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 clayslates). The scope and definition of the Quintuco Fm are shortly reviewed.

Four lithofacies are differentiated in the Vaca Muerta Fm: (1) bituminous shale: grey 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, (3) calcareous shale: carbonate material with varying proportions of fine-grained epiclastic 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: psamatic 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, Choiciensiphinctes, Krantziceras, Catutosphinctes, Mazatepites, Parabaliceras), Neocomitidae (Paradondioceratites, Pseudoparadondioceratites gen. nov., Subtheoneoceras, Blanfordiceras, Neocosmosceras, Argentiniceras, Raimondiceras, Cuyanticeras, Subthurmannia, Thorumarcticeras, Psuedoblanfordia, Liassonia, Psuedofavrelia), Òclogstenianith (Groebericeras, Spiliceras, Aspidagnostus), Himalayitidae (Windhauseniceras, Corongoceras, Himalayites), Aspidoceratidae (Physodoceras, Pseudophilammites, Tulsaiphisites), Haploceratidae (Haploceras), Lissoceratidae (Pseudolissoceras), and Oppellidae (Metahaploceras, Pasottia, Parastrebities, 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 Choiciensiphinctes 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 chronostratigraphic 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 standardized 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 calcarreas 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 calcarreas y abundantes fósiles, (2) lutita arenosa: color mas claro, contenido de material orgánico moderado, niveles de areniscas tobáceas intercalados, pocos fósiles, (3) lutita calcarrea: material calizo con proporciones variadas de material epiclástico finamente granulado y materia orgánica, formando capas gruesas masivas con aspecto margoso y fractura conoidal, fósiles moderadamente abundantes (ammonites y reptiles marinos), y (4) areniscas finas: componentes psamíticos (granos de cuarzo) con total ausencia de componentes pélicos 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 someterización progresiva con condiciones anóxicas-exúxicas pasando a dysoxicas, y un incremento del
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 (Lithococeras, Choiciensiphanites, Krantziceras, Catutusiphanites, Mazatipites, Parabalbiceras), Neocomitidae (Paradontoceras, Pseudoparadontoceras gen. nov., Subteuerceras, Blanfordiceras, Neocosmoceras, Argentiniceras, Raimondiceras, Cuyamiceras, Subthurmannia, Thurmanniceras, Pseuobalbiceras, Lissonia, Pseudofavrella), Olocostephanidae (Groebliceras, Spicicoloceras, Aspidostephanes), Himalayitidae (Windhanseniceras, Corongoceras, Himalayites), Aspidoceratidae (Physodoceras, Pseudhimalayites, Tourilipinctes), Haploceratidae (Haploceras), Lissoceratidae (Pseudolissoceras), y Oppeliidae (Metahaploceras, Pasottia, Parastrabrelikes, Cieneguitaceras). La fauna (especialmente los perispintocódeos) está dominada por macroconchas adultas y juveniles mientras que las microconchas son muy escasas. Lithococeras picunlefaune está muy bien representada por macroconchas adultas que muestran claramente el aspecto de los sucesivos transients a partir de base de la secuencia del Titóniano andino.

La detallada distribución estrictógrafica de las 55 especies de amonites permite, considerando la sucesión de asociaciones, establecer una consistente subdivisión estrictógrafica de la columna a nivel zonal. Además, el reconocimiento de catorce biohorizontes de amonites (cuatro de ellos tentativamente) incrementa sustancialmente la resolución de la subdivisión estratigráfica, lo cual posibilita correlaciones temporales mucho más precisas, e.i. alta resolución. Tres de estos biohorizontes son nuevos: el Hz. internispinum alf (base de una Zona Internispinosum estándar), el Hz. azulense (Zona Alternans), y el Hz. koeneni (Zona Koeneni). La Z. Internispinosum (Titóniano 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 permite correlacionar temporalmente algunos horizontes andinos con partes del Titóniano y Berriasiano de la Escala Primaria Estándar del Tethys. Por primera vez el berriaselido 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 • Titóniano-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 (Kimmeridgian), 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) had 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-Berriasian, as well as part of the Lower Valanginian. On the other hand, the lithologic monotony 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 sedimentaries 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
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 Tithonian 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 Neuquén.” (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 elastic deposits, conformal 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). 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 fine-grained 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 domain 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.

Interpretation: These deposits represent episodes of major clastic influx, whereas the associate structures indicate relationship with sporadic occurrence of high and medium-energy 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-26 to 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 Tríl 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).
Lithacoceras picunleufuense Parent, Garrido, Schweigert & Scherzinger, transient alpha [M], complete adult (unumbered specimen), level PT-A, picunleufuense alpha Hz., Picunleufuense Z. \( L = 330°, D = 203 \text{ mm} \). A: transverse section (body chamber gray) at \( D = 146 \text{ mm} \) (indicated with a line in A). A, A: innermost whorls (x2). A: Lytoceras montanum (Oppel), phragmocone (MOZ-PI 8494), level PT-42, Alternans Z. B: 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, A, A, B, B), and 5 mm for double size views (A, A, B, B).

Figure 6.

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 Koenedi 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 occurrence 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 ["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 Bioestratigrafía, 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 (Dₙ) and diameter at adult peristome (Dₚ), all given in millimeters [mm]; umbilical width (U), whorl width (W), whorl height (H), and whorl ventral (or apertural) height (Hᵥ), all given as dimensionless proportions of D; length of bodychamber (Lᵥ) in degrees [°]. The numbers of primary (P) and ventral (V) ribs are per half whorl; the numbers of umbilical (Tᵥ), lateral (Tₙ) and ventrolateral (Tᵥ) tubercles are per half whorl. Levels of occurrence of 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.
Figure 8. Lithacoceras picunlefuense Parent, Garrido, Schweigert & Scherzinger [M]. Picunlefuense Z. A-B: Adult [M] phragmocones (MOZ-PI 7870/1, MOZ-PI 7870/2, respectively) of transient alpha, level PT-6, picunlefuense alpha Hz.; B: innermost whorls (x2). C: Apertural view (last part of body chamber 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 (x2).
Figure 9. *Lithococeras picunleufuense* Parent, Garrido, Schweigert & Scherzinger [M], complete adult with peristome (MOZ-PI 8376/2), level PT-8, Picunleufuense Z. [$L_c = 270^\circ, D_c = 265$ mm]. Apertural view in Fig. 8C. $A_1$: lateral view (x1) of the complete ammonite with last half of the bodychamber 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. \(L_w = 280^\circ, D_p = 294 \text{ mm}\). \(A_1\): 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. \[L_{w}=310°, D=205\text{ mm}\]. – 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 Neumayr, 1875**

**Genus Lytoceras Suess, 1865**

Type species: *Ammonites fimbriatus* J. Sowerby, 1817

(ICZN Opinion 130)

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**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.
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, Fözy & 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 (Fözy & 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
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.


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.

**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 ($D_2 = 160-200$ mm).

(b) A large morphotype (Figs. 8C, 9-10), level PT-8: large
 specimens ($D_a = 260-350$ 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 Picú 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 guide assemblage 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).
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

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; C1: innermost whorls (x2), C2-C5: inner whorls, last whor removed. – The asterisk indicates the last septum. All natural size (x1), except C1 (x2). The bar represents 10 mm except for C1 (5 mm).

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 polyschizotomics. In the last whorl of the phragmocone most primaries polyfurcate in three to six secondaries projected forwardly, irregularly in virgatomite 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

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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 shell-shape 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* = 50-200 mm (juvenile to adult).
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 homeomorphism 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); A: 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 (Douville, 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. Intercalary ribs are not clearly developed. Secondary 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 body chamber (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. (Zittelli ["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].


1903 *Perisphinctes cf. nikitini* Michalski. – Burckhardt: 49, pl. 6: 8.

1903 *Virgatites scythicus* Vischniakoff. – Burckhardt: 45, pl. 7: 1-8.

* 1900 *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.


1959 *Virgatosphinctes lenaensis* n. sp. – Corvalán: 22, pl. 4: 14-15.

1959 *Perisphinctes aff. erinus* D’Orbigny. – Corvalán: 26, pl. 3: 12.


Figure 21. *Choicensisphinctes* cf. *burckhardti* (Douvillé). A: phragmocone (MOZ-PI 7912), level PT-8, Picunleufuense Z. B: complete? adult [M] phragmocone (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).

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.: 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 Zittel ['Mendozanus'] Z. – The asterisk indicates the last septum. 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

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**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).
Figure 25. Choicensisphinctes erinoides (Burekhardt, 1903) [M], level PT-12, *erinoides* Hz., Zittel ["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, Knetechel 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
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.

**Choicensiphinctes 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. Choicensissphinctes 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 body chamber of a juvenile [M] (MOZ-PI 7952), level PT-12, erinoides Hz. C: Adult [m] with beginning of body chamber (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 body chamber (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 Substeuerceras steueri
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 stratigraphic horizon in several other localities.

**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...
**Choensisphinctes 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).

**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 level PT-1, below the *picunleufuense* alpha Hz., probably uppermost Kimmeridgian.

This specimen from level PT-1, associated with *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 ($W/H_i$ c. 0.72), with flat flanks and well-rounded 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 whor 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.

**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* 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* = 135 mm. The bodychamber is poorly preserved, possibly *L* about 270° at an estimated *D* = 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. 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* = 195 mm). The bodychamber is longer than three quarters of whorl: *Lbc* = 320°. 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*.
(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 complete adult [M] (MOZ-PI 8493), level PT-40, *azulense* Hz. (new), Alternans Z.; A: 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.
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 Taunya, 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


**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); A: ventral view of the inner whorls showing the groove at $D = 50$ mm; A: innermost whorls (x2); A: 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 A (x2). The bar represents 10 mm, except for A. 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

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

**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. *Catastrophinctes 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, (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, ventral view of the inner whorls. B: Phragmocone (MOZ-PI 8048); B, innermost whorls (x2). C: Juvenile [M] (MOZ-PI 8035/1); C, innermost whorls (x2). D: Adult [M] phragmocone (MOZ-PI 8035/2); shell laterally asymmetric with the right side (D) typical of the transient of the species, and left side (D) more finely and densely ribbed. – All natural size (x1), except B and C, (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: 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, verustum Hz., Alternans Z. – All natural size (x1), except A, (x2). The bar indicates 10 mm, except for A, (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 body chamber (MOZ-PI 7578); ventral views showing the weakening of the ventral groove from the end of phragmocone (*A* 2) through the beginning of the body chamber (*A* 3); *A* 1: ventral view of the inner whorls; *A* 2: innermost whorls (x2); note in *A* 1, the ventral spines broken off (arrows). B: Nearly complete adult [M] (MOZ-PI 8110), last portion belongs to the body chamber; *B* 1: innermost whorls (x2). – All natural size (x1), except *A* 2, *B* 1 (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, shows the basis of two ventral spines broken off. This tendency to form ventral spines is similarly manifested 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, subradially 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 phylectic relationships. Superficial resemblance with some simoceratids was discussed by Scherzinger et al. (2010). Inclusion in the Torquispsphinctinae 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 = 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 claw 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 \( (\theta_{m} = 140^\circ) \) ending in a peristome \( (D_{r} \text{ estimated 65 mm}) \) 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.; A₁A₂, ventral views in two positions (x1); A₃ lateral view (x1); A₄ 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 Uhlg., 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 beginning 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 rise 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* Behrends, 1891; by original designation.

*Parodontoceras calistoides* (Behrends, 1891)
Figs. 45-52


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* = 7-8 mm 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 phragmcone is identical to the remaining specimens and the bodychamber is finely and densely ribbed as the phragmcone. No lappets are preserved preventing a definitive dimorphic assignment.

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 phragmcones, 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 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 phragmcones within *24 < U/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* = 150-180 mm, whereas in level PT-40 (Fig. 48) is *D* = 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 phragmcone 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 whors 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); A₃: ventral view of the innermost whorls (x2). B: ?Adult [m] with complete body chamber (MOZ-PI 8063). C: Adult [M] phragmocone (MOZ-PI 8061). D: [M] phragmocone with beginning of body chamber (MOZ-PI 8074). E: Juvenile [M] with part of body chamber (MOZ-PI 8079). F: Nearly complete adult [M] (MOZ-PI 8058). – All natural size (x1), except A₃. The bar indicates 10 mm, except for A₃ (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); A1: ventral view of the bodychamber, A2: ventral view of the last whorl of phragmocone, A3: lateral view of the beginning of the last whorl of phragmocone, bodychamber removed. B: Adult [M] phragmocone (MOZ-PI 8478); lateral (B1) and ventral views (B2) of the inner whorls (x2). C: Juvenile with beginning of bodychamber (MOZ-PI 8102). D: Phragmocone (MOZ-PI 8577). – All natural size (x1), except B1-B2 (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
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. Furthermore, 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 tubercule 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 tubercules; 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.

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 paralectotype (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); A1-A4: 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 \((24 < D < 80 \text{ mm})\) 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.

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 \(A_3\).

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 (transgressiens 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:
- 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.
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 $D = 53$ mm, $L_{\text{max}}$ 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 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 body chamber 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 body chamber 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
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 ($D = 320$ 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 figurens, 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

**Description.** - A single, well-preserved, complete adult (M) phragmocoone (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 = 0.88 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 Himalaya 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 Mazerot, 1939), a synonym of Subalpinites Mazerot, 1939 (Type species: S. fauriensis Mazerot, 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, Mazerot 1939: pl. 22: 4, 59). Figure 58. A-B: Blanfordiceras vetustum (Steuer), Alternans Z. A: Adult [m?] phragmocoone (MOZ-PI 8085), level PT-36, vetustum Hz.; A1: innermost whorls (x2). B: Adult [M] phragmocoone with beginning of bodychamber (MOZ-PI 81119), level PT-46. C: Blanfordiceras cf. bardense (Krantz), phragmocoone (MOZ-PI 81142), level PT-38, Alternans Z.– All natural size (x1), except A1 (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 Occitania 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)

**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
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 I, 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 evolve, 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 \( D_a = 70-80 \) 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 body chamber. One specimen seems to have the last septum at \( D = 52 \text{ mm} \) 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 boisieri* of Pictet (1867: 79-80), especially the specimens from level PT-68 with more flexuous ribs. The lectotype of *A. boisieri* Pictet (1867: pl. 15: 1), was designated and figured 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). Tavares (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 Mallin 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. *octicanicus* (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 two 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 wichmannii (Gerth), lectotype (designated herein), photographic refuguration from Gerth (1925: pl. 3: 6); Paläontologische Institut Universität Tübingen (GPIBO Haupt). Arroyo de La Manga, Mendoza Province, possibly Upper Berriasian. Almost complete [m²]. – Natural size (x1). The asterisk indicates the last septum.](image)

**Krantziceras elliptostomum** (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 fasiculatus* (Steuer, 1897). – Damesi Z.


This specimen described by Gerth (1925b) as *Thurmannia aff. thurmanni* var. allobrogica Kilian was illustrated by a hand-drawing 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 *Thurmannniceras otopena* [m] from the Otopena 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. persiana-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 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.
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 uninterrupted 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 (\(D_5\) 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 ototeta* (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. allogrobica 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-plumum 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.

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**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 refuged by a hand-drawing 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/intercalarys on the upper flank, and (2) the holotype of *Hoplites molinensis* Burckhardt (1903: pl. 11: 13-14, refuguration 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 64. *Subturmannia 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: innermost whorls (x2). E: Phragmocone (MOZ-PI 8172), level PT-66, Damesi Z.; evolute 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 (x2). The bar indicates 10 mm for natural size views (x1), but 5 mm for D (x2). The asterisk indicates the last septum.
**Genus Lissonia Gerth, 1925b**
Type species: *Hoplitites 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 ventrolateral shoulder and are interrupted on the venter. On the adult body chamber the ventral ribs (secondary plus indistinct intercalatories) reach the ventro-lateral 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 body chamber, 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 Cerro 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 *Lissiosa riveroi* and "Thurmanniceras" sp. a in their fig. 3I-J, from the Riveroi Z. of Cerro 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 Ararobos (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 Anguliformis Zone (Upper Valanginian) of the Pichahue 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 swell 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.
(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. 31-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 matches 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).


(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 & Rawson (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 body chamber is markedly
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 & Alvarez (1999), both concluding an early Berriasian age.

Genus Spiticeras Uhlig, 1903
Type species: Ammonites spitiensis Blanford, 1863; by subsequent designation of Roman (1938).

\( Spiticeras \) fraternum (Steuer, 1897)
Fig. 71


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. 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 Djanelidze (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; C₁: enlarged view (x2) of the specimen in C, 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 C₁ (x2). The bar indicates 10 mm for natural size views (x1), but 5 mm for C₁ (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); **A2**: 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 *Spiticeras 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, transgressiens Hz., lowermost Damesi Z. In Arroyo Cienguita 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, transgressiens 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.; A₁ lateral view of the right side; A₂ ventral view; A₃ view of the inner whorls from the left side—Natural size (x1).

**Genus Aspidostephanus Spath, 1925**

Type species: *Holocostephanus 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 ($D = 55-66$ 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 whors would produce the flexure of the ribs which do not shorten accordingly, maintaining 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: *Perispinctes internispinosus* Krantz, 1926; by original designation.
\textit{Windhauzeniceras 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.- Twomorphs 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.

\textbf{Transient alpha (level PT-19).} [M] (Fig. 74): Inner whorls \((D > 10 \text{ mm})\) evolute \((U/D = 0.48-0.50)\), subcircular to subovate-depressed in whorl section, with widely spaced, radial sharp primary ribs \((P = 13-14\) through \(D = 25-35 \text{ mm}\)), bi- or trifurcated from a spiny swellings on the upper flank. Through the middle whorls, from \(D = 50\) up to \(D_\alpha = 115 \text{ mm}\), most ribs are bifurcated from the upper third of the flank \((P = 15-18\) through \(D = 40-90 \text{ mm}\)); 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 \(D = 135 \text{ mm}\). The adult size at peristome must have been \(180-200 \text{ mm}\) 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 trifurcated 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; \(D_p = 92 \text{ mm}\).

\textbf{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 trifurcated 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 \(D = 20-35 \text{ mm}\) there is a ventral groove bounded by the end of the ventral ribs which form a mild swelling, and (2) at \(D = 100 \text{ mm}\) 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 \(D_\alpha = 170 \text{ mm}\); 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 \(D = 280 \text{ mm}\).

[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 end of the adult phragmocone). The transient alpha shows coronate inner whorls followed by a \textit{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 coronate stage begins in the innermost whorls but persists through the middle whorls, up to \(D = 75-80 \text{ mm}\); 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 \textit{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 \textit{Catutosphinctes}; Fig. 41B with deformed whorl section and widely spaced primaries in the inner whorls; or Fig. 74C very similar to \textit{C. proximus} in lateral view can be distinguished from its coronate inner whorls. The specimen of \textit{C. proximus} shown in Fig. 41A has the ribbing of the outer whorls very similar to \textit{W. internispinosum} transient alpha at comparable diameter, but can be distinguished by the

Figure 73. \textit{Windhauzeniceras internispinosum} (Krantz) transient alpha [m], level PT-19, \textit{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 (×1). Asterisk at last septum.
Figure 74. Windhauseniceras internispinosum (Krantz) transient alpha [M], level PT-19, internispinosum alpha Hz. (new), Internispinosum Z. A: Adult phragmocone with beginning of body chamber (MOZ-PI 7571); note the wide smooth ventral band (A₁). B: Adult [M] with part of the body chamber (MOZ-PI 8050). C: Adult phragmocone (MOZ-PI 8018); C₁: inner whorls (x2) showing the irregularly distributed tuberculate primaries. D: Phragmocone (MOZ-PI 8021). E: Phragmocone (MOZ-PI 8039). – All natural size (x1), except C₁ (x2). The bar represents 10 mm for natural size views. The asterisk indicates the last septum.
Figure 75. *Windhauenseiceras internispinosum* (Krantz) transient beta [M], level PT-20, Internispinosum Z. Almost complete adult with bodychamber (MOZ-PI 8465). $A_1$: Lateral view; $A_2$: apertural view showing the ventral spines on the adult phragmocone; $A_3$, $A_4$: ventral views at $D = 88$ and 70 mm, respectively; $A_5$, $A_6$: 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: development of the spines from about \( D = 90 \text{ mm} \). A: spines located on the roof of the body chamber when the shell has \( D = 210 \text{ mm} \). A: spines located around the last septum and beginning of body chamber when the shell is fully grown, at about \( D = 300 \text{ mm} \). Ph: phragmocone, BC: body chamber, sp: ventral spines (see Fig. 75A). – All same scale, reduced x0.2.

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 body chamber (MOZ-PI 8090/1), level PT-36, vetustum Hz., Alternans Z. – All natural size (x1).

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 \( C. \text{proximus} \). The co-occurrence of abundant specimens of both species in the same level, intergrading in shell morphology and sculpture, strongly suggests \( W. \text{internispinosum} \) originated from \( C. \text{proximus} \). 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), 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 body chamber (Fig. 76A), and (3) in the adult age the spines become partially covered by the subsequent whorl (Fig. 76A), 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 findings 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 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 representatives 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 Queemado.

**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); D2: 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: ventral view showing the bodychamber (displaced) and last whorl of phragmocone; F3: phragmocone apertural view; F: lateral view. – All natural size (x1), except D2 (x2). The bar indicates 10 mm for natural size views (x1), but 5 mm for D, (x2). The asterisk indicates the last septum.
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 \( D = 30-40 \)

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

The sculpture of the innermost whorls \((D < 20 \text{ mm})\) is poorly preserved but can be seen to be composed of sharp prosocline primary ribs. From about \( D = 20 \text{ mm} \) 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 \( D = 135-140 \text{ mm} \), 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 lateral 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.
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


**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 tri-ribulation (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 Internispinosum 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 *falcatus* Hz. or equivalent positions within the Proximus Z., somewhat older than the present material from the base of the Internispinosum Z. The available 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 throughout most sectors of the Neuquén Basin (see Leanza & Olóriz 1987, Parent 2001, PSS 2011).

**Genus Toulisphinctes** Sapunov, 1979

Type species: *Toulisphinctes ziegeri* 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 [*"Mendoz anus"*-]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 Barra Negra, figured as *Aspidoceras cf. euomphalum* (Steuer, 1897) by Parent et al. (2007: fig. 5A), is most likely a *Toulisphinctes* considering the 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. 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 [*"Mendoz anus"*] 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, \( U/D = 0.18 \), \( W/H = 0.67 \).

**Remarks.** – The specimens completely match those figured by Zeuschner (1846: pl. 4: 3) and Zitteli (1870: pl. 27: 2-3). All our material comes from the Zitteli [*"Mendoz anus"*] 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, Fözy & Scherzinger 2013a). The earliest Pseudolissoceras (P. olorizi Fözy, 1988) occurs in the lowermost Tithonian and with gradual morphologic changes towards more compressed and involute forms, the genus-lineage 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


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 the level PT-14. Z. A: Adult [M] phragmocone (MOZ-PI 7970/20) of a compressed variant, level PT-12. Z. B: Inner whorls (MOZ-PI 7970/15), level PT-12. Z. C: Adult [m] phragmocone with beginning of bodychamber (MOZ-PI 7933/11), level PT-14. Z. D: Subadult [M] phragmocone (MOZ-PI 7933/14) of an inflate variant, level PT-14. – All natural size (x1). The asterisk indicates the last septum.

Figure 83. Pseudolissoceras zitteli (Burckhardt), Zitteli ["Mendozanus"]

A. Z. A: Adult [M] phragmocone (MOZ-PI 7970/20) of a compressed variant, level PT-12. Z. B: Inner whorls (MOZ-PI 7970/15), level PT-12. Z. C: Adult [m] phragmocone with beginning of bodychamber (MOZ-PI 7933/11), level PT-14. Z. D: Subadult [M] phragmocone (MOZ-PI 7933/14) of an inflate variant, level PT-14. – All natural size (x1). The asterisk indicates the last septum.

Family Oppelliidae Douville, 1890
Subfamily Taramelliceratinae Spath, 1928
Genus Metahaploceras Spath, 1925
Type species: Ammonites Strombecki Oppel, 1857
(objective synonym: Metahaploceras affinis Spath, 1925).

Remarks.- Accepting the renaming of Ammonites lingulatus

Metahaploceras aff. acallopistum (Fontannes, 1879)

Fig. 84A-B

Remarks.- Accepting the renaming of Ammonites lingulatus

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

"Ammonites lingulatus nuda" 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 nuda" 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.
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 $D = 43$ 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 Quequeno, 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.


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.
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


Material.- 4 pphragmocones from level PT-10c; 11 [M] pphragmocones from level PT-12; 12 [M] pphragmocones 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 lunuloid structures in the mid-flank. The adult bodychamber begins at Dₘ = 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 lowest Zittelii ("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 microconch 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 Fallauzi X. of Le Pouzin (L’Ardeche, SE France), are indistinguishable from the corresponding sexual dimorphs of *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.

**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, *internispinosum* 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 lunuloid 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. internispinosum* (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 time-correlations 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. reproducible) 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 standard 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 inaccurate 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 "Mendozianus" 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 ammonite-biostratigraphy-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 Burchhardt (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 time-correlation between distant regions of the basin.

The fauna of the Virgatosphinctinae Bed of Leanza (1980) has long been considered the guide-assembly of the Mendozianus 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. mendozianus* [m] (see PSS 2011, and discussion above), the index-species of the Mendozianus 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*, *guzenakenakensis*, *C. guzenakenakensis*, 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 *Choicensiphisntes*. This *Choicensiphisntes* 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 Mendozianus 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 Vigmaticincticinae Bed.

Krantz (1928: 49) proposed the Calistoides Zone (index-species: P. calistoides) with type locality at Arroyo Durazo and characterized by the guide-assemblage composed of C. mendozanum (including Berriasella submendozanum Krantz, 1928 and B. duraznensis Krantz, 1928), Blanfordiceras? argentinium Krantz, 1926, B. vetustum (as Berriasella subprimavasenst 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 (Geth), 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., as suggested by Leanza (1981: 78), but part of the current 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 well-established twofold subdivision of Leanza (1945), (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 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 osteoids moderately abundant. 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 Tithonian, 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*, *Lithacoercas 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.

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*. The level PT-9 displays a fauna of *L. guenenakenensis*, and *L. picunleufuense* tr. alpha, as well as *C. cf. platyconus*, *Choicensisphinctes?* n. sp. A, *Krantziceras?* sp. A, and *C. cf./aff. platyconus*.

**Picunleufuense beta 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-10a displays a fauna 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 staszyczi*, *Metahaploceras aff. acallopistum*, *Pasottia andina*, *Parastreblites?* cf. *comahuenensis*, *Cieneguiticeras perlaevis*, *P. calistoides* (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 (Geth), 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., as suggested by Leanza (1981: 78), but part of the current 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 well-established twofold subdivision of Leanza (1945), that is the Noduliferum and Danesi 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" fauna of Aguirre-Urreta & Alvarez 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" trigonomatum. 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 outliers 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 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).
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 - the number 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 *Choicicosphinctes cf. platycosmos* (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 matches 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 falculturatum. Most of these species have been attributed to the Zitteli and/or “Mendozanus” zones (Burchhardt 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. burchhardtii which probably indicates the malaurensian Hz. of the lowermost Zitteli (“Mendozanus”) Z. (PGSS 2011).

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

Perlaves Hz. (PGSS 2011), level PT-10c: The ammonites from this level (C. erinoides, P. zitteli, and C. cf. perlaves) 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; this interval between the uppermost occurrence of P. zitteli and the standard base of the Internispinosum Z., that is the internispinosum alpha Hz. (see below).


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 co-occurrence of the figured morphotypes of the following species is taken as the assemblage which defines the new horizon: P.? cf. comahuensis, C. proximus, Choiciennisphinctes sp. A (in PSS 2011), Cieneguiticeras n. sp. A, W. internispinosum transient alpha, P. subpretiosus, 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], Choiciennisphinctes striolatus [M], Choiciennisphinctes cf. striolatus, Parodontoceras calistoides [M & m], P. cf. calistoides, Pseudoparodontoceras dezi 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 assemblage 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.

Perlaves Hz. (PGSS 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 species with the most densely and finely ribbed phragmocones, (2) Pseudoparodontoceras dezi 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: Choiciennisphinctes striolatus, Pseudoparodontoceras cf. dezi 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 paratype 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,
**Boletín del Instituto de Fisiografía y Geología 86, 2015**

**Groebrierceras 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 malhosiforme, 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. malhosiforme. The transgrediens Hz. in herein proposed as the base for a Transgrediens Standard Chronostratigraphic 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 Neocosmoceras wichmanni (Leanza, 1945), not Neocosmoceras wichmanni (Gerth). As pointed out by Aguiire-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 Neocosmorceras 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 the local occurrence of a single species (Leanza 1945: table in PSS 2011: fig. 40): (1) Picún Leufú. Only the Tithonian succession is considered (PGSS 2011). (2) Portada Covunco-Cerrito Caracoes. 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.

**Riveroi Zone, levels PT-86 to PT-106.** The species recorded in this interval are Pseudothelaeformia cf. australis and Lissonia cf. riveroi. Immediately 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 Caracoes. 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.

**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 opportunity to refine the time-correlation of the zonation of the Andean Tithonian-Lower Valanginian with the primary standard. For this purpose, 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 Cario & 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 Kimmeridgian (upper Beckeri Z.). Early Tithonian (Hybonotum Z.).

The perlaevis and erinoides horizons, and the whole Zittelii ["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 Darwin 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. internispinosum in the internispinosum 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 Krantzioceras besides the spiceratid G. bifrons. Within the Late Tithonian to Early Berriasian faunas from southern Spain described by Tavera (1985), Andalusosphinctes and Neoperisphinctes (both genera published as new by Tavera 1985 but published earlier by Olóriz & Tavera 1983) are partially comparable with Krantzioceras. These similar ammonites range through the interval upper Microcanthum (= Transitori. Z. in Tavera 1985) to Durangites (nominally equivalent to the conjugate zone of the Folgaris 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 transgressivus HZ. includes S. boissieri, S. fraternum, and N. malbosiforme (most likely the macroconch of N. sayni). These species are con-specific (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 Faurella gr. boissieri-rectifurcata) and Spiticeras geveyi, which is almost indistinguishable from S. fraternum. Thus, the transgressivus Hz. can be assigned to the Boissieri Z. Furthermore, N. sayni has also been recorded from the Occitanica-Boissieri zones (Mazenot 1939).

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