?], level PT-36, *vetustum* Hz.;  $B_4$ - $B_5$ : innermost whorls (x2). C: Nearly complete juvenile (MOZ-PI 8112), level PT-38. D: Juvenile with part of the bodychamber crushed (MOZ-PI 8491), level PT-40, *azulense* Hz. (new). E: Adult phragmocone (MOZ-PI 8488), level PT-40, *azulense* Hz. (new);  $E_2$ - $E_3$ : innermost whorls (x2). – Natural size (x1), except  $B_4$ - $B_5$  and  $E_2$ - $E_3$  (x2). The bar indicates 10 mm for natural size views. The asterisk indicates the last septum.

- Neocosmoceras malbosiforme (Steuer, 1897)

- Argentiniceras noduliferum (Steuer, 1897), see remarks below

- Argentiniceras malarguense (Steuer, 1897)

- Argentiniceras? argentina (Steuer, 1897)

- Argentiniceras loncochense (Steuer, 1897)

- Argentiniceras incompositum (Steuer, 1897), indistinguishable from *A. malarguense*.

- Krantziceras cf. compressum [cited as Odontoceras theodorii (Oppel)]

- Spiticeras bodenbenderi (Steuer, 1897)

- Protacanthodiscus? quadripartitus (Steuer, 1897). The outermost whorl of the holotype by monotypy (Steuer 1897: pl. 19: 4-5) is similar (although at smaller size) to the outermost whorls of *N. malbosiforme*, but the inner whorls are *Berriasella*-like as in *Protacanthodiscus* Spath, 1923a. Leanza (1945), Rivera (1951), and more recently with doubts Enay et al. (1996) have already included this species in *Protacanthodiscus*, a genus mostly known from Late Tithonian

records. *P.? quadripartitus* could be a late representative of the genus.

- "Hoplites aff. hookeri (Strachey) Blanford"

- "Odontoceras" rotula Steuer, 1897

- "Odontoceras" [nov. gen.?] fallax Steuer, 1897. This species was included in the genus "Andiceras" Krantz, 1926 (nomen dubium, see PSS 2011) by Vennari et al. (2012), but the holotype is the phragmocone of a large platycone ammonite very different from the type species "Andiceras" trigonostomum Krantz, 1926. "O." fallax has irregular ribbing in the outermost whorl, formed by primaries which tend to bifurcate on the umbilical shoulder with formation of a small bulla, then some of them bifurcate again on the upper flank; the venter has a wide depression crossed by the ventral ribbing. This ventral depression is a very conspicuous structure not frequent in the Late Tithonian-Berriasian ammonites. This structure has surely been well entrenched in the literature, as it would be present in "Andiceras" trigonostomum after the erroneous drawing illustrating the species in Krantz (1928: pl.



Figure 55. *Pseudoparodontoceras* cf. *dezai* n. gen. n. sp., adult? phragmocone (MOZ-PI 8127), level PT-50, Alternans Z. – Natural size (x1).

2: 1). Nevertheless, from the photographic refiguration by Vennari et al. (2012: fig. 3C) it is clear that the venter has a very different structure, consisting of a narrow groove or sulcus all throughout the last preserved whorl.

- "Odontoceras" [nov. gen.?] planum Steuer, 1897. A single specimen (holotype by monotypy) was described by Steuer (1897: pl. 2: 4-5), showing the venter widely depressed crossed by the ventral ribbing unchanged. This structure and the same style of ribbing of "O." fallax, suggest it corresponds to the inner whorls of another specimen of this latter species.

This association indicates that the level Malargüe-III belongs to the Andean Berriasian, and the abundance and diversity of morphospecies of *Argentiniceras* points to the Noduliferum Z., probably including the *noduliferum* Hz. (see discussion below).

#### *Neocosmoceras wichmanni* (Gerth, 1925b) Fig. 59C-D, 60

Lectotype.- The name Acanthodiscus wichmanni was cited by Gerth (1921: 140) but with neither figuration nor indication of author, "new species" or similar statement, thus the date of fundation must be considered 1925. However, the nude mentioning of the name does not invalidate its application to his species in the publication of 1925: Acanthodiscus wichmanni Gerth, 1925b. Furthermore, the correct name is indicated in the figure caption of Gerth (1925b: pl. 3: 6), but wrongly in the header of the description (Gerth 1925b: 101, a printing error manuscript corrected in his own copy). The species was proposed based on two specimens from Arroyo de La Manga, but with no designation of a type specimen. We designate as lectotype the specimen figured by Gerth (1925b: pl. 3: 6), re-figurated herein (Fig. 60). It is an adult specimen, as indicated by the uncoiled end of the last whorl. The bodychamber begins at  $D = 53 \text{ mm}, L_{BC}$  about 290°; maximum preserved diameter is 93 mm, probably at peristome. It is likely a microconch.

**Material**.- 1 fragmentary specimen (MOZ-PI 8179) from level PT-72; crushed specimens or impressions from levels PT-71-72.

**Description.**- The phragmocone at about D = 20-30 mm is moderately evolute with primary ribs born on the umbilical shoulder from a small tubercle, some bifurcate from the



**Figure 56**. *Substeueroceras*? sp. A., phragmocone (MOZ-PI 8477), level PT-36, *vetustum* Hz., Alternans Z.;  $A_3$ : innermost whorls (x2). – Natural size (x1), except  $A_3$ . The bar indicates 10 mm for  $A_1$ - $A_2$ , and 5 mm for  $A_3$ .

tubercle. The outer whorl of the observed specimens, possibly around the end of the adult phragmocone, is involute with high flanks; sculpture composed of strong radial primaries with three tubercles along each one: a small umbilical tubercle, a mid-flank bulla, and a large recurved spine on the uppermost flank or ventrolateral shoulder.

The specimen preserved in volume (Fig. 59D) is a fragment of bodychamber with suboval, higher than wide whorl section and flat narrow venter. Primary ribs sharp, born on the umbilical shoulder from a conical tubercle, few of them obscurely bifurcate, others are looped. All ribs end in a bulla or tubercle on the ventrolateral shoulder. The first rib preserved is trituberculate.

**Remarks.-** The material is poorly preserved, but allows to recognize the three successive ornamental stages observed in the lectotype (Fig. 60): (1) inner whorls with fine, prosocline ribs born on the umbilical shoulder from a tubercle, (2) adult phragmocone and beginning of the bodychamber with strong trituberculation, and (3) strong prosocline primaries irregularly spaced, losing the mid-flank tubercle towards the adult peristome.

*N. sayni* (Berriasian) is similar to the present species but the inner whorls are significantly different. In *N. wichmanni* they are finely and densely ribbed up to about D = 30-40 mm, whereas *N. sayni* is already strongly ornamented by widely spaced primary ribs with tubercles from D = 20 mm or less (see the lectotype in Mazenot 1939: pl. 29: 1). This difference is also evident in the several Berriasian specimens of the genus figured by Mazenot (e.g. 1939: pls. 28: 9, 29: 2, 4-6, 30: 1, 2-4). On the other hand, the specimens of *N. breistrofferi* Mazenot (1939: pl. 31: 3.4) have a more extended stage of dense ribbing with periumbilical tubercles, being similar in this respect to *N. wichmanni*.

*N. malbosiforme*, which occurs in lower stratigraphic levels (PT-65-66), differs from *N. wichmanni* not only in the adult stage of macroconch style, but comparably in the inner whorls, as in *N. sayni*, by the earlier bi- and trituberculation on strong primaries.

Gerth (1925b: 101) has already pointed out the proximity of *N. wichmanni* with *Hoplites sayni* Simionescu (1899: pl. 1: 7 lectotype, 8).

**Occurrence and distribution**.- Levels PT-71-72, Wichmanni Z., somewhat higher than the type material. The lectotype was



Figure 57. Substeueroceras koeneni (Steuer), Koeneni Z. A: Phragmocone (MOZ-PI 8495), level PT-54, koeneni Hz. (new). B: Field photograph of an incomplete specimen, level PT-54, koeneni Hz. (new). C: Fragment of an adult [M] bodychamber (MOZ-PI 8503), level PT-56. – All natural size (x1).

collected from a thin limestone bank at Arroyo de La Manga section (Gerth 1925b: 120), associated with: (1) the holotype by monotypy of *Argentiniceras curvatus* (Gerth 1925b: pl. 5: 5) representing the inner whorls of *A. malarguense* (for a photograph of this specimen see Salazar 2012: fig. 4.76.a-c), (2) "*Andesites turgidus*" (Steuer, 1897), not figured, and (3) "*Acanthodiscus* aff. *hystricoides*" (Uhlig, 1902), which was not figured but whose description (Gerth 1925b: 102) indicates a strong similarity with *Neocosmoceras wichmanni*. The only ammonite significant for correlation seems to be *A. curvatus* (= *A. malarguense*), which suggests a position within the Noduliferum or lower Damesi zones as discussed above.

# Subfamily Neocomitinae Salfeld, 1921 Genus Argentiniceras Spath, 1924 Type species: Odontoceras malarguense Steuer, 1897; by original designation.

# Argentiniceras noduliferum (Steuer, 1897) Fig. 61

Synonymy.- See Leanza (1945).

**Material**.- 6 more or less complete macroconchs (MOZ-PI 8189/1-6) from level PT-61.

Description.- Evolute platycone throughout the ontogeny (U/D = 0.37-0.40 at D = 80-200 mm); maximum preserved diameter about D = 520 mm with one whorl of bodychamber, apparently at peristome. Inner whorls with subrectangular, higher than wide whorl section with vertical umbilical wall, passing to suboval from D = 190-200 mm. Inner whorls with fine and dense ribbing (P = 20-23); primaries born on the umbilical wall, swollen on the shoulder, and are prosocline on the flank, many are simple and some bifurcated or twinned on the shoulder, then bi – or trifurcated on the uppermost flank. From D = 190-200 mm the primaries (P = 18-19) are regularly trifurcated from a lateral tubercle, and the swollen of the umbilical shoulder becomes more prominent; ventral ribbing is interrupted at the sides of a wide smooth band which tends to disappear towards the peristome. From the beginning of the bodychamber ( $D_{ls} = 320$  mm) the lateral tubercles tend to fade off and the ribbing is stronger. The bodychamber is uncoiled, U/D > 0.48 from last septum.

**Remarks.**- Our material perfectly match the specimen figured by Steuer (1897: pl. 1: 1); the specimen in Fig. 61A is identical to the specimen figured by Leanza (1945: pl. 23) from the *noduliferum* Hz., Noduliferum Z. of Arroyo del Yeso.

**Occurrence and distribution.**- Argentiniceras noduliferum occurs in several localities of the basin. Most important records

are those including figurations, e.g. bed h of Arroyo del Yeso (in Leanza 1945), level Malargüe-III (of Steuer 1897, discussed above), and level PT-61 in our section (Fig. 5).

In the level PT-66 occur impressions of large specimens up to 600 mm in diameter, which can be assigned to Argentiniceras fasciculatus (Steuer, 1897). This species was defined from its holotype only (Steuer 1897: 64, pl. 3; see photograph of this specimen in Salazar 2012: fig. 4.77, erroneously indicated as lectotype), which was collected in Malargüe (see Fig. 1A), level Malargüe-I (type horizon). The ammonites from this level are (Steuer 1897: 19), under current taxonomy: Argentiniceras malarguense (Steuer, 1897), Cuyaniceras raripartitum (Steuer, 1897), and Argentiniceras? argentina (Steuer, 1897). The association of the first two species would indicate a stratigraphic position somewhere in the interval Noduliferum-Damesi zones. Gerth (1925b: 125) provided a more precise stratigraphic occurrence from material of Arroyo Durazno, in a horizon intercalated between Spiticeras damesi (below) and Cuyaniceras transgrediens (above). These data suggests that the earliest representative of Argentiniceras (lower Noduliferum Z.) would be A. *noduliferum* and the latest A. fasciculatum (lower Damesi Z.)

> Genus *Raimondiceras* Spath, 1924 Type species: *Hoplites raimondii* Lisson, 1907; by original designation.

## Raimondiceras alexandrense Howlett, 1989 Fig. 62

**Description.**- A single, well-preserved, complete adult [M] phragmocone (MOZ-PI 8911) from level PT-62 (Noduliferum Z.). It is evolute throughout the ontogeny: U/D = 0.43 at D =110 mm, passing to U/D = 0.50 at D = 140 mm (last whorl preserved). Whorl section of inner and middle whorls subrectangular, passing to suboval-subrectangular, slightly higher than wide on the last whorl  $(W/H_1 = 0.88 \text{ at } D = 140$ mm). Inner whorls with flexuous primary ribs, which born on the upper umbilical wall and form a little bulla on the shoulder; most of them bifurcate in narrowly splayed secondaries from the upper third of the flank. In the outer whorl, from about D =100 mm, there are primaries trifurcated irregularly on the upper third of the flank after a bulla; there are few simple ribs intercalated. Ventral ribbing is prosocline and interrupted on mid-venter at the sides of a narrow groove. The incipiently uncoiling, indicating maturity, and remains of bodychamber, suggest this latter could be longer than a half whorl.

**Remarks and comparison**.- The holotype and paratype of *Raimondiceras alexandrense* Howlett (1989: pl. 5: 1 and pl. 4: 1-2) from Leda Ridge, and Himalaia Ridge, Antarctica perfectly match our specimen at corresponding diameters. The fragmentary specimens from the Springhill Fm at Lago San Martin figured by Riccardi (1976: pls. 1-2; 1977: fig. 4c-e, fig. 5a-b) as *Jabronella* aff. *michaelis* (Uhlig) belong to *R. alexandrense. Jabronella* Nikolov, 1966 (Type species: *Berriasella jabronensis* Mazenot, 1939), a synonym of *Subalpinites* Mazenot, 1939 (Type species: *S. fauriensis* Mazenot, 1939), can be easily distinguished from *Raimondiceras* by the strong forward projection (chevrons) of the ventral ribbing of this latter.

The ontogeny of our specimen is similar to that of the representatives of *Malbosiceras* (Wright et al. 1996), and in particular is closely comparable with *M. andrussowi* (e.g. Retowski 1893: pl. 10: 10 lectotype, Mazenot 1939: pl. 22: 4,

A3
Image: Constraint of the second secon

Figure 58. A-B: Blanfordiceras vetustum (Steuer), Alternans Z. A: Adult [m?] phragmocone (MOZ-PI 8085), level PT-36, vetustum Hz.; A<sub>i</sub>: innermost whorls (x2). B: Adult [M] phragmocone with beginning of bodychamber (MOZ-PI 8119), level PT-46. C: Blanfordiceras cf. bardense (Krantz), phragmocone (MOZ-PI 8114/2), level PT-38, Alternans Z.– All natural size (x1), except A<sub>1</sub> (x2). The bar indicates 10 mm for natural size views (x1). The asterisks indicates the last septum.

Tavera 1985: pl. 37: 1-3) which is a species confined to the Occitanica Z. (Middle Berriasian). These similarities cannot be evaluated for the scarce material available, but the stunning similarity of the present specimen with those figured by Tavera, strongly suggest they are closely related and similar in age.

Genus Cuyaniceras Leanza, 1945 Type species: Odontoceras transgrediens Steuer, 1897; by original designation.

> Cuyaniceras transgrediens (Steuer, 1897) Fig. 63

Synonymy.- See Leanza (1945).

**Description.**- A single specimen (MOZ-PI 8126) collected from level PT-65. It is a well-preserved phragmocone with less than a half whorl of the bodychamber, crushed, which begins at about D = 63 mm, but it is not clear if the specimen is adult with maximum diameter estimated in 90 mm. The phragmocone is involute (U/D c. 0.15) with subrectangular, higher than wide whorl section. The ribbing is dense (P = 16), primary ribs gently flexuous, bifurcating irregularly at the umbilical shoulder or upper on the flank; all ribs reach the ventrolateral



**Figure 59**. **A-B**: *Neocosmoceras malbosiforme* (Steuer), lower Damesi Zone. **A**: Adult [M] (MOZ-PI 8175), crushed specimen (x0.5), level PT-65, *transgrediens* Hz.;  $A_1$ : inner whorls (x1). **B**: Phragmocone (MOZ-PI 8148), level PT-66. **C-D**: *Neocosmoceras wichmanni* (Gerth), level PT-72, lower Wichmanni Z. **C**: Cast of a phragmocone (LPB-M 151). **D**: Portion of phragmocone (MOZ-PI 8179). – All natural size (x1), except  $A_2$  (x0.5). The bar indicates 10 mm for natural size views (x1), but 20 mm for  $A_2$ (x0.5).

shoulder forming a small tubercle; the venter, poorly preserved, is flat with an apparently narrow smooth band. The bodychamber preserved is covered by primary ribs coarser and more widely spaced than in the phragmocone.

**Remarks.**- The present specimen closely matches the holotype of the species (Steuer 1897: pl. 16: 11-12). *Cuyaniceras* is known from few localities, mostly occurring within a single horizon in each section, in a variety of forms which could likely be but variants of a single species (PSS 2011). These several morphospecies were carefully described by Leanza (1945) from abundant material. All this material was collected from his 0.4 m-thick bed l, which was later used to define the *transgrediens* Hz. by PSS (2011: 84).

# Genus Subthurmannia Spath, 1939 Type species: Subthurmannia fermori Spath, 1939; by original designation.

# Subthurmannia boissieri (Pictet, 1867) Fig. 64

**Material**.- 21 specimens, mainly phragmocones from levels PT-63, 65-66 and 68.

**Description.**- Compressed to somewhat inflate platycones, moderately involute to evolute, whorl section subrectangular to suboval with high and gently convex flanks convergent to the rounded venter. Ribbing from about D = 10 mm fine and dense, mostly flexuous and rather irregularly polyfurcated. The primary ribs commonly divide on the umbilical shoulder and many divide again on the upper third of the flank. From D = 40-50 mm the periumbilical bifurcation is the most frequent and mostly from a lamellar tubercle or bulla. Ventral ribbing is evenly spaced and cross the venter mostly unchanged. Most of the specimens show at D = 40-50 mm a short stage with some ventral ribs slightly raised on the ventro-lateral shoulder. The adult bodychamber begins at about  $D_{\rm is} = 70$ -80 mm with no

changes in ribbing but showing the onset of uncoiling, mean U/D passing from 0.28 in the pre-adult phragmocone to 0.33 at the beginning of the bodychamber. One specimen seems to have the last septum at D = 52 mm but this would be pre-adult for it does not show signs of uncoiling.

Remarks and discussion.- The only consistent difference between the samples is that the specimens from the lower level (PT-63) show the ribbing less flexuous than those of the upper level (PT-68). The present specimens fit the diagnosis of the genus Subthurmannia (Wright et al. 1996: 55) as well as the original description of Ammonites boissieri of Pictet (1867: 79-80), especially the specimens from level PT-68 with more flexuous ribs. The lectotype of A. boissieri Pictet (1867: pl. 15: 1), was designated and refigured by Mazenot (1939: 107, pl. 16: 4). Our specimens can be closely compared with those figured by Mazenot (1939: pls. 15: 2, 16: 1, 4 lectotype). Tavera (1985: pl. 43: 4, 6, 7. pl. 44: 1-4, pl. 45: 2, 4) has figured several specimens from the Boissieri Z. of Spain which are closely comparable, if not identical, with our material. These specimens, identical or barely differentiable between them at comparable diameter, were included in different morphospecies of the genera Fauriella and Tirnovella Nikolov, 1966, both considered synonyms of Subthurmannia in accordance with Wright et al. (1996).

The two specimens figured by Leanza (1945: pl. 10: 8-10) as *Thurmannites duraznensis* (Gerth) var. lateumbilicata, from the Damesi Z. of Mallín Redondo (level MR-1773), clearly belong to this species. Moreover, these specimens occur associated, in the same 0.20 m-thick bed MR-1773 (in Leanza 1945: 89), with *Spiticeras fraternum* and *S. bodenbenderi* like in the interval PT-63-68 of our section (discussed below). *Thurmannites* sp. indet. and *Neocomites* cf. occitanicus (Pictet) in Leanza (1945: pl. 11: 1-4), from the Damesi Z. of Arroyo del Yeso (level m-n) are also assignable to *S. boissieri*.

Windhausen (1918) has early cited the occurrence of the present, or a closely related species in the north of the basin, below levels with *Olcostephanus*, and associated or slightly above the horizon with *Cuyaniceras transgrediens*, in the same position of the occurrence of *S. boissieri* in our section levels PT-65-68.

The specimen figured by Krantz (1928: pl. 2: 5; refigured in Fig. 65 this report) as Thurmannia aff. boissieri from Casa Pincheira is very similar to the present specimens, only differing by the somewhat stronger primary ribs but with the same distinctive sculptural style of S. boissieri. Moreover, this specimen is indistinguishable from Thurmannia aff. thurmanni var. allobrogica Kilian (in Gerth 1925b: pl. 5: 2) from the same locality. This latter specimen comes from the "horizon 8" of Gerth (1925b: 123) associated with material assigned to the enigmatic "Blanfordiceras" fraudans (Steuer, 1897). "B." fraudans has been cited everywhere but never figured out of the lectotype (refigured by PGSS 2011: fig. 25D, wrongly indicated holotype in the caption) from an unknown type horizon, and the Alternans Z. specimen from Cerrito Caracoles in PGSS (2013a: fig. 20A). This "horizon 8" is sandwiched by two ammonite assemblages which indicate clearly its position within the Noduliferum-Damesi zones. The succession presented by Gerth (1925b) is very interesting for it includes well delimited levels with ammonites that mostly are present in Pampa Tril too. This succession is from below and under current taxonomy, as follows:

- "Horizon 10" (base): *Choicensisphinctes striolatus* (Steuer 1897), including the synonym "*Steueroceras steueri*" Gerth (see PSS 2011), *Substeueroceras koeneni* (Steuer, 1897), and

\*

**Figure 60**. *Neocosmoceras wichmanni* (Gerth), lectotype (designated herein), photographic refiguration from Gerth (1925: pl. 3: 6); Paläontologische Institut Universitat Tübingen (GPIBO Haupt). Arroyo de La Manga, Mendoza Province, possibly Upper Berriasian. Almost complete [m?]. – Natural size (x1). The asterisk indicates the last septum.

Krantziceras ellipsostomum (Steuer, 1897). – Koeneni Z. - "Horizon 8": Subthurmannia cf. boissieri (as Thurmannia aff. thurmanni var. allobrogica Kilian), and "Blanfordiceras" fraudans. – Noduliferum-Damesi zones.

- "Horizon 7": Spiticeras damesi (Steuer, 1897), Spiticeras fraternum (Steuer, 1897), Argentiniceras turgida (Steuer, 1897), and Argentiniceras fasciculatus (Steuer, 1897). – Damesi Z.

- "Horizon 6": "Neocomites" senilis Gerth, 1925b, "Neocomites regalis (Bean) forma andina" (merely a phragmocone of N. senilis), Cuyaniceras transgrediens, "Neocomites inflatus" (= Cuyaniceras transgrediens), and Pseudoblanfordia australis (Burckhardt, 1903). – Damesi-Wichmanni zones.

This specimen described by Gerth (1925b) as *Thurmannia* aff. *thurmanni* var. allobrogica Kilian was illustrated by a handdrawing on which can be seen, in the outermost whorl, that the ribbing is flatten on the flanks. This distinctive feature is present in some specimens of *Thurmanniceras otopeta* [m] from the Otopeta Subzone (e.g. Company & Tavera 1982: pl. 1: 7-8)–uppermost Boissieri Z. (Reboulet et al. 2014).

**Occurrence and distribution**.- Levels PT-63 (Noduliferum Z.) and 65-68 (Damesi Z.). Considering the distribution of the species in the well controlled successions of Spain (Tavera 1985), it can be assumed the levels PT-63-68 represent a time-interval within the Late Berriasian Boissieri Z. of southern Europe (further discussed below). *Berriasella broggi* Rivera (1951: pl. 2: 1-2) and *Berriasella* cf. *peruana-B. broggi* Rivera (in Romero et al. 1995: pl. 18: 1-2) from Peru are very similar and can be assigned to *S. boissieri. Hoplites* cf. *thurmanni* (in Burckhardt 1906: pl. 42: 1) from Mexico can also be assigned to *S. boissieri*. From India it has been figured by Uhlig (1910:



Figure 61. Argentiniceras noduliferum (Steuer), level PT-61, noduliferum Hz., Noduliferum Z. A: Virtually complete adult [M] (MOZ-PI 8189). B-C: Fragment of adult [M] bodychamber (MOZ-PI 8189/1). D: Fragmentary adult [M] (MOZ-PI 8189/2). – All reduced (x0.5). The asterisk indicates the last septum.



Figure 62. Raimondiceras alexandrense Howlett, adult [M] phragmocone (MOZ-PI 8911), level PT-62, Noduliferum Z. – Natural size (x1). The asterisk indicates the probable last septum.

pl. 80) according to Mazenot (1939: 106). Thus, it can be assumed the species has a Tethyan and peri-Gondwanian distribution.

Genus Thurmanniceras Cossmann, 1901 Type species: Ammonites thurmanni Pictet & Campiche, 1860; by original designation.

# *Thurmanniceras* sp. A Fig. 66C

**Remarks.**- A small phragmocone from level PT-68 (Damesi Z.) similar to the specimens described below as *Thurmanniceras* sp. B in lateral view but differs by the rounded venter crossed by uninterrupeted ribs. This specimen is similar to *S. boissieri* but coarsely ribbed with bifurcate primaries and some simple ribs, and could likely be a transitional form between this latter species and *Thurmanniceras* sp. B, in a very similar way as known in the southern Tethys (further discussed below).

*Thurmanniceras* sp. B Fig. 66A-B **Material.** 1 small phragmocone (MOZ-PI 8181) from level PT-72; 1 adult [M] phragmocone with the beginning of the bodychamber (MOZ-PI 8182) from level PT-76.

**Description.**- Inner whorls compressed, subrectangular, higher than wide with tabulate venter. Ribbing fine and dense, gently flexuous, irregularly bi- or trifurcate from the umbilical shoulder, some again near mid-flank. Outer whorls (from about D = 30 mm) similar but somewhat wider in whorl section and more widely umbilicated. Ribbing as in the inner whorls but coarser with umbilical bullae and raised on the ventrolateral shoulder before crossing unchanged the wide and flat venter.

The largest specimen is adult as indicated by the uncoiled end of the phragmocone ( $D_{is}$  at about 105-110 mm); the remains of bodychamber indicate three quarters whorl or longer. The ribbing at the beginning of the bodychamber is composed by stronger primaries.

**Remarks.-** The present specimens show the typical shell morphology and sculpture ontogeny of *Thurmanniceras* (*sensu* Wrigth et al. 1996). The inner whorls are comparable with slight differences to *Thurmanniceras otopeta* (Thieuloy *in* Busnardo et al., 1979) from the uppermost Berriasian Otopeta Subzone. For example, the phragmocones of the two microconchs figured by Company & Tavera (1982: pl. 1: 7-8) are very similar to our specimens at comparable size, although the ribs divide somewhat higher on the flanks. Within the Andean ammonites in the literature, the specimen figured by Gerth (1925b: pl. 5: 2) as *Thurmannia* aff. *thurmanni* var. allobrogica from the Damesi Z. is also similar as discussed above.

Company (1987: 112) has pointed out that *S. boissieri* is the berriaselid most similar to the earliest *Thurmanniceras*. We agree about this close similarity what, moreover, suggests a direct phyletic relationship. However, *Thurmanniceras* sp. B seems to be closely related to *S. boissieri* as represented in the studied section, and *Thurmanniceras* sp. A could likely be a transitional form.

This succession, which of course needs more collections for confirmation, is very similar to the equivalent in the southern Tethys and seems to be very important for consistent time-correlation of the Andean successions based on comparable assemblages.

Present species shows similarities in shell-shape and ribbing with "*Odontoceras*" [nov. gen.?] *fallax-planum* discussed above, but the venter does not seem to be so depressed and there is a stratigraphic gap with these forms which occur in the Noduliferum Z.

Occurrence.- Levels PT-72 and 76, Wichmanni Z.

#### Genus Pseudoblanfordia Spath, 1925

Type species: *Hoplites australis* Burckhardt, 1903; by original designation.

**Remarks.-** Thomson (1979: 26) and Enay (2009: 207) discussed and accepted the genus, but Gerth (1925), Arkell (1957), and Wright et al. (1996) considered *Pseudoblanfordia* a synonym of *Blanfordiceras*.

The lectotype of *H. australis*, designated herein, was illustrated photographically by Burckhardt (1900: pl. 27: 5) as Hoplites aff. privasensis Pictet. This illustration indeed shows an ammonite which could be superficially assigned to Blanfordiceras. Later, this ammonite was refigured by a handdrawing by Burckhardt (1903: pl. 11: 9-10) and described as H. australis (both figurations are reproduced in Fig. 67A-B for direct comparison). The specimen comes from his level 12b of Molinos Colgados. His figuration of 1903 is evidently idealized, showing the sculpture of the penultimate whorl which in the photographic figuration of 1900 is covered by the last whorl. From the same level 12b of Molinos Colgados come two other specimens which Burckhardt used for defining two species. These are: (1) the holotype of Hoplites peregrinus Burckhardt (1903: pl. 11: 1-2), involute and discoidal, high whorled, with sharp distant primary ribs and two or three secondaries/intercalatories on the upper flank, and (2) the holotype of Hoplites molinensis Burckhardt (1903: pl. 11: 13-14, refiguration from Burckhardt 1900: pl. 27: 6), virtually identical to the lectotype of H. australis. These two species are considered synonyms of H. australis. Thus, the genus Pseudoblanfordia must be retained.

According to Leanza (1945), *P. australis* occurs in the uppermost Damesi Z. and/or Wichmanni Z. (see discussion below). It is worth to note that *P. australis* shows much resemblance, especially in the inner whorls, with *Lissonia* Gerth, 1925b and some forms of *Pseudofavrella* Leanza & Leanza, 1973 which is well developed somewhat higher in the stratigraphic succession, in the Andean Upper Valanginian Angulatiformis Z. (A.-Urreta & Rawson 2010).



**Figure 63.** *Cuyaniceras transgrediens* (Steuer), phragmocone with half whorl of bodychamber (MOZ-PI 8126), level PT-65, *transgrediens* Hz., base of the Damesi Z. – Natural size (x1). The asterisk indicates the last septum.

# Pseudoblanfordia cf. australis (Burckhardt, 1903) Fig. 68

**Material.**- Abundant crushed specimens from level PT-86. 1 specimen from level PT-88.

**Description**.- Phragmocone through D = 20 to 50 mm involute with high flanks. Primary ribs sharp and widely spaced, obscurely bifurcated on the upper half of the flank; there are one or two short intercalatory ribs per each primary; the secondaries and the intercalatories are more or less projected forward. Through D = 50-90 mm the number of intercalatories becomes gradually lower. The bodychamber is only poorly preserved in the larger specimens, showing a wide umbilicus.

**Remarks.-** The inner whorls of the phragmocone (at D < 40 mm) are very similar to the holotype of *H. peregrinus*, whereas the outer whorls match the holotype of *H. molinensis* and the specimen from Arroyo del Yeso figured by Leanza (1945: pl. 10: 1-2). Respect to our specimens and to that of Leanza, the lectotype (Fig. 67) is similar in involution but has a more regularly bifurcated ribbing and no intercalatory ribs. Under the interpretation of the species discussed above, these differences could be due to intraspecific variation.

The specimen in Fig. 68D is, in lateral view, indistinguishable from the Upper Valanginian examples of *Pseudofavrella angulatiformis* (Behrendsen, 1892) figured by A.-Urreta & Rawson (2010: fig. 6C and I). This close similarity suggests that the origin of *Pseudofavrella* could be in ammonites resembling, or belonging to, *Pseudoblanfordia* perhaps via *Lissonia* (see discussion below).

**Occurrence.-** Our specimens were collected from levels assigned to the Riveroi Z. The specimen from Arroyo del Yeso was assigned by Leanza (1945) to the upper Damesi Z. The lectotype comes from an uncertain horizon assigned by Burckhardt (1903) to the Lower Cretaceous.



**Figure 64**. *Subthurmannia boissieri* (Pictet), Noduliferum and Damesi zones. **A**: Adult [M] with beginning of bodychamber (MOZ-PI 8156), level PT-68, Damesi Z. **B**: Adult [M] with beginning of bodychamber (MOZ-PI 8158), level PT-68, Damesi Z. **C**: Adult? phragmocone (MOZ-PI 8159), level PT-68, Damesi Z. **D**: Adult [M] with part of bodychamber (MOZ-PI 8162), level PT-68, Damesi Z.; **D**<sub>3</sub>: innermost whorls (x2). **E**: Phragmocone (MOZ-PI 8172), level PT-66, Damesi Z.; **e**volute variant with marked ventral groove. **F**: Adult [M] with incomplete bodychamber (MOZ-PI 7580/1), level PT-63, Noduliferum Z. **G**: Adult [M?] phragmocone (MOZ-PI 7580/2), level PT-63, Noduliferum Z. **H**: Adult [M] phragmocone (MOZ-PI 7581), level PT-63, Noduliferum Z. – All natural size (x1), except D<sub>3</sub> (x2). The bar indicates 10 mm for natural size views (x1), but 5 mm for D<sub>3</sub> (x2). The asterisk indicates the last septum.

Genus Lissonia Gerth, 1925b Type species: Hoplites riveroi Lisson, 1907; by original designation.

> *Lissonia* cf. *riveroi* (Lisson, 1907) Fig. 69A-F

Material.- Abundant material, mostly crushed from levels PT-88, 104, 106.

**Description.-** Platycone, moderately involute. Whorl section suboval to subrectangular with high flanks and vertical umbilical wall. Densely ribbed, throughout the ontogeny, by prosocline primary ribs bifurcated irregularly around the middle of the flank. In the inner and middle whorls, one of the secondary ribs is directed backwards at the beginning and soon becomes parallel to the other secondary, which stands like a prolongation of the primary rib. The ventral ribs may swell on the ventrolaterial shoulder and are interrupted on the venter. On the adult bodychamber the ventrolaterial shoulder with a tendency to form a little bullae each one and swells in the point of furcation. The ventral area, poorly preserved in most specimens, is narrow, weakly ribbed or smooth.

The largest specimen (Fig. 69F), a macroconch, is an adult as indicated by the uncoiling of the bodychamber, which begins at D = 100 mm and seems to be complete at D = 146 mm.

Remarks.- The outer whorls of the present material closely resembles L. riveroi as illustrated by Leanza (1945: pl. 12: 1) from the Riveroi Z. of Mallín Redondo, probably from the same stratigraphic position that our material. Nevertheless, the inner whorls are more densely ribbed (cf. Wrigth et al. 1996: fig. 42.1). The inner whorls of P. cf. australis and Thurmanniceras sp. A are very similar in ribbing style and shell-shape, suggesting our specimens could represent an early form of Lissonia. It is possible that the forms from Cerrito de la Ventana cited as "Thurmanniceras/Lissonia intermediates" by A.-Urreta & Rawson (1999: fig. 2) have a comparable stratigraphic position. On the other hand, the fragment figured by A.-Urreta & Rawson (1999: fig. 3G-H) as Lissonia riveroi and "Thurmanniceras" sp. a in their fig. 3I-J, from the Riveroi Z. of Cerrito de la Ventana are similar but more densely and finely ribbed than our material.

*Lissonia* n. sp. (in Aguirre-Urreta et al. 2007: fig. 6F) from the Riveroi Z. of Quebrada Los Algarrobos (Chile) with densely ribbed flanks, is very similar to our specimens.

The present specimens differ from *Pseudoblanfordia* cf. *australis* (described above) in the denser ribbing with few intercalatory ribs and less projected secondaries.

The closest resemblance of our larger specimens (e.g. Fig. 69F) is with the specimens of *Pseudofavrella garatei* Leanza & Leanza, 1973 figured by A.-Urreta & Rawson (2010: fig. 5A, L-N) from the lower Angulatiformis Zone (Upper Valanginian) of the Pichaihue Valley (W Neuquén Province). However, these specimens from level PT-106 as well as the others of the range of the species, show differences apparently significant from *P. garatei*, especially the inner whorls which are more densely ribbed and these ribs have no swells on the umbilical shoulder. In the outer whorls, the ventral ribs are not projected forwardly as in *P. garatei*, and bear, irregularly distributed, small tubercles or bullae on the ventro-lateral shoulder.

**Occurrence and distribution**.- All the material comes from the upper part of the studied section, levels PT-88, 104-106 assigned to the Riveroi Z.

<u>10 mm</u>

**Figure 65.** *Subthurmannia boissieri* (Pictet), Casa Pincheira, Berriasian. Photographic refiguration of the specimen in Krantz (1928: 2: 5). – Natural size (x1).

Genus *Pseudofavrella* Leanza & Leanza, 1973 Type species: *Hoplites angulatiformis* (Behrendsen, 1892); by original designation

# **Pseudofavrella sp. A** Fig. 69G

**Remarks.**- A single specimen collected from the lower part of the Mulichinco Fm, above the studied section overlying the Quintuco Fm (Fig. 2, inset). It is assigned to *Pseudofavrella* by the style of ribbing with the upper flank ribbing projected forwardly, and involution. It could match *P. garatei*, but its preservation is very poor and the material scarce for a closer comparison.

The close resemblance of this specimen with P. garatei could suggest that the lower Mulichinco Fm in the study area belongs to the Upper Valanginian. Nevertheless, in the upper part of the Mulichinco Fm (Fig. 2 inset) occur levels of greenish silty sandstones with abundant large macroconchs of Olcostephanus atherstoni (Sharpe, 1856). The record of O. atherstoni in this position of the upper Mulichinco Fm and so profusely represented, likely indicates the Atherstoni Zone of the middle part of the Valanginian (see A.-Urreta et al. 2007, A.-Urreta & Rawson 2010). However, the present specimen of Pseudofavrella sp. A, which occurs above the uppermost records of L. cf. riveroi and below the levels with O. atherstoni, could represent the earliest occurrence of P. garatei or a close form (cf. A.-Urreta & Rawson 2010: 329), and could be attributed to the lowermost Atherstoni Z. or to the uppermost Riveroi Z.

Origin of Pseudofavrella: A.-Urreta & Rawson (1999: 526) have suggested, based on material from Cerrito La Ventana and Cerro La Parva, that Lissonia could likely have originated from their "Thurmanniceras" sp. a. A.-Urreta & Rawson (2010: 329) pointed out they failed to recognize any inmediate predecessor for P. garatei, apparently the earliest component of the lineage Pseudofavrella, which they recorded ranging from the upper Atherstoni Z. Pseudofavrella sp. A occurs in a lower stratigraphic position, and the records in our section (Fig. 5) show a succession of neocomitids through the Wichmanni Z. to the Riveroi Z. that can be fitted to those records. The composed succession of these apparently phyletically related forms allows to connect Andean forms of Thurmanniceras with Pseudofavrella via Pseudoblanfordia-Lissonia. The recorded succession of representatives of this lineage would be, from below:



Figure 66. A-B: *Thurmanniceras* sp. B, Wichmanni Z. A: Phragmocone (MOZ-PI 8181), level PT-72. B: Adult [M] phragmocone with beginning of bodychamber (MOZ-PI 8182), level PT-76. C: *Thurmanniceras* sp. A (MOZ-PI 8169), level PT-68, Damesi Z. – All natural size (x1). The asterisk indicates the last septum.

- (1) *Thurmanniceras* sp. B (Fig. 66A-B), levels PT-72-76, lower Wichmanni Z.: sculpture ontogeny typically necomitid, resembling
- (2) "Thurmanniceras" sp. a (in A.-Urreta & Rawson 1999: fig. 3I-J), upper? Wichmanni Z. The material was collected loose from the scree, but the authors have given confidence to the stratigraphic position they assumed (A.-Urreta & Rawson 1999: 524).
- (3) Pseudoblanfordia cf. australis (Fig. 68), levels PT-86-88, lower Riveroi Z. The specimen in Fig. 68C is very similar to P. angulatiformis in A.-Urreta & Rawson (2010: fig. 6C, I). The specimen in Fig. 68D is an adult with the outermost whorl uncoiled, which matchs in the small adult size, wide umbilicus and ribbing with the specimen in A.-Urreta & Rawson (2010: fig. 6E). Both of these specimens could be microconchs.
- (4) *Lissonia* cf. *riveroi* (Fig. 69A-F), levels PT-88-106, Riveroi Z. Some of the figured specimens closely resemble some morphotypes of *P. garatei* (discussed above).
- (5) Lissonia riveroi (in A.-Urreta & Rawson 1999: 3G-H).
- (6) Pseudofavrella sp. A. (Fig. 69G):
- (7) Pseudofavrella garatei and succeeding species of the lineage (see Leanza & Leanza 1973, A.-Urreta & Rawson 2010).

This preliminary succession shows a rather well-marked tendency, from the inner whorls, to develop umbilical and ventrolateral tubercles or swells, and to become less densely ribbed. These changes lead gradually to the typical sculptural style of *Pseudofavrella* as described by A.-Urreta & Raswon (2010). The constant difference from *Pseudofavrella* is the more densely ribbed inner whorls of *P*. cf. *australis* and *L*. cf.

*riveroi*. Although for the time being there is a single specimen of *Pseudofavrella* sp. A, it gives consistency to the tentatively proposed phylogeny *Thurmanniceras – Pseudoblanfordia – Lissonia – Pseudofavrella*.

Family Olcostephanidae Haug, 1910 Subfamily Spiticeratinae Spath, 1924 Genus Groebericeras Leanza, 1945 Type species: Groebericeras bifrons Leanza, 1945; by original designation.

### Groebericeras bifrons Leanza, 1945 Fig. 70

Synonymy.- See Aguirre-Urreta & Álvarez (1999).

**Material**.- 3 [M] phragmocones (MOZ-PI 8496/1-3) and 1 complete adult [m] (MOZ-PI 8496/4) from level PT-60.

**Description**.- *Macroconch*: suboxyconic, involute, whorl section subtriangular, higher than wide, with subvertical umbilical wall, flat to gently rounded flanks and narrow, rounded venter. Ribbing on the lower flank is very weak, especially in the outer whorls; on the upper half the ribs are moderately strong, regularly spaced and narrowly spaced, crossing the venter unchanged. Three to four well marked constrictions per whorl.

*Microconch*: phragmocone like in the inner whorls of the macroconch, showing the strong constrictions and ribbing of the inner whorls that vanish gradually on the lower half of the flank towards the outer whorls. The bodychamber is markedly

**Figure 67**. **A-B**: *Pseudoblanfordia australis* (Burckhardt, 1903), lectotype (designated herein), Molinos Colgados, Valanginian. **A**: Refiguration of the hand-drawing picture in Burckhardt (1903: pl. 11: 9-10). **B**: Original figuration by Burckhardt (1900: pl. 27: 5) as *Hoplites* aff. *privasensis* Pictet. **C**: Ventral view of the ?lectotype, modified from Burckhardt (1900: pl. 27: 7). –All natural size (x1).

в

10 mm

C

uncoiled, about a half whorl long; the peristome bears long curved lappets. Diameter at last septum 30 mm, and at peristome 45 mm.

**Remarks.**- The macroconchs are identical to the lectotype and the material in A.-Urreta & Alvarez (1999: pl. 1: 1-2, 6-7); the microconch is described for first time. The species was described in detail by Leanza (1945), Howarth (1992), and A.-Urreta & Alvarez (1999). These later authors have described an apparent size-dimorphism with two size-classes of adult individuals: D = 70-80 mm and D > 300 mm. However, considering the smaller size of the lappeted microconch (Fig. 71A), this size-dimorphism, if statistical significant, would be but a phenomenon of polymorphotypism (sensu Parent & Garrido 2015) but not sexual dimorphism.

**Occurrence and distribution.**- Present material comes from level PT-60, *compressum* Hz., basal Noduliferum Zone. The age of *G. bifrons* has been discussed in detail by Howarth (1992) and A.-Urreta & Álvarez (1999), both concluding an early Berriasian age.

#### Genus Spiticeras Uhlig, 1903

Type species: *Ammonites spitiensis* Blanford, 1863; by subsequent designation of Roman (1938).

**Figure 68**. *Pseudoblanfordia* cf. *australis* (Burckhardt), Riveroi Z. A: crushed phragmocone (MOZ-PI 8183), level PT-86, lower Riveroi Z. B: Crushed adult [M?] phragmocone (MOZ-PI 8185), level PT-86. C: Crushed ?phragmocone (MOZ-PI 8186), level PT-86. D: Adult phragmocone (MOZ-PI 8178), level PT-88. –All natural size (x1).

# Spiticeras fraternum (Steuer, 1897) Fig. 71

Synonymy.- See PSS (2011).

**Material**.- 1 well-preserved macroconch phragmocone (MOZ-PI 8143/1) loose; 3 fragmentary specimens (MOZ-PI 8143/2) and 1 almost complete specimen (MOZ-PI 8123). All from level PT-65.

**Remarks and comparison.**- The species was revised in detail by PSS (2011) based on material from Arroyo Cieneguita. The present specimens match to that material as well to the lectotype; the only difference is that our larger specimen (Fig. 71A) is somewhat more involute. The specimen in Fig. 71A can be safely attributed to the level PT-65, although collected loose, considering not only the identical matrix but its identity with another one crushed. The specimen in Fig. 71C appears to be a microconch for it is an evolute bodychamber with no signs of tubercles and strong bourrelets, which in the microconchs of the genus *Spiticeras*, typically precede the peristome with long lappets.

An identical although fragmentary specimen from the "Berriasian" of S Longing Gap (Nordenskjöld Fm, Ameghino Member) was figured by Whitham & Doyle (1989: fig. 6j).

The holotype of Spiticeras gevreyi Djanélidzé (1922: pl.





**Figure 69**. **A-F**: *Lissonia* cf. *riveroi* (Lisson), Riveroi Z., lower Valanginian. **A-E**: Crushed, incomplete phragmocones (MOZ-PI 8501, 8188/1-3, 8502, respectively), level PT-88; **C**<sub>2</sub>: elarged view (x2) of the specimen in C<sub>1</sub> representing the inner whorls of the species. **F**: Complete adult [M] (MOZ-PI 8177), level PT-106. **G**: *Pseudofavrella* sp. A, phragmocone (MOZ-PI unnumbered), Mulichinco Fm (see inset Fig. 2). – All natural size (x1), except C<sub>2</sub> (x2). The bar indicates 10 mm for natural size views (x1), but 5 mm for C<sub>2</sub>(x2). The asterisk indicates last septum.



**Figure 70**. *Groebericeras bifrons* Leanza, level PT-60, *compressum* Hz., Noduliferum Z. A: Complete adult [m] (MOZ-PI 8496/4); A<sub>2</sub>: delineation of the lappets. B: Adult [M] phragmocone (MOZ-PI 8496/1). – All natural size (x1). The asterisk indicates the last septum.

20: 2) from the Berriasian of La Faurie, France, is virtually identical with our specimens. The present transient of S. fraternum from level PT-65 shows the same shell-shape and sculpture ontogeny, including the number of constrictions and the separation between them at comparable diameters. S. gevreyi has been recorded by Company & Tavera (1982) as part of an assemblage (their Asociación A) collected under stratigraphic control from the Boissieri Z. of Cehegin, SE Spain. Among the ammonites taking part of this assemblage there is Spiticeras kiliani Djanélidzé, 1922. The several specimens described originally by Djanélidzé (1922), also coming from the Berriasian of La Faurie, are perfect microconch Spiticeras with inner whorls closely comparable, perhaps identical, with those of S. gevreyi by which could be safely assumed that these morphospecies actually represent the sexual dimorphs of a single species.

**Occurrence and distribution.**- The present material comes from level PT-65, *transgrediens* Hz., lowermost Damesi Z. In Arroyo Cieneguita the species was recorded in the *compressum* Hz. (lowermost Noduliferum Z.) so that present specimens clearly represent a later transient which tends to be more involute than the older one.



**Figure 71**. *Spiticeras fraternum* (Steuer), level PT-65, *transgrediens* Hz., Damesi Z. A: Adult [M] phragmocone (MOZ-PI 8143/1), loose from level PT-65. B: Nearly complete juvenile [M] (MOZ-PI 8123). C: Bodychamber, probably of a [m] (MOZ-PI 8143/2). – All natural size (x1). The asterisk indicates the last septum.



Figure 72. Aspidostephanus cf. depressus (Steuer), adult? [M] phragmocone (MOZ-PI 8147), level PT-65, transgrediens Hz., Damesi Z.;  $A_1$ : lateral view of the right side;  $A_2$ : ventral view;  $A_3$ : view of the inner whorls from the left side – Natural size (x1).

Genus Aspidostephanus Spath, 1925 Type species: Holcostephanus depressus Steuer, 1897; by original designation.

# Aspidostephanus cf. depressus (Steuer, 1897) Fig. 72

**Description.**- One adult? phragmocone (MOZ-PI 8147) with maximum preserved D = 110 mm. Inner whorls narrowly umbilicated, with strong and well spaced primary ribs (P = 8) which bear indistinct bullae on the umbilical shoulder and the uppermost part of the flank. Outer whorl coroniform-cadiconic with depressed suboval whorl section with widely rounded venter. The beginning of the outer whorl is only weakly ribbed. From D = 75-80 mm the sculpture is composed of huge, hollow conical tubercles (7 per half whorl) on the umbilical shoulder, or lowermost flank, from which born one to three secondary ribs strongly prosocline. Ventral ribbing cross transversally the venter with no modifications.

**Remarks.**- The specimen comes from level PT-65, *transgrediens* Hz., lowermost Damesi Z. The inner whorls of the present specimen match the holotype at comparable diameter. Part of the last whorl of the holotype belongs to the bodychamber which is ventrally smooth and the flanks only bear bullae with a short rib. At this diameter (D = 55-65 mm) our specimen is not preserved, but nearly (D = 75-80 mm) is similar in whorl section and weakly ribbed. These apparent differences prevent a firm identification.

The holotype by monotypy of Reineckeia latior Steuer

(1897: pl. 13: 3-4) is almost identical with the outer whorl of the present specimen. It appears that the holotype of *A. depressus* represents the inner whorls of a species of which the outer whorls would be represented by the holotype of *R. latior*, both from the same level Loncoche-III of Steuer (1897, 1921).

*A. depressus* has been compared by Steuer (1897) and Gerth (1925b) with *Spiticeras bodenbenderi* (Steuer, 1897). Nevertheless, this latter has different inner whorls at comparable diameter, and the venter of the outer whorls covered by ribs forming the characteristic chevron of most *Spiticeras*.

However, the ventral chevron in many ammonites seems to be a feature which is developed by the compressed morphs but not by the widely depressed morphs - as if the compression of the whorls would produce the flexure of the ribs which do not shorten accordingly, mantaining a constant perimeter.

The holotype comes from Arroyo Loncoche, level Loncoche-III of Steuer (1897). The ammonite fauna described from this level includes (under current taxonomy): *Argentiniceras noduliferum*, *A. loncochense*, *A. argentina*, *S. bodenbenderi* (= *S. fraternum*), and *Aspidostephanus latior*. These ammonites suggest the Noduliferum Z. but only tentatively because *Argentiniceras* range in some localities like Arroyo Durazno, into the Damesi Z. (see Gerth 1925b: 125).

Family Himalayitidae Spath, 1925 Genus Windhauseniceras Leanza, 1945 Type species: Perisphinctes internispinosus Krantz, 1926; by original designation.

# Windhauseniceras internispinosum (Krantz, 1926) Figs. 73-76

Synonymy.- See Parent (2003b) and Parent et al. (2007).

**Material**.- 8 more or less complete [M] and 2 [m] from level PT-19 (Internispinosum Z.); 2 adult [M] from level PT-20.

**Description**.- Two morphs occurring in the successive levels PT-19 and PT-20 may be distinguished, thus considered transients of the species. They differ mainly in the middle whorls are probably in adult size.

*Transient alpha (level PT-19).* [M] (Fig. 74): Inner whorls (*D* > 10 mm) evolute (U/D = 0.48-0.50), subcircular to subovatedepressed in whorl section, with widely spaced, radial sharp primary ribs (P = 13-14 through D = 25-35 mm), bi- or trifurcated from a spiny swellings on the upper flank. Through the middle whorls, from D = 50 up to  $D_{1s} = 115$  mm, most ribs are bifurcated from the upper third of the flank (P = 15-18) through D = 40-90 mm); ventral ribbing is at first unchanged but near the beginning of the bodychamber tends to be interrupted by a smooth mid-ventral band. The beginning of the adult bodychamber is somewhat more compressed; the ribbing bifurcates from the middle of the flank in narrowly splayed secondaries; some irregularly distributed intercalatories occur. Maximum preserved D = 135 mm. The adult size at peristome must have been 180-200 mm in diameter, considering the bodychamber at least three quarters whorl long

[m] (Fig. 73): about a half of the estimated adult size of the macroconch, from which differs by the ribbing of the adult bodychamber which is denser, bi- or trifucated from the mid-flank in narrowly splayed secondaries; some primaries are undivided. The peristome bears short and wide lappets. Bodychamber about a half whorl long, uncoiled;  $D_p = 92$  mm.

Transient beta (level PT-20). [M] (Fig. 75): Inner and middle whorls similar to the transient beta but the coronate stage formed by primary ribs regularly trifucarted from a spiny swelling, persists up to the middle whorls. The secondary ribbing cross the venter unchanged up to the peristome, with the exception of two short modifications through the ontogeny: (1) through D = 20-35 mm there is a ventral groove bounded by the end of the ventral ribs which form a mild swelling, and (2) at D = 100 mm there is a short stage, in which the five ventral ribs end on a spiny, hollow tubercle besides a narrow ventral band. The last whorl of the adult phragmocone becomes higher than wide, more densely ribbed by primary ribs bifurcated around the mid-flank in two narrowly splayed secondaries of the same strength, crossing the venter unchanged. The adult bodychamber begins at an estimated  $D_{is} = 170$  mm; it is compressed, covered by rather flexuous, strong primaries bi- to trifurcated and several intercalatories, all crossing the venter unchanged. It is a little more than three quarters of a whorl long, apparently complete with peristome at  $D_p = 280$  mm.

[m]: see description in Parent et al. 2007).

**Remarks.**- The transient beta shows the typical aspect of the species as characterized by the lectotype (Krantz 1926: pl. 14: 1-2; refigured in Parent 2003b: fig. 1A-B) and the paralectotype, as well as the specimens figured by Weaver (1931), Leanza (1980) and Parent et al. (2007). Thus, this should be the type transient of the species. The fragmentary specimen figured by A.-Urreta (1990: pl. 1: 9) seems to belong to the transient alpha.

Differentiation between the macroconchs of the two transients is mainly from the inner and middle whorls (near the



**Figure 73**. *Windhauseniceras internispinosum* (Krantz) transient alpha [m], level PT-19, *internispinosum* alpha Hz. (new), Internispinosum Z. A: Complete adult with lappets (MOZ-PI 8462/1). B: Adult phragmocone with part of the bodychamber (MOZ-PI 8462/2). – All natural size (x1). Asterisk at last septum.

end of the adult phragmocone). The transient alpha shows coronate inner whorls followed by a *Catutosphinctes*-like stage through about one whorl, with regularly bifurcated ribs and a frequent smooth ventral band which extends up to the end of the adult phragmocone. In the transient beta the coronote stage begins in the innermost whorls but persists through the middle whorls, up to D = 75-80 mm; the adult phragmocone is more densely ribbed with a higher whorl section and a short stage of spiny ventral ribs.

Some specimens of transient alpha show intermediate morphology and sculpture with the more coarsely ribbed representatives of *C. proximus* which co-occur in the level PT-19, in some cases making hard their assignation to one or the other species. For example: Fig. 40A with some trifurcates which are not usual in *Catutosphinctes*; Fig. 41B with depressed whorl section and widely spaced primaries in the inner whorls; or Fig. 74C very similar to *C. proximus* in lateral view can be distinguished from its coronate inner whorls. The specimen of *C. proximus* shown in Fig. 41A has the ribbing of the outer whorls very similar to *W. internispinosum* transient alpha at comparable diameter, but can be distinguished by the


**Figure 74.** *Windhauseniceras internispinosum* (Krantz) transient alpha [M], level PT-19, *internispinosum* alpha Hz. (new), Internispinosum Z. A: Adult phragmocone with beginning of bodychamber (MOZ-PI 7571); note the wide smooth ventral band ( $A_2$ ). B: Adult [M] with part of the bodychamber (MOZ-PI 8050). C: Adult phragmocone (MOZ-PI 8018); C<sub>3</sub>: inner whorls (x2) showing the irregularly distributed tuberculate primaries. D: Phragmocone (MOZ-PI 8039). – All natural size (x1), except C<sub>3</sub> (x2). The bar represents 10 mm for natural size views. The asterisk indicates the last septum.



**Figure 75**. *Windhauseniceras internispinosum* (Krantz) transient beta [M], level PT-20, Internispinosum Z. Almost complete adult with bodychamber (MOZ-PI 8465). **A**<sub>1</sub>: Lateral view; **A**<sub>2</sub>: apertural view showing the ventral spines on the adult phragmocone; **A**<sub>3</sub>-**A**<sub>4</sub>: ventral views at D = 88 and 70 mm, respectively; **A**<sub>5</sub>-**A**<sub>6</sub>: lateral and ventral views, respectively, of the innermost whorls at D = 26 mm. – The asterisk indicates last septum. All natural size (x1).



**Figure 76.** Windhauseniceras internispinosum (Krantz) transient beta [M]. Diagram representing the position of the ventral spines (sp) relative to the growth stages, based on the specimen in Fig. 75.  $A_1$ : development of the spines from about D = 90 mm.  $A_2$ : spines located on the roof of the bodychamber when the shell has D = 210 mm.  $A_3$ : spines located around the last septum and beginning of bodychamber when the shell is fully grown, at about D = 300 mm. Ph: phragmocone, BC: bodychamber, sp: ventral spines (see Fig. 75A<sub>2</sub>). –All same scale, reduced x0.2.

inner whorls, which are more densely ribbed with no trifurcations or coronate stage. The most consistent difference is the dense, bifurcate ribbing of the inner whorls of the specimens assigned to *C. proximus*. The co-occurrence of abundant specimens of both species in the same level, intergrading in shell morphology and sculpture, strongly suggests *W. internispinosum* originated from *C. proximus*. This hypothesis was already suggested in Parent (2001, 2003b). Later, PSS (2011: fig. 29F) figured the nucleus of an intermediate specimen from the base of the Internispinosum Z. of Arroyo Cieneguita which can be assigned to the transient alpha of the species.

The short stage of spiny ventral ribs at the beginning of the last whorl of the phragmocone in the macroconch of transient beta (Figs. 75-76) is a structure which must have had different functions during ontogeny: (1) external during the juvenile age (Fig. 76A<sub>1</sub>), perhaps related with protection against predators or resting on seafloor; (2) in the subadult age the spines would have been located in the roof of the bodychamber (Fig. 76A<sub>2</sub>), and (3) in the adult age the spines become partially covered by the subsequent whorl (Fig. 76A<sub>3</sub>), and could have had some relationships with the attachment of the paired retractor muscles.

**Occurrence and distribution**.- Our material comes from the Internispinosum Z. (upper Middle Tithonian). The species is widely distributed throughout the basin (Leanza & Hugo 1977, Parent 2003b).

## Genus Corongoceras Spath, 1925 Type species: Corongoceras lotenoense Spath, 1925; by original designation.

**Remarks.-** The genus is herein interpreted in the restricted sense of PSS (2011). Its origin has remained elusive, but some recent fidings in different localities begin to shed light about possible ancestors. In basal levels of the Internispinosum Z. at Cerro Lotena and Cerro Granito, nearly equivalent to level PT-22 present section, occurs a group of ammonites, which could represent the earliest *Corongoceras*. These platyconic, evolute and tuberculate, ventrally tabulate ammonites are slightly older



**Figure 77**. **A**: *Corongoceras* aff. *mendozanum* (Behrendsen), unnumbered specimen from level PT-22, Internispinosum Z. **B**: *Corongoceras mendozanum* (Behrendsen), adult [M] phragmocone with beginning of bodychamber (MOZ-PI 8090/1), level PT-36, *vetustum* Hz., Alternans Z. – All natural size (x1).

but similar to the specimen figured by Leanza (1980: pl. 6: 6) as *Corongoceras lotenoense*. These ammonites also show similarities with the upper Proximus Z. *Corongoceras*? sp. A in PSS (2011: fig. 33A). It appears that *Corongoceras* would have derived from late representtives of *Catutosphinctes proximus* in the lower Internispinosum Z.

The poorly preserved specimen in Fig. 77A as *Corongoceras* aff. *mendozanum* (Behrendsen, 1891), from level PT-22 (lower Internispinosum Z.), seems to belong to *Corongoceras* by the aspect of the ribbing of the penultimate whorl. The outer whorl is very evolute and densely ribbed, differing from the sculpture of *C. mendozanum* (e.g. PSS 2011: figs. 33-34). This fragmentary specimen is figured only for it can be matched with a complete specimen of *Corongoceras* we have recently collected from a section at Mallín Quemado.

#### Corongoceras mendozanum (Behrendsen, 1891) Fig. 77B, 78A-E

Synonymy.- See PSS (2011).

**Material**.- 6 specimens from level PT-34; 12 specimens from level PT-36.

**Remarks.**- The species was revised and described in detail in PSS (2011) from material of A. Cieneguita. In the present



**Figure 78.** A-E: *Corongoceras mendozanum* (Behrendsen), Alternans Z. A: Juvenile [M] (MOZ-PI 8510), level PT-34. B: Portion of adult [M] bodychamber (MOZ-PI 8509), level PT-34. C: Phragmocone [M?] (MOZ-PI 8084), level PT-36, *vetustum* Hz. D: [M] phragmocone (MOZ-PI 8089); D<sub>3</sub>: innermost whorls (x2). E: Portion of adult [M] bodychamber (MOZ-PI 8086), level PT-36, *vetustum* Hz. F: *Corongoceras*? *steinmanni* (Krantz), nearly complete adult [M] (MOZ-PI 8086), level PT-36, *vetustum* Hz.; F: *Corongoceras*? *steinmanni* (Krantz), nearly complete adult [M] (MOZ-PI 8086), level PT-36, *vetustum* Hz.; F<sub>1</sub>: ventral view showing the bodychamber (displaced) and last whorl of phragmocone; F<sub>2</sub>: phragmocone apertural view; F<sub>3</sub>: lateral view. – All natural size (x1), except D<sub>3</sub> (x2). The bar indicates 10 mm for natural size views (x1), but 5 mm for D<sub>3</sub> (x2). The asterisk indicates the last septum.



Figure 79. *Himalayites* cf. *treubi* Boehm, level PT-54, Koeneni Z., *koeneni* Hz. (new). Field photographs of material not collected. A: Subadult with bodychamber [M]. B: Adult [M] with bodychamber. Note the abundance of *Substeueroceras koeneni*. C: Inner whorls. – All natural size (x1).

section the species occurs in abundance in two discrete levels of the Alternans Z., represented by specimens somewhat more inflated than the holotype (Behrendsen 1891: pl. 25: 2; 1921: pl. 2: 4) but comparable with the inflate variants from A. Cieneguita.

#### Corongoceras? steinmanni (Krantz, 1926) Fig. 78F

**Material**.- 2 adult macroconchs with parts of bodychamber (MOZ-PI 8082/1-2) from level PT-36 (*vetustum* Hz., Alternans Z.).

**Description.-** Phragmocone moderately involute with suboval whorl section; sculpture composed of radial primary ribs of which one each two is bifurcated on the upper half of the flank; ventral ribs cross the venter with no interruptions and some bear a bullate tubercle just above the ventrolateral shoulder. The bodychamber is poorly preserved, beginning at D=90-100 mm; the ribbing is stronger, forming a lamellar tubercle on the ventrolateral shoulder, then crossing the venter high and acute. In the last parts preserved of the phragmocone (adult) and bodychamber, the flanks appear as very high, but they are actually much lower, deformed by crushing.

**Remarks.**- These specimens perfectly match the lectotype (Krantz 1928: pl. 1: 3) and additionally show partially the bodychamber which remained unknown. The species was recorded in the lower Alternans Z. of Arroyo Cieneguita (PSS

2011: fig. 35). The generic assignation remains unclear for the species of the genus *Corongoceras* show in the adult phragmocone only small tubercles in the ending of all the ventral ribs with a well-defined smooth mid-ventral band (see PSS 2011).

This conspicuous ammonite recorded consistently in the Alternans Z. of the central Neuquén Basin could be a valuable biostratigraphic guide, especially considering that in the studied section is associated in the level PT-36 with other ammonites typical of this zone (see discussion below) and which characterize the *vetustum* Hz.

Genus *Himalayites* Uhlig in Boehm, 1904 Type species: *Himalayites treubi* Boehm, 1904; by subsequent designation of Douvillé (1912).

### *Himalayites* cf. *treubi* Boehm, 1904 Fig. 79

**Material**.- Several moderately well-preserved phragmocones and complete specimens in level PT-54, not collected.

**Description**.- Stout, moderately involute serpenticones with large lateral spines from about D = 15 mm up to the adult bodychamber. Whorl section rounded passing from wider than high (juvenile phragmocone) to slightly higher than wide on the bodychamber. The relative umbilical width tends to enlarge through the ontogeny, passing from U/D = 0.34 (at D = 30-40



Figure 80. A-B: *Pseudhimalayites subpretiosus* (Uhlig), level PT-19, *internispinosum* alpha Hz. (new), Internispinosum Z. A: Inner whorls (MOZ-PI 8013) finely preserved showing the long lateral spines, which are commonly preserved as lateral tubercles. B: Adult [M] phragmocone, field photograph of a not collected specimen. C-E: *Physodoceras* n. sp. A, level PT-12, *erinoides* Hz., Zitteli ["Mendozanus"] Z. C: [M] phragmocone (MOZ-PI 7970/1). D: [M] phragmocone (MOZ-PI 8445/12). E: Adult [m] phragmocone with beginning of bodychamber (MOZ-PI 7970/3). F-H: *Physodoceras* n. sp. B, level PT-12, *erinoides* Hz., Zitteli ["Mendozanus"] Z. C: [M] phragmocone (MOZ-PI 7970/5). H: [M] phragmocone (MOZ-PI 7970/6). -All natural size (x1).

mm) to 0.47-0.50 (at D = 80-135 mm).

The sculpture of the innermost whorls (D < 20 mm) is poorly preserved but can be seen to be composed of sharp prosocline primary ribs. From about D = 20 mm the sculpture consists of 6-7 acute primaries which bear a strong, hollow conical tubercle slightly below the mid-flank from which trifurcates in widely splayed secondaries. Some few primaries with no tubercle are intercalated irregularly between pairs of those tuberculate. This sculpture configuration remains constant up to the beginning of the adult bodychamber where the primaries with no tubercles are weak and tend to disappear. The largest specimen has D = 135-140 mm, probably near peristome.

**Remarks.**- The specimens described are very similar in size, shell-shape and sculpture ontogeny to the holotype of *H. treubi* Boehm (1904: pl. 7: 2), differing by the smooth intercostal spaces in our specimens. However, this difference cannot be definitely evaluated for our specimens are moulds in which some details of the sculpture could have been erased. The holotype of *Himalayites andinus* Leanza (1975: fig. 3a) differs by the occurrence of smaller tubercules and dense laterial ribbing; furthermore the paratype (Leanza 1975: fig. 3b-c) has a very dense ribbing with tubercles from which born shaves of fine secondary ribs, some of which raise on small ventro-lateral bullae.

**Occurrence and distribution.**- The species was only recorded from a thin bank of hard calcareous sandy shale, level PT-54, *koeneni* Hz. (new), Koeneni Z. In this level also occurs abundant *S. koeneni*, ostreids and brachiopods (see Fig. 79B).

### Family Aspidoceratidae Zittel, 1895 Subfamily Aspidoceratinae Zittel, 1895 Genus *Physodoceras* Hyatt, 1900

Type species: Ammonites circumspinosus Oppel, 1863 (= Ammonites circumspinosum Quenstedt, 1849); by original designation.

> Physodoceras n. sp. A Fig. 80C-E

**Material**. - 4 [M] phragmocones (MOZ-PI 7970/1, 8445) and 1 incomplete [m] (MOZ-PI 7970/3) from level PT-12.

**Description.**- *Macroconch*: maximum preserved diameter within 40 and 45 mm: compressed (W/D = 0.33) and rather narrowly umbilicate (U/D = 0.18-0.20) with suboval, higher than wide whorls. Sculpture composed of wide and faint undulations on the upper flank and venter.

*Microconch*: small adult phragmocone with a median sulcus in the flank.



Figure 81. A: *Toulishpinctes* cf. *rafaeli* (Oppel), adult [M] bodychamber (MOZ-PI 8001/2), x0.5, level PT-20 (loose), Internispinosum Z. B: Aspidoceratinae indet. [Laevaptychus] (MOZ-PI 7564), x0.5, level PT-19, *internispinosum* alpha Hz. (new), Internispinosum Z. – The asterisk indicates the last septum.

**Remarks.-** The material comes from a single horizon: level PT-12, *erinoides* Hz., Zitteli ["Mendozanus"] Z. Similar specimens including adults of both sexes were collected from comparable stratigraphic position in Cerro Lotena and Cerro Granito. The combination of wide ventral undulations on a smooth shell with compressed whorl section seems to be not known in other species of *Physodoceras* in the literature.

## Physodoceras n. sp. B Fig. 80F-H

Material.- 6 phragmocones (MOZ-PI 7970/5-6, 8445) from level PT-12.

**Description**.- Compressed, narrowly umbilicate, flanks high and smooth from the inner whorls. From D = 22 mm occasional faint lateral ribbing with weak periumbilical tubercles. The septal suture line is typical of the Aspidoceratidae, with wide and low saddle S1.

**Remarks.-** The material comes from level PT-12, *erinoides* Hz., Zitteli ["Mendozanus"] Z. This species has been recorded in other localities of the Neuquén Basin: (1) Zitteli ["Mendozanus"] Z. of Picún Leufú (PGSS 2011: fig. 32C), (2) same zone in Piuquenes Pass, N Mendoza (Aguirre-Urreta & Vennari 2009: fig. 5f), and (3) Proximus Z. of Arroyo Cieneguita (PSS 2011: fig. 37E).

The compressed and involute shell is not frequent in the Aspidoceratidae. The specimens are similar to *Physodoceras episus* (Oppel, 1856) by the smooth flanks with gentle periumbilical tubercles. *Aspidoceras tenuiculum* and *Aspidoceras eligmoptychum* Fontannes, 1879 are similar to the present species but more inflate with well marked lateral ribbing and periumbilical tubercles, and are significantly older.

Genus Pseudhimalayites Spath, 1925 Type species: Aspidoceras steinmanni Haupt, 1907 (= Cosmoceras subpretiosum Uhlig, 1878); by original designation.

#### Pseudhimalayites subpretiosus Uhlig, 1878 Fig. 80A-B

Synonymy.- See Schweigert (1997) and Parent (2001).

**Material**.- 1 small phragmocone (MOZ-PI 8013), 1 cast from the impression of a macroconch, and several fragmentary specimens. All from level PT-19.

**Remarks.**- The specimens show the typical trituberculation (umbilical, lateral and ventral) of the macroconch phragmocone. The ventral tubercles are known to fade away from the preadult phragmocone, from about D = 100 mm (PGSS 2013a). The microconch was described in PSS (2011).

The small phragmocone of Fig. 80A shows the long lateral spatulate spines (cf. PGSS 2013a: fig. 24C), which form a rounded tubercle in the internal mould. This specimen is identical to the holotype of *Cosmoceras subpretiosum* Uhlig, refigured in Schweigert (1997: pl. 1: 4), giving additional support to the consideration of *P. steinmanni* as a junior synonym proposed by Schweigert (1997).

**Occurrence and distribution.**- The specimens come from level PT-19, *internispinosum* alpha Hz., base of the Internsipinosum Z. This stratigraphic position is comparable to the occurrence levels of the specimen from Cerro Lotena in PGSS (2013a: figs. 24C, 25A). The specimens from Arroyo Cieneguita (PSS 2011) and Portada Covunco (PGSS 2013a: fig. 25B) come from the *falculatum* Hz. or equivalent positions within the Proximus Z., somewhat older than the present material from both occurrences is for the time being somewhat scarce and/or incomplete for detailed comparisons, but it seems that the adult macroconchs should be larger and stouter in the Internispinosum Z. The species is widely recorded through most sectors of the Neuquén Basin (see Leanza & Olóriz 1987, Parent 2001, PSS 2011).

#### Genus Toulisphinctes Sapunov, 1979

Type species: *Toulisphinctes ziegleri* Sapunov, 1979; by original designation

# *Toulisphinctes* cf. *rafaeli* (Oppel, 1863) Fig. 81A

**Remarks.**- 1 adult [M] bodychamber with remains of phragmocone, loose from levels PT-20-22 and a large fragmentary macroconch with laevaptychus from level PT-19 (lower Internispinosum Z.). Large, stout and moderately involute with narrow umbilicus; whorl section suboval, wider than high. The bodychamber begins at about D = 160 mm, it is uncoiled on the last part and more than three quarters long (maximum preserved D = 300 mm), but does not seem to be complete. Sculpture composed of umbilical tubercles from which born one or two gross ribs, and the anterior secondary bears other tubercle on mid-flank; all ribs cross the venter with no interruptions but fading towards the peristome.

Similar ammonites have been recorded virtually all throughout the basin: Cerro Lotena (to be published elsewhere), Zitteli ["Mendozanus"]-lower Internispinosum zones; Pampa Tril (herein), lower Internispinosum Z.; Arroyo Cieneguita (PSS 2011), upper Proximus Z. The large fragment from the lower Internispinosum Z. of Barda Negra, figured as *Aspidoceras* cf. *euomphalum* (Steuer, 1897) by Parent et al. (2007: fig. 5A), is most likely a *Toulisphinctes* considering the



**Figure 82.** A-C: *Haploceras staszycii* (Zeuschner), Zitteli ["Mendozanus"] Z. A: Phragmocone (MOZ-PI 7993/3), level PT-14. B: Phragmocone (MOZ-PI 7970/7), level PT-12, *erinoides* Hz. C: Adult phragmocone (MOZ-PI 7993/2), level PT-14;  $C_1$ : cross section view;  $C_2$ : innermost whorls (x2). – All natural size (x1), except  $C_2$  (x2). The bar indicates 10 mm for natural size views, but 5 mm for  $C_2$ (x2).

sculptural pattern. The possible microconch of this species was described as *Toulisphinctes*? sp. A (PSS 2011).

A large, complete Laevaptychus from level PT-19 is shown in Fig. 81B. It could belong to the *T*. cf. *rafaeli* of this level.

> Superfamily Haploceratoidea Zittel, 1884 Family Haploceratidae Zittel, 1884 Genus Haploceras Zittel, 1870 Type species: Ammonites elimatus Oppel, 1865;

> by subsequent designation of Spath (1923b).

## Haploceras staszycii (Zeuschner, 1846) Fig. 82

**Material**. - 2 phragmocones from level PT-12; 2 phragmocones from level PT-14. Zitteli ["Mendozanus"] Z.

**Description.-** Moderately inflate and involute from the innermost whorls, wide suboval whorl section with flat lower flanks, and narrow umbilicus with high subvertical wall. Almost smooth, faint ribs on the upper flank at about D = 15 mm. All are incipiently uncoiled indicating maturity. At D = 22 mm, U/D = 0.15, and at D = 34-38 mm, U/D = 0.18,  $W/H_1 = 0.67$ .

**Remarks.**- The specimens completely match those figured by Zeuschner (1846: pl. 4: 3) and Zittel (1870: pl. 27: 2-3). All our material comes from the Zitteli ["Mendozanus"] Z., and seems to be the first record of the genus in the Neuquén Basin.

Family Lissoceratidae Douvillé, 1885 Genus *Pseudolissoceras* Spath, 1925 Type species: *Neumayria zitteli* Burckhardt, 1903; by subsequent designation of Roman (1938).

Remarks.- The genus is assigned to the family Lissoceratidae assuming a long evolutionary line Lissoceras Bayle 1879-Lissoceratoides Spath 1923b to which is added Pseudolissoceras as a natural extension into the Tithonian. Parent (2001) suggested Pseudolissoceras could have been originated from Haploceras, but the similarities in shell morphology, septal suture line, and the form of sexual dimorphism with Lissoceratoides (and even with Lissoceras) are much closer. The proposal that Lissoceratoides might be reunited with Lissoceras was already suggested by Roman (1938: 173), Donovan et al. (1981) and, more recently by Callomon (pers. comm. 30/06/2006). The only serious reason for the original separation seems to have been the then perceived stratigraphical gap, between Bathonian and Oxfordian, which has since also been filled (Oxfordian: Fözy et al. 1997), and extended up to the Kimmeridgian (Andelkovic 1966: pl. 4: 1, Sarti 1993, Főzy & Scherzinger 2013a). The earliest Pseudolissoceras (P. olorizi Főzy, 1988) occurs in the lowermost Tithonian and with gradual morphologic changes towards more compressed and involute forms, the genuslineage evolves towards the forms included in Pseudolissoceras zitteli. This species most likely arrived to the eastern Pacific Ocean from the Tethys Ocean in the late Darwini Z. or early Semiforme Z., quickly expanded, and evolved in the Neuquén Basin during the late part of the Zitteli ["Mendozanus"] Zone (Parent 2001), rather equivalent to the Semiforme Z. (see below).

### Pseudolissoceras zitteli (Burckhardt, 1903) Fig. 83

Synonymy.- See Leanza (1980) pars, Parent (2001), Aguirre-Urreta & Vennari (2009), and PSS (2011).

**Material**.- 1 poorly preserved specimen from level PT-10c; 1 specimen form level PT-11; 41 specimens from level PT-12; 8 specimens from level PT-14.

**Remarks.**- The stratigraphic range of the species in Pampa Tril extends from level PT-10c to PT-14, defining the local *Zitteli* (total-range) Biozone. The species can be collected in abundance from the concretions of levels PT-12 and PT-14 where occurs almost exclusively in the form of subadult phragmocones of macroconchs. The species has been described in profusion (Krantz 1928, Leanza 1980, Parent 2001, PGSS 2011). The material from Pampa Tril is typical, so that we have figured only four specimens to show the local aspect of the species. In the level PT-14 most specimens tend to be more inflate from the inner whorls (Fig. 83C-D) than those of the level PT-12 (Fig. 83A-B).

The macroconchs of *P. zitteli* are similar to those of the *Haploceras* with which co-occur in levels PT-12 and PT-14, but these latter are by rule more inflate with flat flanks and deeper umbilicus, and tend to have faint wide ribs on the upper flank of phragmocone. The septal suture lines are very different, but this feature is usually not preserved or not accessible to direct observation.

## Family Oppeliidae Douvillé, 1890 Subfamily Taramelliceratinae Spath, 1928 Genus *Metahaploceras* Spath, 1925

Type species: *Ammonites strombecki* Oppel, 1858 (objective synonym: *Metahaploceras affinis* Spath, 1925).

Remarks.- Accepting the renaming of Ammonites lingulatus



**Figure 83.** *Pseudolissoceras zitteli* (Burckhardt), Zitteli ["Mendozanus"] Z. A: Adult [M] phragmocone (MOZ-PI 7970/20) of a compressed variant, level PT-12, *erinoides* Hz. B: Inner whorls (MOZ-PI 7970/15), level PT-12, *erinoides* Hz. C: Adult [m] phragmocone with beginning of bodychamber (MOZ-PI 7993/11), level PT-14. D: Subadult [M] phragmocone (MOZ-PI 7993/14) of an inflate variant, level PT-14. – All natural size (x1). The asterisk indicates the last septum.

nudus Quenstedt, 1849 as Ammonites strombecki Oppel, 1857, then Metahaploceras affinis Spath, 1925 [= Ammonites lingulatus nudus (Quenstedt, 1887); sic Spath (1925: 113)] is an objective junior synonym of Ammonites strombecki Oppel, 1857.

"Ammonites lingulatus nudus" as defined by Quenstedt consisted of both, microconchs which were mentioned in the text as lappeted specimens but not illustrated and the illustrated example, which is a macroconch. Dimorphism was not recognized in that time, and therefore Oppel restricted "Ammonites lingulatus nudus" for the microconchs (lingulatus refers to the lappet) and Ammonites strombecki for the illustrated macroconch. Quenstedt did not know about sexual dimorphism but he expected that lappeted and unlappeted forms can exist in one species. This would be a rather modern view, however, the material did not come from the same bed and therefore his syntypes consisted of specimens from various taxa.

Metahaploceras aff. acallopistum (Fontannes, 1879) Fig. 84A-B **Material**.- 2 incomplete, well-preserved specimens (MOZ-PI 7974/1-2) from level PT-12.

**Description.-** Inner whorls (D < 20 mm) compressed and involute, smooth. Middle whorls, from about D = 30 mm (last whorl of the adult phragmocone), compressed and involute (U/D = 0.11 at D = 33 mm) with suboval, higher than wide whorl section; the umbilical shoulder and the venter are gently rounded. Primary ribs are feeble, subfalcoid, undivided, stronger on the middle flank; near the end of the phragmocone and beginning of the bodychamber they become wider on the upper flank and fade off leaving the venter smooth. The adult bodychamber is poorly preserved in the two specimens, beginning at  $D_{ls} = 43$  and 48 mm, preceded by the onset of uncoiling (U/D = 0.17 through D = 40.48 mm) in the last portion of the phragmocone.

**Remarks.**- The present specimens come from the level PT-12, *erinoides* Hz., Zitteli ["Mendozanus"] Zone. They are very similar to *Metahaploceras acallopistum* (Fontannes, 1879: pl. 6: 5) as well as to the specimens figured by Berckhemer & Hölder (1959: pl. 19: 90, 94). Nevertheless, our specimens have weaker ribbing on the lowermost flank and the umbilical shoulder is more rounded.

Metahaploceras ranges all throughout the Kimmeridgian, e.g. M. strombecki in the Early Kimmeridgian and M. acallopistum in the late Kimmeridgian. The specimens described come from younger levels, in the Middle Tithonian Zitteli ["Mendozanus"] Zone, but the few typical sculptural characters which characterize the genus are apparently well expressed in them. Thus, it could be expected that some representatives have survived elsewhere than in the Central Tethys and shortly migrated into the Neuquén Basin. This kind of late representatives of Metahaploceras could also be represented by certain ammonites reported from Mexico: (1) the specimen figured by Burckhardt (1906: pl. 18: 4-7) as Oppelia aff. strombecki from the late Kimmeridgian (most likely Beckeri Zone according to Hillebrandt, Smith et al. in Westermann 1992) of Sierra de Santa Rosa, and (2) Haploceras aff. costatum Burckhardt (1906: pl. 25: 1-2), from a similar stratigraphic position in Vereda del Quemado, has a sculpture very similar to our specimens and to the representatives of M. acallopistum cited above.

#### Genus Pasottia Parent, Schweigert, Scherzinger & Enay, 2008

Type species: *Pasottia andina* Parent, Schweigert, Scherzinger & Enay, 2008; by original designation.

Pasottia andina Parent, Schweigert, Scherzinger & Enay, 2008 Fig. 84C-D

**Remarks.**- The species is moderately abundant in levels PT-12 and PT-14, Zitteli ["Mendozanus"] Zone, represented by macro- and microconchs. All these specimens are very similar to the type material from Cerro Lotena and to the material from La Amarga (Cerro Granito). The species is rather widely distributed through the Neuquén Basin, besides the cited localities it occurs also in Arroyo Cieneguita (see PSSE 2008, PSS 2011, PGSS 2013a). There are no significant variations between the samples of different areas, although the adult bodychamber of the macroconch is poorly known. All the recorded specimens come from the Zitteli ["Mendozanus"] Zone.



Figure 84. A-B: Metahaploceras aff. acallopistum (Fontannes), level PT-12, erinoides Hz., Zitteli ["Mendozanus"] Z. A: Almost complete adult [M] with part of the bodychamber (MOZ-PI 8445/1); A<sub>3</sub>: lateral view of the left side showing the sculpture not well preserved in the right side. B: Adult? [M?] phragmocone (MOZ-PI 7974/1). C-D: Pasottia andina, level PT-12, erinoides Hz., Zitteli ["Mendozanus"] Z. C: Adult [M] phrgmocone (MOZ-PI 7970/19). D: Adult [m] (MOZ-PI 7971/17). E-F: Parastreblites? cf. comahuensis Leanza. E: Phragmocone (MOZ-PI 8445/2), level PT-12, erinoides Hz., Zitteli ["Mendozanus"] Z. F: Phragmocone (MOZ-PI 8007), level PT-19, internispinosum alpha Hz. (new), Internispinosum Z. – All natural size. The asterisk indicates the last septum.

Genus Parastreblites Donze & Enay, 1961 Type species: Oppelia circumnodosa Fontannes, 1879; by original designation.

Parastreblites? cf. comahuensis Leanza, 1980 Fig. 84E-F

**Material**.- 1 specimen (MOZ-PI 8445/2) from level PT-12; 1 specimen (MOZ-PI 8007) from level PT-19.



**Figure 85.** A-I: *Cieneguiticeras perlaevis & C. falculatum* (Steuer, 1897), levels PT-12 and 14, Zitteli ["Mendozanus"] Z. Morphotypic classification: A-E: *C. perlaevis*: subadult macroconchs with crushed incomplete bodychamber (MOZ-PI 7558/3, 7970/1-3, 7975), level PT-12;  $D_3$ - $D_4$ : lateral and ventral views inner whorls (x2);  $E_1$ : ventral view inner whorls (x2): F-I: *C. falculatum*; F: adult phragmocone (MOZ-PI 7558/4), level PT-14; G: Juvenil? [M] with part of bodychamber (MOZ-PI 7558/5). Jevel PT-14; H: adult [M] phragmocone (MOZ-PI 7558/2), level PT-14; I: Adult [m] with almost complete bodychamber (MOZ-PI 7558/5). J-K: *Cieneguiticeras* n. sp. A., level PT-19, *internispinosum* alpha Hz., Internispinosum Z.; J: Adult microconch with lappets (MOZ-PI 8006); K: Adult macroconch phragmocone (MOZ-PI 8460). The asterisk indicates the last septum. All natural size (x1), except  $D_3$ - $D_4$  and  $E_1(x2)$ . The bar indicates 10 mm for all, except for  $D_3$ - $D_4$  and  $E_1(5 \text{ mm})$ .

**Remarks.**-The specimen from level PT-12 is very similar to the specimen from the *perlaevis* Hz., Zitteli ["Mendozanus"] Z. of A. Cieneguita described in PSS (2011: fig. 39C). The specimen from level PT-19, base of the Internispinosum Z., is also very similar but larger what allows to compare more closely with the holotype of *P. comahuensis*. The holotype seems to differ in being more involute than our material, but all these ammonites are smooth and *P. comahuensis* was defined on the basis of a single, completely septated specimen, thus the adult bodychamber and variation of the species in its type locality and horizon are unknown. This situation prevents definitive assignation of our scarce and incomplete material, being necessary a sample of topotypes that could provide the necessary information about the species.

The only new information the present material provides is the occurrence of this kind of ammonites in the lowermost Internispinosum Z. Genus Cieneguiticeras Parent, Myczinski, Scherzinger & Schweigert, 2010 Type species: Haploceras falculatum Steuer, 1897; by original designation.

Cieneguiticeras perlaevis (Steuer, 1897) & Cieneguiticeras falculatum (Steuer, 1897) Fig. 85A-E, F-I

Synonymy.- See PSSE (2008).

**Material**.- 4 phragmocones from level PT-10c; 11 [M] phragmocones from level PT-12; 12 [M] phragmocones and 1 complete and 3 fragmentary [m] from lower part of level PT-14.

Description.- Specimens from level PT-12: Macroconch:

Inner whorls (D < 10-12 mm) involute, suboxyconic, smooth. Outer whorls of phragmocone through D = 12-50 mm are involute (U/D = 0.12-0.16) and variably inflated (W/D = 0.26-0.33); most specimens smooth, few with more or less prominent lunuloid primaries on the upper half of flanks; venter generally smooth, but few specimens with ventral ribs forming a ventral chevron. The bodychamber is partially preserved but crushed in most specimens.

Specimens from level PT-14: *Macroconch*: Inner whorls indistinguishable from those of the specimens from level PT-12. Outer whorls with increasingly stronger and denser lunuloid ribs on the upper flank. One specimen is completely septated at D = 50 mm. *Microconch*: The best preserved specimen is almost complete. The last whorl of the phragmocone has a row of lingulate structures in the mid-flank. The adult bodychamber begins at  $D_{\rm ls} = 24$  mm, half whorl is preserved.

Remarks.- The type material of C. perlaevis and C. falculatum described by Steuer (1897, transl. 1921) comes from two well separated horizons in the lowermost Zitteli ["Mendozanus"] (or upper Picunleufuense) and Proximus zones, respectively (PMSS 2010). The lectotypes are differentiated from involution and ribbing of the last whorls of phragmocone, being in C. falculatum more involute, and densely and strongly ribbed. The abundant macroconchiate specimens in the present samples from levels PT-12 and PT-14 include specimens, which intergrade in shell-shape and especially ribbing between C. perlaevis and C. falculatum. Under a morphotypic taxonomy, they would be assigned to C. perlaevis (weakly ribbed or smooth, Fig. 85A-E) and others to C. falculatum (more densely and strongly ribbed, Fig. 85F-H). The smooth or weakly ribbed specimens dominate in level PT-12 and those more strongly and densely ribbed occur only in level PT-14.

The interpretation adopted herein is that these intergrading morphotypes represent two transients of a continuous evolving lineage, which could be classified as *C. perlaevis* in level PT-12 and *C. falculatum* in level PT-14. Ribbed specimens in level PT-12 would be nothing but the first representatives developing incipiently the sculpture, as part of the intraspecific variation, which later dominates in the lineage. This so-called horizontal classification is more natural and helps to understand the evolutionary changes of the species from a close stratigraphic control of sampling. Nevertheless, for nomenclatural purposes the specimens are labelled under morphotypic classification as indicated above and so denoted in Fig. 5. Macroconch phragmocones from level PT-10c although poorly preserved can be assigned to *C. cf. perlaevis*.

The macroconch and microconchs figured by Cecca & Enay (1991: pl: 1: 9 and pl. 2: 6-8) as Neochetoceras sp. [M] and Glochiceras blaschkei [m], from the banc CA-Sud-10 of the Fallauxi Z. of Le Pouzin (L'Ardeche, SE France), are indistinguishable from the corresponding sexual dimorphs of C. falculatum (see PMSS 2010). The adult macroconch phragmocone is suboxyconic as in Cieneguiticeras and with similar adult size; the ribbing is identical, formed by oxycerites-like lunuloid ribs confined to the upper flank. The small adult microconchs are also very closely comparable in shell-shape and sculpture (including the lingulate ribs on midflank) with that of C. falculatum. It could be a case of homoeomorphy with C. falculatum, but more likely they had direct genetical relationship for: (1) the sexual dimorphism is identical, (2) the stratigraphic position is very similar, the Proximus Z. is usually correlated with the Fallauxi Z. (see below), and (3) there are lower and middle Tithonian records of Cieneguiticeras in the migration pathway between the Andes

and the Tethys, namely the Carribean region (Mexico and Cuba, see PMSS 2010).

**Occurrence and distribution.**-*C. perlaevis* and *C. falculatum* occur all throughout the basin, from South: Picún Leufú (PGSS 2011), Cerro Lotena (Leanza 1980: pl. 1: 2-3), Cerro Granito (PSSE 2008), Portada Covunco (PGSS 2013a), Pampa Tril this report, Chacay Melehué (material under study), and Arroyo Cieneguita (PSS 2011). These occurrences are recorded through the range from the Picunleufuense Z. to the Proximus Z.

Cieneguiticeras n. sp. A Fig. 85J-K

**Material.** 2 adult [M] phragmocones (MOZ-PI 8460) and 1 complete, but poorly preserved adult microconch (MOZ-PI 8006). All the specimens come from the level PT-19, *internsipinosum* alpha Hz. (new), lower Internispinosum Z.

**Description.**- *Macroconch*: the last whorl of phragmocone is covered by falcoid primary ribs which are stronger on the upper flank, separated by several fine intercalatories. Involute with compressed whorl section, venter rounded and smooth. *Microconch*: the adult phragmocone is rather evolute. The bodychamber is strongly uncoiled with falcoid primary ribs projected forward on mid-flank in the form of lingulate marks. These projections of the ribs become more pronounced and transformed in long lappets projected from the peristome.

**Remarks and comparison.**- These specimens are unique within the genus for the dense and fine ribbing on the upper flanks in the macroconchs. The microconch is similar but more evolute than those of *C. falculatum*. This is an undescribed species which occurs in the basal horizon of the Internispinosum Z. (*internispinosum* alpha Hz., new), above the horizons where *C. falculatum* typically occurs (Proximus Z.) in Arroyo Cieneguita. In levels of this section, equivalent to PT-19, is known a small specimen described as *C.* cf. *falculatum* (in PMSS 2010: fig. 5F) which has strong ribs on the upper flank of its outermost preserved whorl at D = 23 mm; unfortunately the present specimens cannot be observed at this size for comparison.

## **BIOSTRATIGRAPHY AND TIME-CORRELATION**

Methodological remarks.- Time-correlation is an estimation of stratigraphic age respect to a chronostratigraphic standard scale. The quality of an estimation has two main properties to consider: (1) accuracy and (2) precision. Precise timecorrelations would allow the reproducibility: new samplings would reproduce the estimation. Accurate time-correlation is that which agrees with, or is as close as possible to, the true value of the standard scale of reference. Precise (i.e. reproductible) results in fine time-correlation can be obtained only by working out successions of ammonite associations (see discussion in Gabilly 1971, Callomon 1985, 1995, Rogov et al. 2012, Garrido & Parent 2013, Schweigert 2015). The accuracy of time-correlations depends on the number of common morphotypes of the different ammonite species in the studied assemblage with respect to those of the guide-assemblage on which the stadard unit is defined.

First and last occurrences of single species in the fossil record are phenomena strongly controlled by the local palaeoecologic and taphonomic conditions, and statistically dependant of the contingencies and type of sampling. These punctual occurrences are frequently used for defining chronostratigraphic units, although they can provide neither chronostratigraphic stability nor consistency through different localities, even sections, at the scale of the ammonite-zone. On the other hand, these records generate non-standard scales, with gaps and/or overlaps, and so unaccurate correlations. These gaps and overlaps are detected by comparative studies of faunal successions, but usually remain imperceptible in most other geologic studies, introducing strong bias and errors in every interpretation dependant on time-correlation. A significative example is the overlapping of the "Mendozanus" and Zitteli zones discussed below. For overriding these strong limitations of the criteria of first and/or last occurrences of single species in time-correlation, whenever possible there must be worked out time-correlation by means of successions of ammonite assemblages.

It is very important to avoid confusions about the alleged numerical datations and time-correlations based on samples from Andean successions. The base of the (standard) Berriasian stage (the so-called Jurassic/Cretaceous boundary which is nothing but an ideal time-plane belonging neither to the Tithonian nor to the Berriasian) has not been established, or properly described yet in modern terms. Thus, time-correlation with supposed strata of the base of the Berriasian cannot be achieved in the Andes (probably neither in any region out of France for the time being). The base of the Berriasian, that would be the base of a Jacobi Standard Chronostratigraphic Zone, cannot be traced in the Andes simply because it is not yet so defined in the type locality. Moreover, the known Tethyan elements in the ammonite faunas of the Andean successions are not enough for accurate time-correlation with Tethyan horizons. Thus, it cannot be claimed to have dated the base of the Berriasian in Argentina using radiometric (numerical) datations because the materials to be dated are of unknown stratigraphic age respect to the Primary Standard Chronostratigraphic Scale. Furthermore, radiometric datations are much less accurate and precise than the ammonitebiostratigraphy-based chronostratigraphy.

The successions described in the present paper include some assemblages with ammonites which allow discrete comparisons attempting time-correlation with Tethyan assemblages or zones. As pointed out above, pending a definition of the Standard Jacobi Z., the recognition of the base of the Berriasian is far from been determined in the Andes. Considering that for the time being there are no reliable or exact time-correlations available with the base of the Tithonian and Berriasian, we refer to Andean Tithonian and Andean Berriasian.

Time-correlation of the Andean zonation with the Tethyan scale is frequently attempted by moving downwards or upwards the zonal boundaries when different ammonites are supposed to be of a certain age. Nevertheless, comparison of successions of ammonite assemblages is the consistent way to obtain accurate and precise time-correlations (Enay 1966: 594, Gabilly 1971, Callomon 1985, Cariou & Hantzpergue 1997). However, in favourable cases ammonite biohorizons can be defined from some ammonite assemblages occurring in a single or few beds of a local succession. Some biohorizons are excellent markers, in some cases over distances of thousands of kilometres (e.g. Callomon 1994, 1995, Blau & Meister 2000, Meister 2010). Our bottom-upwards approach is based on the construction of a scale of ammonite biohorizons referred to the chronostratigraphical zonal subdivision, and an effort to standardize its zones for enhancing time-correlation (e.g. PGSS 2011, PSS 2011, PGSS 2013a, 2013b, Parent & Garrido 2015). The biostratigraphic chronostratigraphy presented below, based on ammonite horizons, follows this programme.

#### The Andean chronostratigraphic scale

The chronostratigraphic classification adopted herein is shown in Fig. 86. Most of the zonal subdivision of the Andean Tithonian is derived from different kinds of biozones originally proposed from Burckhardt (1900, 1903) onwards (see details in Leanza 1981, PGSS 2011, PSS 2011). This zone scale is not yet wholly standardized in modern terms; only the Picunleufuense Zone was defined originally as a standard chronostratigraphic zone, by means of an ammonite horizon as its base (PGSS 2011). In consequence, considering that the zones are recognized by their ammonite content, the boundaries between those not yet standardized zones are herein approximated by the first occurrence of one or more ammonites which are characteristic of the zone. However, as discussed above, this procedure generates poor and unstable limits vulnerable to new findings, above and/or below the boundary drawn this way. Differently the ammonite horizons which are recognized into these zones are strong markers which can be used for fine timecorrelation between distant regions of the basin.

The fauna of the Virgatosphinctinae Bed of Leanza (1980) has long been considered the guide-assemblage of the Mendozanus Z. (ex Scythicus Z.) as occurring below the Zitteli Z., e.i. below the first occurrence of *P. zitteli* (e.g. Leanza 1980, 1981). The fauna of this Virgatosphinctinae Bed would consist mainly of C. erinoides (see Leanza 1980) which has been demonstrated to be the corresponding macroconch of C. mendozanus [m] (see PSS 2011, and discussion above), the index-species of the Mendozanus Zone. Nevertheless, this fauna has never been found below the Zitteli Z. (or first occurrence of P. zitteli), in our studies throughout the Neuquén Basin (PGSS 2011: Picún Leufú, PSS 2011: Arroyo Cieneguita, PGSS 2013a: Portada Covunco) nor in the present section, or the large samplings under study from Mallín Quemado, Estancia María Juana, and Cerro Lotena-Cerro Granito. Furthermore, below the first occurrences of P. zitteli in the totality of all these localities occur consistently an important fauna composed of L. picunleufuense, C. platyconus, C. guenenakenensis, C. perlaevis, and other ancillary ammonites, which characterizes the Picunleufuense (standard) Zone (PGSS 2011), including several differentiable horizons (Fig. 86). This latter fauna occurs widely, and is frequently very abundant and very clearly differentiable. As shown above (see Fig. 5), and in the cited papers, C. erinoides [M & m] occurs associated with P. zitteli, and frequently above the first occurrence of this latter species. The co-occurrence of these species has already been mentioned by Weaver (1931) as pointed out by PGSS (2011:93).

Finally, it is worth to note that in the section of Cerro Lotena we have collected 5 m above the basal conglomerate bed of the Vaca Muerta Fm, just below the Virgatosphinctinae Bed of Leanza (1980), several specimens of *P. zitteli* associated with complete macroconchs of a species of *Choicensisphinctes*. This *Choicensisphinctes* is intermediate in size and morphology between *C. platyconus* (which occurs below) and *C. erinoides*. *C. erinoides* is well represented by large and complete macroconchs, again associated with abundant complete macro- and microconchs of *P. zitteli*, in the same section of Cerro Lotena from about 10 m above the basal conglomerate bed.

In consequence, the Mendozanus and Zitteli zones can not be discriminated because of the overlapping, and frequent inversion, of the local biostratigraphic ranges of *C. erinoides* 

[M & m = C. mendozanus] and P. zitteli (see, e.g. Fig. 5) in different localities. This inconsistency observed virtually all throughout the Neuquén Basin is solved, preliminary, considering the Mendozanus Z. included into the Zitteli Z. (see Fig. 86), and denominated Zitteli ["Mendozanus"] Zone. Much of this problem has been created by several factors: (1) the new discoveries enlarging the biostratigraphic ranges of species of the assemblage of the "Mendozanus Z.", like C. erinoides, as well as that of P. zitteli below the type horizon, from the work of Burckhardt (1900, 1903), (2) the unstability of time-correlation by means of the local first and/or last occurrences (discussed above), like the usual concept of the Zitteli Z. (based on the total-range-biozone of P. zitteli, never to be known), and possibly (3) the fauna of the Picunleufuense Z. which seems to have been overlooked by most workers, could have been confused with those of the assemblage of the Scythicus Z. of Burckhardt (1900, 1903) named by Leanza (1980) as the fauna of the Virgatosphinctinae Bed.

Krantz (1928: 49) proposed the Calistoides Zone (indexspecies: P. calistoides) with type locality at Arroyo Durazno and characterized by the guide-assemblage composed of C. mendozanum (including Berriasella submendozana Krantz, 1928 and B. duraznensis Krantz, 1928), Blanfordiceras? argentinum Krantz, 1926, B. vetustum (as Berriasella subprivasensis Krantz, 1928), P. calistoides and Aspidoceras andinum Steuer, 1897. This assemblage was revised and assigned to the vetustum Hz. by PSS (2011), by which the Calistoides Z. is not partially equivalent to the Koeneni Z., as suggested by Leanza (1981: 78), but part of the current Alternans Z. The supposed occurrences of P. calistoides in the Koeneni Z. could likely correspond, actually, to Parodontoceras discoidalis (Gerth), as discussed above (see also PSS 2011). Windhausen (1918) proposed a zonation for the Tithonian-Valanginian interval of the Neuquén Basin which is very similar to that currently accepted. In this zonation, the Calistoides Z. was correctly placed below the Koeneni Z. in a position nearly equivalent to the current (upper?) Alternans Z. The Calistoides Z. has been almost ignored, only cited by some authors, e.g. Leanza (1945: 92) who proposed the alternative Alternans Z. This latter zone has been entrenched in the literature although the Calistoides Z. would have been of choice because its original definition is precise.

The zonation of the Andean Berriasian follows the wellestablished twofold subdivision of Leanza (1945), that is the Noduliferum and Damesi zones. These two zones are standardized herein by means of an ammonite biohorizon at the base of each one as discussed below.

Aguirre-Urreta (2001) defined the Trigonostomum Zone (= "Andiceras" faunule of Aguirre-Urreta & Álvarez 1999) as an interval of rocks between the Koeneni and Noduliferum zones in the "Malargue sector"; the only ammonite said to occur in this interval is "Andiceras" trigonostomum. Later, Vennari et al. (2012), although not stated explicitly, seem to have renamed this zone in their table 2 as the ("Andiceras") Planulatum Zone from material collected in the upper Vaca Muerta Fm and lower Chachao Fm from the far north located outcrops of the Real de Las Coloradas (Mendoza). There are some ammonites, other than Krantziceras planulatum, that Vennari et al. (2012) cite nominally for this interval: "Himalayites" egregius (Steuer, 1897), Micracanthoceras lamberti (Leanza, 1945), and Parodontoceras? subfasciatum (Steuer, 1897). We prefer, at least for the time being, to adopt the well-established twofold subdivision of Leanza (1945), especially considering the above mentioned nominal units are not defined consistently and seem to can be differentiated as an ammonite biohorizon, which would be named *planulatum* Hz. as indicated above. Considering the discussion given above for *Krantziceras compressum*, the position of this assemblage would be in the uppermost Koeneni Z., just below the *compressum* Hz. (standard base of the Noduliferum Z., discussion below).

The zonal subdivision of the lower part of the Andean Valanginian as represented in the studied section consists of the Wichmanni Zone (Leanza 1945) and the Riveroi Zone (Aguirre-Urreta & Rawson 1999).

#### Biostratigraphy of the studied section

The biostratigraphy and the derived chronostratigraphy of the ammonite succession of Pampa Tril based on the present study (Fig. 5) is interpreted as follows:

Level PT-1. This 2 m-thick level yields ammonites mainly as impression or crushed and decalcified; bivalves of thin shell are abundant (lucinids?) at all growth stages including larvae, and ostreids moderately abudant. A small assemblage of poorly preserved ammonites, including *Choicensisphinctes* cf. *platyconus*, *Choicensisphinctes*? n. sp. A and other form (a narrowly umbilicate and coarsely ribbed ammonite) not yet identified. This assemblage is the first record of ammonites below the *picunleufuense* alpha Hz. all throughout the basin. This level belongs to a horizon, which could be late Kimmeridgian or earliest Tithonan, older than the Picunleufuense Z.

**Picunleufuense (standard) Zone, levels PT-2 to PT-10a.** The species recorded in this zone are: *Choicensisphinctes platyconus, Catutosphinctes guenenakenensis, Lithacoceras picunleufuense, Choicensisphinctes* cf. *platyconus, Choicensisphinctes* n. sp. A, *Krantziceras*? sp. A, *Choicensisphinctes* cf./aff. *platyconus,* and *Choicensisphinctes* cf. *burckhardti.* The base of this standard zone is by definition the *picunleufuense* alpha Hz. which has been clearly recognized. This zone is characterized by a conspicuous assemblage recorded from the base of the Vaca Muerta Fm virtually in every sector of the Neuquén Basin.

*picunleufuense* alpha Hz. (PGSS 2011), levels PT-2-6: Abundant specimens of the typical assemblage, *C. platyconus*, *C. guenenakenensis*, and *L. picunleufuense* tr. alpha, as well as *C. cf. platyconus*, *Choicensisphinctes*? n. sp. A, *Krantziceras*? sp. A, and *C. cf./aff. platyconus*.

The level PT-8 could represent a differentiable horizon with a large, coarsely ribbed variant (transient?) of *L. picunleufuense*, the most compressed variant of *C. platyconus*, *C.* cf./aff. *platyconus*, *C.* cf. *burckhardti*, and *C. guenenakenensis*.

*picunleufuense* beta Hz. (PGSS 2011), level PT-10a: Late representatives of *C. platyconus*, *L. picunleufuense* tr. beta, and *C. guenenakenensis* (transitional to *Catutosphinctes* windhauseni).

Zitteli ["Mendozanus"] Zone, levels PT-10b to PT-14. The species recorded in this interval are: Choicensisphinctes cf. burckhardti, Choicensisphinctes erinoides, Pseudolissoceras zitteli, Cieneguiticeras cf. perlaevis, Mazatepites arredondense, Catutosphinctes n. sp. aff. guenenakenensis, Physodoceras n. sp. A, Physodoceras n. sp. B, Haploceras staszycii, Metahaploceras aff. acallopistum, Pasottia andina, Parastreblites? cf. comahuensis, Cieneguiticeras perlaevis,



**Figure 86.** Chronostratigraphic zone scale adopted in this paper (based on Leanza 1945, Leanza 1981, Aguirre-Urreta 1999, PGSS 2011 and PSS 2011 as explained in text). The *quinchoai* Hz. (ex *altum* Hz.) and the *catutosensis* Hz. have been introduced by Leanza & Zeiss (1992) for the local succession of Los Catutos. Biostratigraphic time-correlation chart for selected localities based on the recognition of ammonite bio-horizons in selected successions well constrained stratigraphically (see transect in Fig. 1A). Level numbers indicated into the boxes taken from the source of the information: PGSS (2011) for Picún Leufú (PL); PGSS (2013a) for Cerrito Caracoles-Portada Covunco (CC-PC); this report for Pampa Tril (PT); Leanza (1945) for Mallín Redondo (MR) and Arroyo del Yeso (AY); PSS (2011) for Arroyo Cieneguita (AC). Firm recognition of horizons indicated with gray boxes, tentative with white boxes. The asterisk indicates the type locality or section of the horizon. In every succession there are levels with ammonites between most of the horizons - unmber of horizons is expanded every time a new one is differentiated in the succession. The height of the boxes of each zone does not indicate time-duration neither content of horizons, they are sized for convenience of design. The limits between the stages are indicated in the sense of the Andean classification, not meaning necessarily exact time-correlation with the Primary Standard Scale (see Fig. 87). Abbreviation Kimm.: latest Kimmeridgian.

Notes: (1) After the results obtained in the present study the indicated horizons can now be recognized in the successions of Portada Covunco-Cerrito Caracoles described in PGSS (2013a). (2) The "unnamed Hz." (PGSS 2011: 95) is mainly characterized by the conspicuous *Choicensisphinctes* cf./aff. *platyconus* (in PSS 2011: fig. 6C-E), but in the studied section these ammonites are recorded in a lower position. (3) *W*. cf. *internispinosum* (in Leanza 1945: pl. 21: 6) perfectly matchs the transient alpha of the species as described above, strongly suggesting the horizon; in Arroyo Cieneguita the specimen in PSS (2011: fig. 29F) likely belongs to *W internispinosum* tr. alpha. (4) In Arroyo del Yeso the bed c of Leanza (1945: 89) yields *Corongoceras mendozanum* (as *Aulacosphinctes* sp.) and *Catutosphinctes australis* (Leanza, 1945) which is indistinguishable from *C. inflatus* of the *vetustum* Hz. (5) The specimen of *N. malbosiforme* described from bed 1771 of Mallín Redondo by Leanza (1945) as *Octagoniceras egregium* (Steuer), discussed above, suggests equivalence of this level with the *transgrediens* Hz., lying below the the levels with abundant *Spiticeras* like the horizon in its type locality, Arroyo del Yeso.

#### and Cieneguiticeras falculatum.

Most of these species have been attributed to the Zitteli and/or "Mendozanus" zones (Burckhardt 1900, 1903, Weaver 1931, Leanza 1980, Parent 2001, PGSS 2011, PSS 2011). The lower limit of the zone is tentatively drawn at the level PT-10b with the first occurrence of *C*. cf. *burckhardti* which probably indicates the *malarguense* Hz. of the lowermost Zitteli ["Mendozanus"] Z. (PGSS 2011).

*?malarguense* Hz. (PGSS 2011), level PT-10b: *C.* cf. *burckhardti* is the only species recorded in this poorly fossiliferous level and one of the guide species of the horizon (PGSS 2011).

*?perlaevis* Hz. (PGSS 2011), level PT-10c: The ammonites from this level (*C. erinoides*, *P. zitteli*, and *C. cf. perlaevis*) are not enough for a firm recognition of the horizon.

*erinoides* Hz. (PSS 2011), level PT-12: The assemblage of this level includes the ammonites which characterizes the horizon as defined in its type locality Arroyo Cieneguita. The index species is definitely assigned to *C. erinoides* leading to rename the "cf.-*erinoides* Hz." (PSS 2011) as *erinoides* Hz.

**Proximus Zone, levels PT-15 to PT-18.** This segment of the section is poorly exposed by which collection was very limited; the only species recorded is *Catutosphinctes proximus*. Considering this poor record, the zone is delimited as the interval between the uppermost occurrence of *P. zitteli* and the standard base of the Internispinosum Z., that is the *internispinosum* alpha Hz. (see below).

Internispinosum (standard) Zone, levels PT-19 to PT-31. The species recorded in this interval are: *Parastreblites*? cf. comahuensis, Catutosphinctes proximus, Choicensisphinctes sp. A (in PSS 2011), Cieneguiticeras n. sp. A, Windhauseniceras internispinosum, Pseudhimalayites subpretiosus, Toulisphinctes cf. rafaeli, Krantziceras cf. disputabile, Corongoceras aff. mendozanum, Paraboliceras? sp. A, and Catutosphinctes inflatus.

Most of these species have been reported to occur in the Internispinosum Z. (Weaver 1931, Leanza 1945, Leanza 1980, 1981, Parent et al. 2007). The lower limit of the zone is fixed at the level PT-19, the *internispinosum* alpha Hz.

*internispinosum* alpha Hz. (new), level PT-19: The cooccurrence of the figured morphotypes of the following species is taken as the assemblage which defines the new horizon: *P*? cf. *comahuensis*, *C. proximus*, *Choicensisphinctes* sp. A (*in* PSS 2011), *Cieneguiticeras* n. sp. A, *W. internispinosum* transient alpha, *P. subpretiousus*, and *T.* cf. *rafaeli*. The *internispinosum* alpha Hz. is herein proposed as the base for an Internispinosum Standard Chronostratigraphic Zone.

Alternans Zone, levels PT-32 to PT-50. The species recorded in this interval are: *Catutosphinctes inflatus* [M], *Choicensisphinctes striolatus* [M], *Choicensisphintes* cf. *striolatus*, *Parodontoceras calistoides* [M & m], *P. cf. calistoides*, *Pseudoparodontoceras dezai* n. gen. n. sp. [M & ?m], *Blanfordiceras vetustum* [M & ?m], *Blanfordiceras* cf. *bardense*, *Corongoceras mendozanum*, *Substeueroceras*? sp. A, *Corongoceras*? steinmanni [M], *Krantziceras azulense* [M], and *Lytoceras montanum*.

Most of these species have been reported to occur in the Alternans Z. (Leanza 1945, Leanza 1981, PSS 2011). It is interesting to note that the genus *Steueria* PSS, 2011 to which

belong the index-species *Steueria alternans* (Gerth, 1921), typical and abundant in this zone in several localities, has not been recorded in the studied section. The level PT-32 is tentatively considered the base of the local Alternans Z. for the first occurrence of *P. calistoides*, slightly below the assemblage of the *vetustum* Hz.

*vetustum* Hz. (PSS 2011), level PT-36: The association of *C. mendozanum, C. inflatus* and *P. calistoides* indicates the horizon. There is a strong similarity of the morphotypes of these three species with those described from the type locality Arroyo Cieneguita. Additionally a probable microconch of *B. vetustum* occurs.

*?bardense* Hz. (PSS 2011), level PT-38: The occurrence in this level of *Blanfordiceras* cf. *bardense* could indicate the horizon, but it cannot be confirmed by the occurrence of just similar specimens of a single species.

*azulense* Hz. (new), level PT-40: The assemblage, which characterizes this horizon consists of (1) *P. calistoides* including the specimens with the most densely and finely ribbed phragmocones, (2) *Pseudoparodontoceras dezai* n. gen. n. sp.; (3) the earliest transient of *C. striolatus*, consisting of the specimens with the most densely and finely ribbed phragmocones matching the lectotype and the material figured by Leanza (1945) from the bed d of Arroyo del Yeso; and (4) the index-species *Krantziceras azulense*. The index-species in isolation would indicate nothing but some part of its total-range biozone whose vertical extension is unknown.

Koeneni Zone, levels PT-51 to PT-59. The species recorded in this interval are: *Choicensisphinctes striolatus*, *Pseudoparodontoceras* cf. *dezai* n.gen. et n.sp., *Substeueroceras koeneni*, *Himalayites* cf. *treubi*, *Catutosphinctes* sp. A, and *Krantziceras* cf. *planulatum*. The youngest occurrence of herpetofauna was recorded in the level PT-56 (see Fig. 2), in the middle of a thick succession of homogeneous lithology (see discussion above, pp. 6, 10).

*C. striolatus* and *S. koeneni*, as well as representatives of *Himalayites*, occur typically in the Koeneni Z. (Gerth 1925a, 1925b, Leanza 1945, Leanza 1975, 1981, PSS 2011). The base of the zone is tentatively drawn at PT-51 because the occurrence of a morphotype of *C. striolatus* similar to the specimens from Arroyo Cieneguita where is defined the *striolatus* Hz.

*?striolatus* Hz. (PSS 2011): The levels PT-51-52 could represent this ammonite bio-horizon by the occurrence of morphotypes of *C. striolatus* similar to those known from the type locality, but it is tentative for the occurrence of a single species is not enough for recognition of the guide-assemblage which defines the horizon.

*koeneni* Hz. (new), level PT-54: The assemblage composed by *S. koeneni* closely matching the lectotype and paralectotype and *H.* cf. *treubi*, both occurring in great abundance in a single, conspicuous bank, is distinctive enough for defining this new local ammonite horizon.

*Planulatum* Hz. (Vennari et al. 2012): This horizon is probably represented by level PT-58 where occurs *K*. cf. *planulatum* in isolation.

Noduliferum (standard) Zone, levels PT-60 to PT-64. The species recorded in this interval are: *Krantziceras compressum*,

Groebericeras bifrons, Argentiniceras noduliferum, Raimondiceras alexandrense, and Subthurmannia boissieri.

*K. compressum, G. bifrons,* and *A. noduliferum* are typical species of the zone (Leanza 1945, Leanza 1981, PSS 2011). The base of the zone is drawn at level PT-60 which represents the *compressum* Hz.

*compressum* Hz. (PSS 2011), level PT-60: A thin bank of calcareous shale where *K. compressum* dominates in large abundance; additionally it has been collected macro- and microconchs of *G. bifrons*. This association indicates clearly the *compressum* Hz. The stratigraphic position of this horizon is now confirmed below the *noduliferum* Hz. (cf. PSS 2011). The *compressum* Hz. is herein proposed as the base for a Noduliferum Standard Chronostratigraphic Zone.

*noduliferum* Hz. (PSS 2011): The ammonites from level PT-61, all concentrated in a band of calcareous concretions within a thick bed of calcareous shale, are abundant large macroconchs of *A. noduliferum* (species confined in this level) and *K. compressum*. This association and the mode of occurrence indicate clearly that the level PT-61 represents the *noduliferum* Hz.

**Damesi (standard) Zone, levels PT-65 to PT-70.** The ammonites recorded in this interval are *Subthurmannia boissieri* (total range through PT-63 to PT-68), *Cuyaniceras transgrediens, Aspidostephanus* cf. *depressus, Spiticeras fraternum, Neocosmoceras malbosiforme*, and *Thurmanniceras* sp.A.

The base of the zone (level PT-65) is drawn at the first occurrence recorded of *C. transgrediens*, a species which characterizes the zone (Leanza 1945) and seems to be confined to a single horizon in most of the basin (discussed above).

*transgrediens* Hz. (PSS 2011), level PT-65: This level has an interesting association composed of *C. transgrediens*, *S. fraternum*, *A.* cf. *depressus*, *S. boissieri*, and *N. malbosiforme*. The *transgrediens* Hz. in herein proposed as the base for a Transgrediens Standard Chronostratigrahic Zone.

Wichmanni Zone, levels PT-71 to PT-85. The ammonites recorded in this interval are *Neocosmoceras wichmanni* (Gerth) and *Thurmanniceras* sp. B. The index-species of the Wichmanni Zone is *Neocomites wichmanni* (Leanza, 1945), not *Neocosmoceras wichmanni* (Gerth). As pointed out by Aguirre-Urreta (2001: 80) this zone was ill defined by means of the local occurrence of a single species (Leanza 1945: table in p. 96) of which the holotype is a fragmentary ammonite. The finding of *Neocosmoceras wichmanni* and *Thurmanniceras* sp. B above a rich fauna of the Damesi Z. and below the occurrence of ammonites of the Riveroi Z. is very valuable for giving consistence to the Wichmanni Z., as an interval which could be characterized by at least this assemblage (see Fig. 5).

**Riveroi Zone, levels PT-86 to PT-106.** The species recorded in this interval are *Pseudoblanfordia* cf. *australis* and *Lissonia* cf. *riveroi*. Inmediatly above the level PT-120 starts the Quintuco Fm (devoid of fossils), followed by the Mulichinco Fm consisting of calcareous sandstone with abundant bivalves and few ammonites at base. Our uppermost record of ammonites in the Vaca Muerta Fm is in level PT-106, *Lissonia riveroi* (Fig. 5). Nevertheless, Leanza & Hugo (1977: 259) have reported the occurrence of this species in the calcareous sandstones of the lower Mulichinco Fm, by which the Riveroi Z. could be extended beyond the top of the Vaca Muerta Fm.

#### **Regional biostratigraphic time-correlation**

Time-correlation down of the zone level between different localities of the basin is constrained by the few published studies of ammonite successions collected with fine stratigraphic control. The results obtained from a set of selected localities of a S-N transect through the Neuquén Basin (Fig. 1A) are summarized in Fig. 86, which is a refinement of the chart in PSS (2011: fig. 40):

(1) Picún Leufú. Only the Tithonian succession is considered (PGSS 2011).

(2) Portada Covunco-Cerrito Caracoles. Interval Tithonian-Lower Berriasian (PGSS 2013a).

(3) Pampa Tril. Tithonian-Lower Valanginian (this report).

(4) Mallín Redondo and (5) Arroyo del Yeso. Based on the study by Leanza (1945) which includes lists of the ammonite assemblages from each level collected bed-by-bed; labelling of levels taken from pages 89-90 of his paper.

(6) Arroyo Cieneguita. Interval Tithonian-Berriasian (PSS 2011).

#### Time-correlation with the Tethyan Primary Standard

The most complete of the Tethyan Tithonian-Valanginian successions are in the Submediterranean/Tethys Province, and the ammonite zonation has been taken by general agreement to provide the Primary Standard Chronostratigraphic Zonation (primary standard hereafter) for this interval.

The rich succession of the studied section gives the oportunity to refine the time-correlation of the zonation of the Andean Tithonian-Lower Valanginian with the primary standard. For this pupose, the studied assemblages are compared with the most similar Tethyan ones. The best correlations that can be obtained at present are summarized in Fig. 87. The horizons which cannot be compared because of the endemism of their ammonites are placed in the scale considering their relative positions as they are bracketed within the zone to which they belong. The Tethyan zone scales adopted are those of Enay & Geyssant (1975) and Geyssant (in Cariou & Hantzpergue 1997) for the Tithonian, and Reboulet et al. (2014) for the Berriasian-lowermost Valanginian (Pertransiens Z.) which has proven to be stable since at least Hoedemaeker et al. (1995).

The age of the basal Andean Tithonian *picunleufuense* alpha Hz. (Picunleufuense Z.) was discussed in detail by PGSS (2011) indicating an age within the interval latest Kimmerigian (upper Beckeri Z.)-Early Tithonian (Hybonotum Z.).

The *perlaevis* and *erinoides* horizons, and the whole Zitteli ["Mendozanus"] Z. are, at least in part, Semiforme Z. in age (Leanza 1981, Parent 2001, Schweigert et al. 2002, PSS 2011). The lower part of the zone could likely be equivalent to the upper part of the Darwini Z. in some localities (Cerro Lotena, Cerro Granito).

The Proximus Z., poorly sampled in the studied section by being covered, has been attributed to the middle part of the Middle Tithonian, nearly the Fallauxi Z. (Leanza 1981, Parent 2001, PSS 2011). The co-occurrence of late *C. proximus* with the earliest representative of the himalayitid *W. internsipinosum* in the *internispinsosum* alpha Hz. (new) gives additional support to this correlation assuming a Ponti Z. age for the Internispinosum Z. where occur the earliest himalayitids in the Neuquén Basin.

The *vestustum* Hz. (Alternans Z.) can be recognized by their ammonites over long distances from its type locality, i.e. in Madagascar and most likely Antarctica (see PSS 2011). However, we do not know such an assemblage, or a similar one in the Tethys. The fauna of the Alternans Z. includes several himalayitids, which support time-correlation with some part of the Microcanthum Z. (cf. Leanza 1981; see discussion in Parent 2003b).

The ammonites recorded in the interval planulatum?compressum horizons (levels PT-58-60) are mainly of the genus Krantziceras besides the spiticeratid G. bifrons. Within the Late Tithonian to Early Berriasian faunas from southern Spain described by Tavera (1985), Andalusphinctes and Neoperisphinctes (both genera published as new by Tavera 1985 but published earlier by Olóriz & Tavera 1983) are partially comparable with Krantziceras. These similar ammonites range through the interval upper Microcanthum (= Transitorius Z. in Tavera 1985) to Durangites (nominally equivalent to the conjugate zone of the Vulgaris Biozone of Sarti 1988 and to the Andreaei Z. of Wimbledon et al. 2013 and Frau et al. 2015) zones, suggesting a similar age for K. planulatum. On the other hand, the association of G. bifrons with K. compressum in the level PT-60 strongly suggests an Early Berriasian, Jacobi Z. age for the compressum Hz., standard base of the Noduliferum Z.

The assemblage of the *transgrediens* Hz. includes *S. boissieri*, *S. fraternum*, and *N. malbosiforme* (most likely the macroconch of *N. sayni*). These species are conespecific (*S. boissieri*) or very close to European forms from which they are hard to separate as discussed above. For example, the Asociación A of Company & Tavera (1982) of the Boissieri Z. includes *S. boissieri* (as *Fauriella* gr. *boissieri-rarefurcata*) and *Spiticeras gevreyi*, which is almost indistinguishable from *S. fraternum*. Thus, the *transgrediens* Hz. can be assigned to the Boissieri Z. Furthermore, *N. sayni* has also been recorded from the Occitanica-Boissieri zones (Mazenot 1939).

The interval of levels PT-66-76 (upper Damesi Z. to lower? Wichmanni Zone) yielded the succession S. boissieri-Thurmanniceras sp. A-Thurmanniceras sp. B, closely resembling the Tethyan succession S. boissieri (= Subthurmannia alpillensis (Mazenot) [M] / Subthurmannia donzei (Le Hegarat) [m]) - Thurmanniceras romani (Mazenot) [M] / Thurmanniceras otopeta (Thieuloy) [m] through the Alpillensis-Otopeta subzones of the upper Boissieri Z. (e.g. Tavera 1985, Company 1987: pls. 4-5).

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**Figure 87.** Time-correlation of the Andean chronostratigraphic zones with the Tethyan Primary Standard based on estimated age of the ammonite horizons and selected assemblages of the Neuquén Basin (as explained in the text). Some of the horizons are only roughly correlated by their relative position within the zone (see text). Updated from PSS (2011, and references therein) with results in this paper. Standard zones with solid line at base. Non-standard zones with broken lines at base.

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