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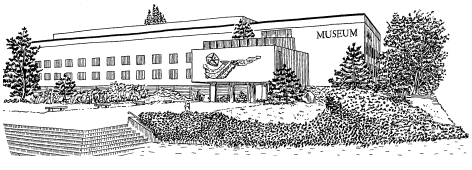

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The Tithonian ammonite fauna and stratigraphy of Picún Leufú, southern Neuquén Basin, Argentina

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Abstract

A Tithonian section of the Vaca Muerta Formation (362 m in thickness) in Picún Leufú (southern Neuquén Basin, Argentina) was measured and sampled for ammonites. There were recognized seven different lithofacies which represent at least five different episodes of sedimentation. The ammonite fauna is dominated by perisphinctids belonging to three genera of the Ataxioceratidae. The classification proposed for the Andean lower-middle Tithonian Ataxioceratidae includes three genera: two phyletic lineages, *Choicensisphinctes* LEANZA (Lithacoceratinae) and *Catutosphinctes* LEANZA & ZEISS (Torquatisphinctinae), and "*Lithacoceras*" HYATT represented by apparently two species in the lower Tithonian. Each one of these three genera is rather well characterized by its different ontogeny of sculpture, shell shape and coiling and, moreover, their sexual dimorphism is different, especially by the morphology of the microconchs. Both phyletic lineages include several Andean ammonites described in the literature as unrelated species but showing progressive differentiation with independent evolutionary trends. The ammonite fauna includes accessory elements (in terms of abundance) which belong to the following genera: *Physodoceras* (macro- and microconchs, *Sutneria*), *Pseudolissoceras*, *Cieneguiticeras* and *Pasottia*. The Picunleufuense (Standard Chronostratigraphic) Zone for the Andean Tithonian is introduced, including two horizons: the *picunleufuense* α horizon (standard base of the Picunleufuense Zone) and the *picunleufuense* β horizon. Upper in the section, within the biozone, or biostratigraphic range, of *Pseudolissoceras zitteli*, is introduced the *perlaevis* horizon.

Keywords

Tithonian, Southern Neuquén Basin, Vaca Muerta Formation, Lithofacies, Ammonite fauna, Biostratigraphic chronostratigraphy.

Resumen

La fauna de amonites y stratigrafía del Tithoniano de Picún Leufú, sur de la Cuenca Neuquen, Argentina.- Una sección tithoniana de la Fm. Vaca Muerta (362 m de espesor) en Picún Leufú (sector sur de la Cuenca Neuquina, Argentina) fue medida y su fauna de amonites muestreada. Se han reconocido siete diferentes litofacies las cuales representan cinco episodios de sedimentación. La fauna de amonites está dominada por perisfínctidos correspondientes a tres géneros de Ataxioceratidae. La clasificación propuesta para estos Ataxioceratidae andinos del Tithoniano inferior y medio incluye tres géneros: *Choicensisphinctes* LEANZA (Lithacoceratinae) y *Catutosphinctes* LEANZA & ZEISS (Torquatisphinctinae), y "*Lithacoceras*" HYATT, aparentemente representado por dos especies en el Tithoniano inferior bajo. Cada uno de estos tres géneros puede caracterizarse diferencialmente a partir de la ontogenia de su ornamentación, forma de la concha y arrollamiento, y además su dimorfismo sexual es distintivo de cada grupo, especialmente por la morfología de las microconchas. Los dos primeros géneros mencionados incluyen numerosos amonites típicamente andinos descriptos en la literatura como especies de diversos géneros y sin relaciones entre sí; además muestran una progresiva diferenciación con tendencias evolutivas propias. La fauna de amonites incluye además varios elementos que, en términos de su abundancia relativa, pueden considerarse accesorios: *Physodoceras* (macro- y microconchas, *Sutneria*), *Pseudolissoceras*, *Cieneguiticeras* y *Pasottia*. Se introduce la Zona (cronoestratigráfica estándar) Picunleufuense para la base del Tithoniano andino, la cual incluye dos horizontes de amonites: el horizone *picunleufuense* α (base estándar de la zona) y el horizonte *picunleufuense* β. Dentro de la biozona, o intervalo bioestratigráfico, de *Pseudolissoceras zitteli* se define el horizone *perlaevis*.

Palabras clave

Tithoniano, Cuenca Neuquina, Formación Vaca Muerta, Litofacies, Fauna de amonites, Cronoestratigrafía bioestratigráfica.

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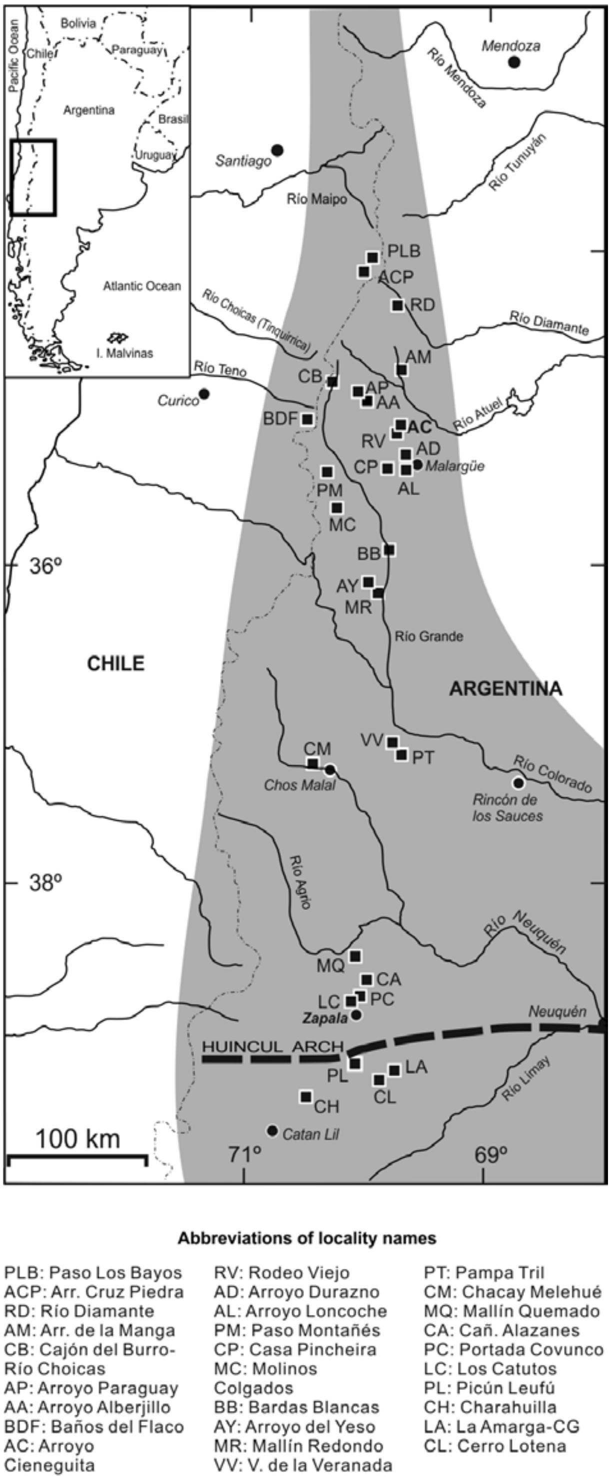
I. INTRODUCTION

Picún Leufú is one of the most cited localities for the Upper Jurassic of the Neuquén Basin (Fig. 1; hereafter abbreviated as NB), indistinctly referred to as the Neuquén-Mendoza Basin for other authors (e.g. PARENT *et al.*, 2006). Nevertheless, its Tithonian ammonite fauna has not been monographed till today. The lower and middle Tithonian rocks in this locality belong to the Vaca Muerta Fm. which is widely distributed throughout all the Neuquén Basin (see LEANZA *et al.,* 1977). The regional geology and stratigraphy have been described by WEAVER (1931), GROEBER (1952), LEANZA (1973) and LEANZA & HUGO (1977, 1997), among others. In these papers the authors have provided lists of the recorded ammonites. Bivalves have been described, e.g., by WEAVER (1931) and LEANZA (1993), whereas gastropods have received attention more recently (see GRÜNDEL & PARENT, 2001, 2006).

The chronostratigraphic scale of the Andean Tithonian consists of a subdivision into six zones: Mendozanus, Zitteli, Proximus, Internispinosum, Alternans and, the youngest, Koeneni (see LEANZA, 1981 for a recent review). These zones have been neither standarized nor subdivided yet, with the exception of the upper middle Tithonian Internispinosum Zone which was subdivided into two subzones by LEANZA & ZEISS (1992). Non-standard zones include gaps and overlaps across different localities, especially in what has been a so large and tectonically active, back-arc basin like the Neuquén Basin, in which a wide variety of lithological changes and numerous local subbasins were developed. Regional and intercontinental time-correlation at the zone level or below, must be invariably based on a standard scale in terms of standard zones. In modern terms the standarization of a zone requieres the definition by only its base in a stratotype by means of a marker or "golden-spike", in this case a bio-horizon or ammonite horizon (rather equivalent to the concurrent-range, assemblage biozone), which represents a time-plane respect to which time-correlations would be made. Following this procedure the base of the next overlying standard zone is the top of the underlying one, leaving open the field for inclusion of newly discovered horizons of the zone which could be unrecorded in the type locality. Further details and advantages of this procedure have been extensively discussed (e.g., GABILLY, 1971; CALLOMON, 1995, 2003; PAGE, 1995), including the important feature of being by far the most precise method for dating of rocks in the marine Jurassic. The pre-requisite for the application of this procedure of sudivision of the successions in terms of bio-horizons is the obtention of samples collected bed-by-bed. Collections of such samples from several localities of the basin have been obtained in the last years, including those from Picún Leufú which are described in this paper.



Abbreviations of locality names

PLB: Paso Los Bayos
ACP: Arr. Cruz Piedra
RD: Río Diamante
AM: Arr. de la Manga
CB: Cajón del Burro-Río Choicas
AP: Arroyo Paraguay
AA: Arroyo Alberjillo
BDF: Baños del Flaco
AC: Arroyo Cieneguita
RV: Rodeo Viejo
AD: Arroyo Durazno
AL: Arroyo Loncoche
PM: Paso Montañés
CP: Casa Pincheira
MC: Molinos Colgados
BB: Bardas Blancas
AY: Arroyo del Yeso
MR: Mallín Redondo
VV: V. de la Veranada
PT: Pampa Tril
CM: Chacay Melehué
MQ: Mallín Quemado
CA: Cañ. Alazanes
PC: Portada Covunco
LC: Los Catutos
PL: Picún Leufú
CH: Charahuilla
LA: La Amarga-CG
CL: Cerro Lotena

Fig. 1: Map of West-Central Argentina and Central Chile showing the location of the fossiliferous localities cited in text and approximate limits of the Neuquén Basin (gray area).

The studied outcrops have yielded an important and interesting ammonite fauna. The fauna of the lowermost part of these outcrops was preliminary presented in a previous paper (PARENT *et al.,* 2006) as conforming an assemblage which was named ‘Fauna A’ awaiting for a systematic description. In this paper we present the description of this assemblage which is divided in three ammonite bio-horizons and assigned to a new standard chronostratigraphic zone at the base of the Andean Tithonian. The overlying assemblages are also described. The description of the fauna needs a previous revision of the genera to which the studied species are assigned. This is necessary to stabilize the taxonomy of several old-defined species which have not been typologized, and to consider the much new information on the Tithonian ammonites, biostratigraphy and paleogeography published in the last years all around the world.

II. STRATIGRAPHY

Geological setting

The studied section is located near the bridge of the National Road 40 over the Picún Leufú River (Neuquén Province, Argentina), along a secondary road connecting small villages and local schools (Fig. 2). This area shows large Jurassic and Early Cretaceous outcrops of marine and continental deposits of the Neuquén Basin. The sedimentary sequences are tectonically affected by the Dorsal de Huincul (or Huincul Arch), an underground tectonic structure that operated intermittently during

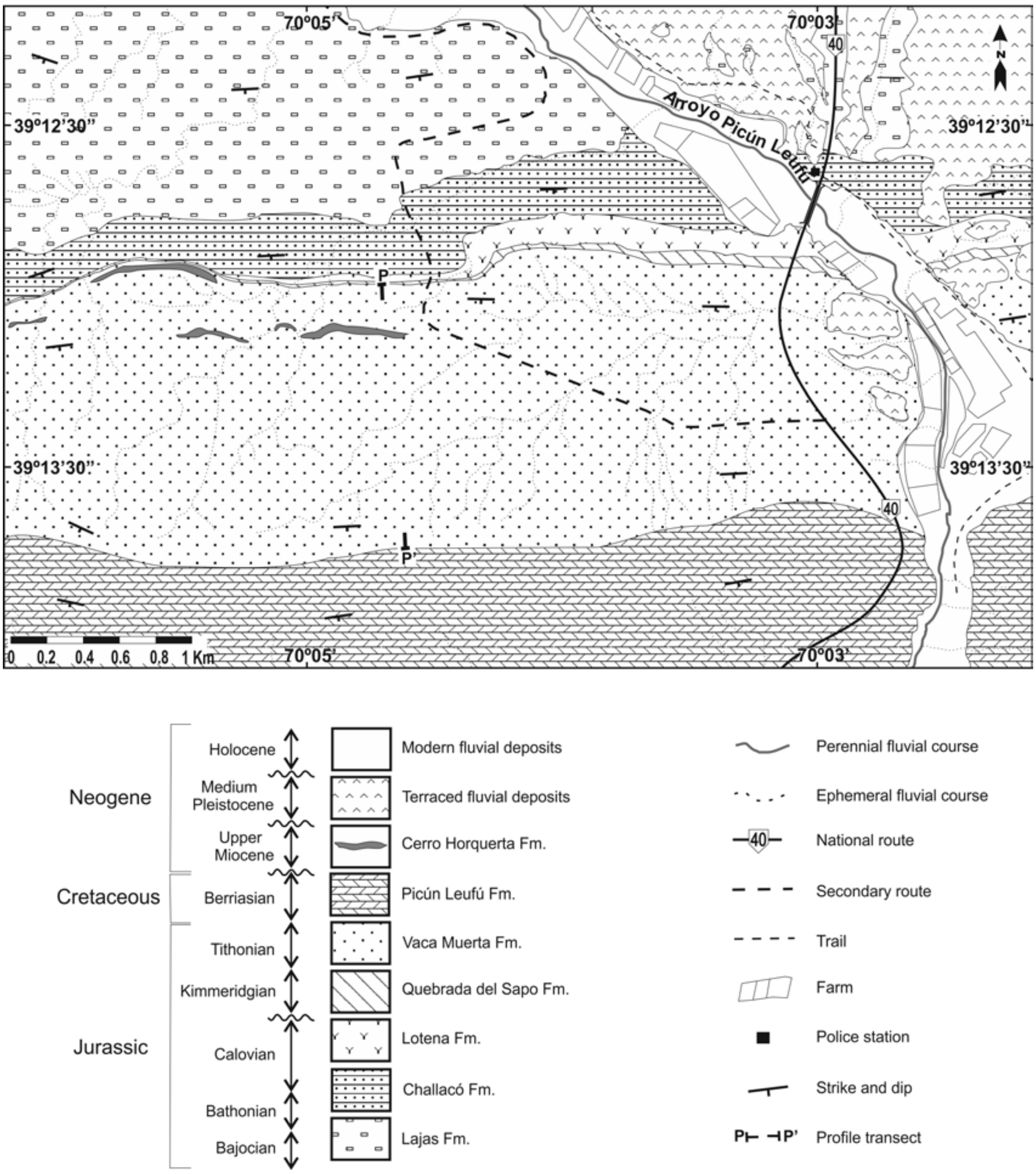


Fig. 2: Geological map of the studied region with indication of the section Picún Leufú (PP´) detailed in Fig. 3.

the Mesozoic as a stratigraphic barrier, controlling the deposition cycles and facies distribution in this area of the basin (DE FERRARIIS, 1947; HOGG, 1993; CRUZ *et al.,* 2000). During the Cenozoic the Andean deformation exposed the Mesozoic sequence and there were intrusions of areally restricted basaltic sills and necks.

The Tithonian ammonite fauna described in the present report was collected from deposits of the Vaca Muerta Formation of the Mendoza Group (STIPANICIC *et al*., 1968). These rocks contain abundant faunas of invertebrates and marine reptiles (see e.g. WEAVER, 1931; LEANZA, 1980; LEANZA & ZEISS, 1990, 1992, 1994; GASPARINI & FERNÁNDEZ, 1997, 2005; GASPARINI *et al.,* 2007). These deposits have been considered by several authors as the by-product of a quick marine transgression (GROEBER, 1952: 352), controlled by regional subsidence during a phase of intensive tectonic inversion which affected the basin during the Late Jurassic (VERGANI *et al.,* 1995; SPALLETTI *et al.,* 1999; CEVALLOS, 2005). According to SPALLETTI *et al.* (2000) the succession of the Vaca Muerta Fm. was deposited on a shallow, tidally dominated, mixed carbonate-siliciclastic ramp.

Description of the section

The log-section of the studied profile is shown in Fig. 3 with indication of the bed numbers, lithology, thickness and fossils occurring in each bed to which we refer below. The lithostratigraphic profile was recorded along an outcrop located in the western flank of the Picún Leufú anticline, started at 39°12’56.1’’S, 70°04’47.4’’W (Fig. 2). In this point the beds are dipping in average 35º W, being the total measured thickness of the Vaca Muerta Fm. about 362 m. This later unit rests, with erosive contact, over aeolian and alluvial deposits of the Quebrada del Sapo Fm. (considered as the Tordillo Fm. by PARENT *et al.,* 2006, 2008), passing gradationally towards the top, to tidal barrier deposits of the Picún Leufú Fm. The basal contact of the Vaca Muerta Fm. has been defined in the studied section at the base of the bed PL-2 (Fig. 3). This boundary is characterized by a marked erosive surface, followed by 5.5 m of sandstones and conglomerate lens (beds PL-2-4), contrasting respect the major part of the sequence. This basal deposit can be correlated with the conglomeratic sandstones of the so called “Basal Parasequence of the Vaca Muerta Formation” (BOLL & VALENCIO, 1996). According to these authors, those levels constitute a short depositional event well represented along the Huincul Arch, being interpreted as transgressive lag deposits formed by the reworking of the underlying sediments. In this sense ZAVALA *et al*. (2008) concluded that in the area of the Picun Leufú River the Vaca Muerta Fm. deposits overlay, indistinctly, deposits of the Tordillo and Quebrada del Sapo formations (Kimmeridgian sensu lato) when considered as independent units.

Within the study area, several basaltic Upper Miocene sills intrude the lowermost part of the Vaca Muerta Fm. (Fig. 2), affecting the deposits comprised between beds PL-2 and PL-13. These intrusives which belong to the Cerro Horqueta Formation, are arranged in parallel form to the stratification planes, conforming lensoid bodies of several hundred meters long with maxium thickness less than 10 m.

Lithology: Usually the deposits of the Vaca Muerta Formation have been typified as a monotonous succession of organic-carbon-rich strata. According to the relatively high concentration of organic matter, these rocks have been described as “black shales” or “bituminous lutites” (GROEBER, 1929; WINDHAUSEN, 1931; DIGREGORIO, 1978; DIGREGORIO & ULIANA, 1980). WEAVER (1931) described originally the Vaca Muerta Fm. deposits, outcropping in the vicinities of Cerro Lotena and Río Picún Leufú, as a thick succession of calcareous sandy shales with subordinate amounts of interbedded sandstones and limestones. In the same sense LEANZA (1973) measured in the Río Picún Leufú area a 336 m thick succession, composed by marls and shales with intercalations of limestones and calcareous sandstones. Along the profile presented in this work, we recognized seven lithofacies:

Lithofacies 1. Conglomerates: This facies is represented by a single bed PL-3 of poorly consolidated, medium-sized, polymictic conglomerate. The clasts are rounded, moderately-sorted, ranging from 12 to 65 mm in diameter. Internally, the bed shows crude stratification, forming a continuous tabular bed less than 0.3 m thick. No fossils were found in this lithofacies.

Lithofacies 2. Medium to fine-grained sandstones: This facies is composed by medium to fine-grained, poorly to moderately-sorted, unconsolidate, quartz-lithic sandstones. The color of these levels vary from yellowish orange (10 YR 8/6) to dark yellowish orange (10 YR 6/6), forming tabular beds ranging from 1.5 to 3.0 m in thickness. These deposits are formed by the beds PL-2 and PL-4, conforming with the conglomeratic bed PL-3, the basal deposits of the Vaca Muerta Fm. The base of the bed PL-2, which is the lower contact of the Vaca Muerta Fm., is clearly delineated by a continuous gravelly mantle of variable thickness. These beds change laterally from massive to cross-bedded sandy deposits, evidencing switches in the depositional mode. No fossils were found in this lithofacies.

Lithofacies 3. Massive fine-grained sandstones: This facies consists of massive, poorly consolidated, fine-grained quartzitic sandstones; occasionally a faint lamination can be observed. The color varies from whitish yellow to pale yellowish orange (10YR 8/6). These beds occur from the medium to the upper parts of the profile

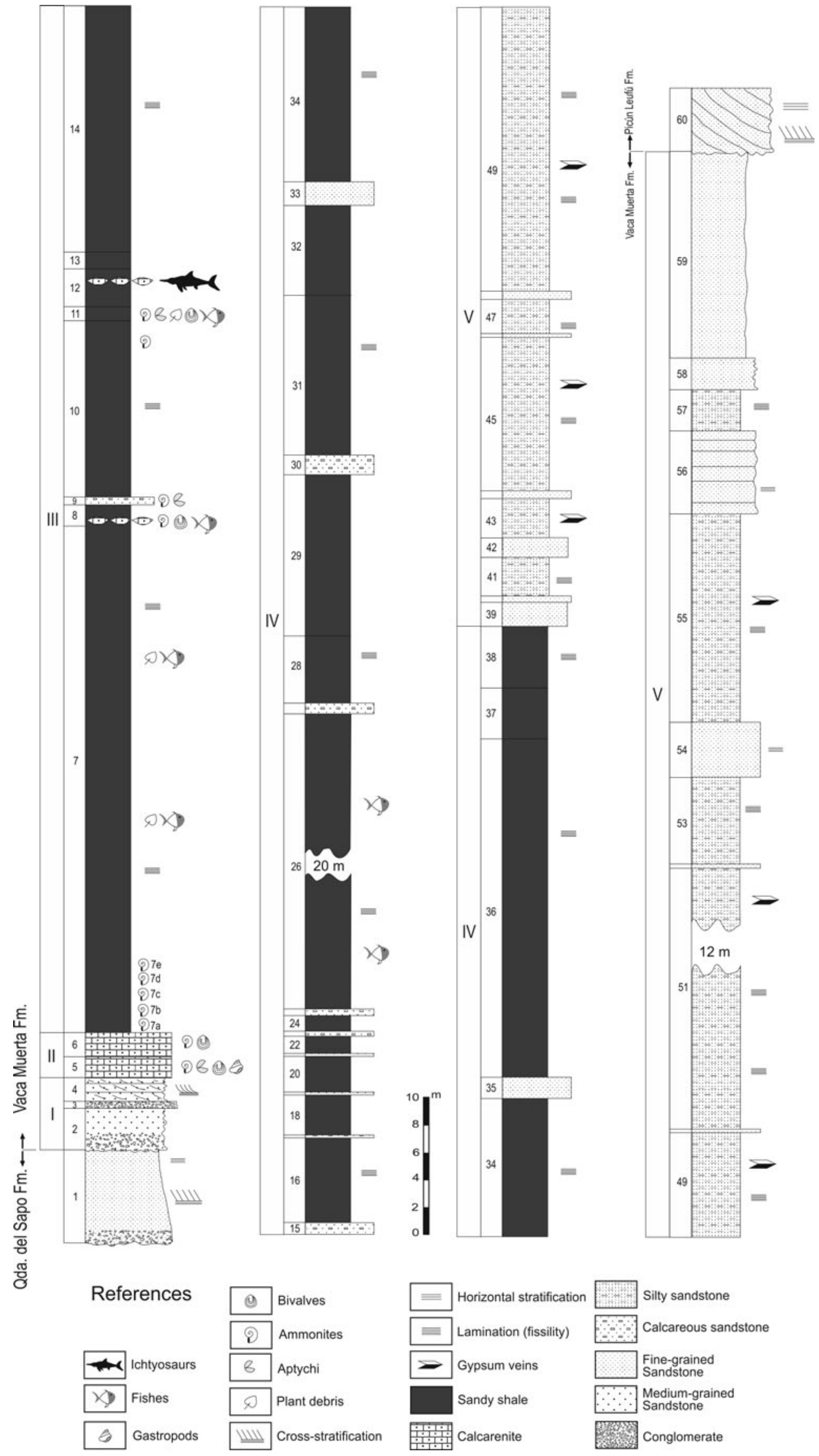


Fig. 3: Log-section of the studied outcrops at Picún Leufú indicated as PP´ in Fig. 2.

(beds PL-33, 35, 39-40, 42, 44, 46, 48, 50, 52, 54, 56, 58-59), constituing the third dominant lithological type of the sequence (nearly 9 % of the total thickness). Toward the top, a clear increase in the frequences and thicknesses of the individual beds is observed. No fossils were found in this lithofacies.

Lithofacies 4. Calcareous sandstones: This facies is formed by pale greenish yellow (10Y 8/2), laminated, calcareous fine-grained sandstones. Sometimes, a high proportion of a muddy fraction gives a wacky aspect to these rocks. These deposits form extensive and continuous beds less than 0.2 m in thickness, reaching exceptionally 1.2 m. These beds occur in the lower section of the profile (beds PL-9, 15, 17, 19, 21, 23, 25, 27 and 30), intercalating into the thick sandy shale deposits. In this lithofacies ammonites occur only in bed PL-9.

Lithofacies 5. Calcarenites: This facies is formed by compact, drab to buff color coquiniferous calcarenites. Internally they are massive or crudely stratified. The sandy fraction is conformed by moderate-rounded, quartz grains; ranging from medium-grained (bed PL-5) to fine-grained size (bed PL-6). These are the only calcarenite levels, located in the lowermost part of the sequence and characterized by a rich content of fossils (see details below).

Lithofacies 6. Silty sandstones. This facies is conformed by finely laminated, dusky yellow (5Y 6/4) to grayish (5Y 8/4) silty sandstones. The sandy fraction is composed of fine-grained, rounded, well-sorted quartz grains; sometimes associated with scarce proportions of muscovite. The development of thin veins of secondary gypsum is characteristic in these deposits. These rocks represent the second dominant lithology in the sequence (nearly 28 % of the total thickness), characterizing the uppermost section of the profile (beds PL-41, 43, 45, 47, 49, 51, 53, 55 and 57). No fossils were found in these deposits, and the proportion of organic matter is very low or lacking.

Lithofacies 7. Sandy shales: This facies consist of fissil, poorly calcareous, finely sandy shales. These deposits form the dominant lithology of the first 220 m of the sequence, constituing nearly 60 % of their total thickness. In the lowermost beds (beds PL-7-8, 10-14) the dominant color is grey to black, while in the upper beds (beds PL-16, 18, 20, 22, 24, 26, 28-29, 31-32, 34, 36-38) the color varies between greenish yellow to greenish gray. This change in color may be due to differences in the content of organic matter. In this sense, results of geochemical analysis of these deposits indicate values of organic content ranging between 0 % and 5 % (DANDERFER, 1977). Likewise, the dark colored sandy shales exhibit an homogeneous, very thin, regular or varve-like lamination; while in the light color sandy shales the development of a continuous, uneven parallel lamination predominates. This latter lamination-type is given by a cyclic and irregular alternance into the sandy shale deposits of thin (< 10 mm thick) and continuous fine-grained sandstone horizons. The sandy shale succession yields some of the most ammonitiferous beds (beds PL-7-8, 10-11), sometimes characterized by the development of diagenetic, calcareous concretions rich in fish and marine reptile remains.

Taphonomic features of the fossiliferous beds: The taphonomic features of the sequence studied exhibit notorious variation in accordance with the lithological variation observed. We have not found strong evidence of significant condensation.

Bed PL-5: This bed is formed by the calcarenite facies, being very rich in fossils. Shell debris is scarce. The fossils are almost exclusively molluscs: ammonites (very abundant, dominating the fauna), gastropods (abundant) and bivalves (moderately abundant); a single brachiopod was collected among hundreds of ammonites. Gastropods are preserved in different ontogenetic stages but all of them belong to local, small-sized species, most likely benthic (see GRÜNDEL & PARENT, 2001, 2006). Gastropods and small juvenile bivalves mostly occur as clusters in the rock matrix and into the body chambers of ammonites, almost exclusively in the macroconchs. Larger bivalves, including oysters, occur as isolated single valves.

Ammonites occur as more or less complete and well preserved adults (macro- and microconchs) with their body chambers typically crushed; complete juveniles or subadults with crushed body chamber; and uncrushed phragmocones. The macro-/microconch ratio is larger than the unit in all species, except for oppeliids where microconchs are more frequently preserved. Some scarce concentrations of ammonitellae have been observed, some of them clustering with small bivalves and tiny gastropods. The specimens are commonly well preserved with the test, and the microconchs commonly with the lappets. The orientation of the specimens in mainly horizontal, parallel to the stratification plane, but mainly small juveniles occur in different orientation. The sediment inside the body chambers is always the matrix of the bed, and the phragmocones are completely filled or replaced by calcite. Aptychi are scarce: Laevaptychi occur loose in the bed in single valves, and a large macroconch oppeliid contains in its body chamber the pair of Lamellaptychus complete and finely preserved. It may be assumed that condensation, if occurred, has been insignificant.

In the face underside most ammonites are covered with epizoans, cemented oysters encrusting the umbilicus and, in some cases, even the lower part of the flank of the outermost whorl. This mode of encrustation was analyzed by COPE (1968b) concluding that oysters colonized empty ammonite shells lying on the bottom of the sea.

Bed PL-6: This bed is formed by the fossiliferous calcarenite facies. Fossils occur mainly in well formed concretions, including one or two ammonites and occasionally abundant small juvenile and adult gastropods and juvenile bivalves, adult bivalves being scarce. Ammonites, only perisphinctids, are mostly well preserved, adult macroconchs and less abundant microconchs. Compression has crushed both the phragmocone and the body chamber with few exceptions of uncrushed juveniles. Some specimens have their peristome preserved but not the lappets in the microconchs. The compression of the whole ammonite, phragmocone and body chamber, and the occurrence concentrated in concretions clearly indicate a post-depositional, diagenetic mechanic action.

Bed PL-7: This bed is formed by the sandy shale facies. The only fossils in these levels are ammonites, abundant in the lower part of the bed (PL-7a-e). Most of them are poorly preserved, mainly as impressions which become visible in the surface of the blocky fractures. Very rare, thin levels of small concretions have yielded few well preserved ammonites. In the upper part of the bed fishes and plant debris occur.

Bed PL-8: This bed shows the same lithology as the underlying bed with a conspicuous band of large concretions which defoliate in sheets. Fossils are abundant, horizontally arranged in the faces of the sheets. The fauna includes mainly ammonites of compressed shell shape, and accessory bivalves and fishes. No strictly benthic elements have been observed. Ammonites are preserved as complete micro- and macroconchs with their body chambers crushed. Even so, preservation is fine, a large part of the specimens is preserved with the test, some microconchs with their lappets and both, macro- and microconchs usually have their aptychi within the body chamber. Some paired aptychi occur isolated. Adhered to the surface of some concretions larger and stouter ammonites occur, but they are poorly preserved and very hard to collect in a single piece, as typical in this kind of poorly calcareous sandy shales.

Bed PL-9: This bed is formed by the fine-grained, calcareous sandstone facies. Fossils are moderately abundant, including ammonites and bivalves. Preservation of ammonites is similar to that of the underlying bed but they are less abundant.

Bed PL-10: The lithology of this level corresponds to the sandy shale facies. The only recorded fossils are scarce ammonites in the upper part of the bed. The preservation modes are similar to those of bed PL-7.

Bed PL-11: This bed corresponds to the sandy shale facies. Fossils observed are ammonites (including rare aptychi), bivalves, fishes and plant debris in abundance. Crushed bivalves and ammonites are seen in the plane of fracture of the shales. Ammonites also occur, well preserved, in small, very hard concretions which sparsely occur. The phragmocones are finely preserved in these cases and typically complete with the test, but the body chamber is crushed, mainly in the outer part of the concretion.

Bed PL-12: This bed is lithologically similar to the underlying bed (sandy shale facies), but includes at least one row of large calcareous concretions with blocky fractures. Fossils observed are ammonites and ichthyosaurs. The occurrence is in the form of complete, large ammonites and isolated fragments in the concretions. Most specimens are embedded in the external part of the concretions so that about a half of the ammonite is eroded. Nevertheless, is not clear if this eroded part is a weathering effect or, alternatively, fresh concretions were in this condition.

Interpretation: Along the profile we have recognized at least five different episodes of sedimentation. The first episode is represented by the conglomerate and sandstone facies of the beds PL-2-4. The interpretation of this succession has been discussed previously. In general, it is assigned to a short erosional event and reworking of the underlying substrate, produced during the rapid marine transgression of the "early" Tithonian sea in the Neuquén Basin. According to BOLL & VALENCIO (1996), these sediments have been accumulated along the coast line as bars or transgresive lag deposits.

The second episode of sedimentation is represented by the calcarenite facies of the beds PL-5-6. These deposits represent a more or less short sedimentation event under relative low energy conditions in a well oxygenized, shallow marine environment.

The third episode is represented by the grey to black, varve-like laminated, sandy shale deposits (beds PL-7-14). The continuous fine-lamination in these organic-carbon-rich sediments, indicates the absence of benthic organisms producing bioturbation and anaerobic to anoxic conditions (BYERS, 1974; ARTHUR *et al.,* 1984; ISAACS, 1984; MOON & HURST, 1984). The low oxygen content in low-deep water mass may be due to basin conditions of restriction or poor circulation (TWENHOFEL, 1939). Similar deposits of the Vaca Muerta Formation have been interpretated by SPALLETTI *et al.* (2000) as sediments formed in anoxic to dysoxic basinal environments.

The fourth episode is conformed by the association of the greenish yellow to greenish gray, uneven parallel laminated, sandy shale deposits, and the fine-grained calcareous sandstone facies (beds PL-15-38). The minor content of organic matter in this succesion can be attributed to several causes, such as minor supply of organic matter in the basin, decreasing of the rate of sedimentation, or increasing of the oxygen content of the water mass overlying the sediment (ARTHUR *et al.*, 1984;

ROBERTSON, 1984). The uneven parallel lamination that characterizes these shale deposits is attributed to cyclic fluctuations (seasonal or annual) in the sediment supply and sedimentation rate (ISAACS, 1984; ARTHUR *et al.,* 1984). The thicker intercalated calcareous sandstone beds indicate short and highly rated supply of sediment, possibly originated from storms. In general this section shows evidence of more heterogeneous supply of sediments and conditions of more oxygenized basin environments.

The fifth episode is conformed by the association of the silty sandstones and massive fine-grained sandstones facies (beds PL-39-59). This section shows an increase in the grain size of the sediment and absense of organic matter, suggesting a tansition towards shallower marine and well-oxygenized conditions.

III. SYSTEMATIC PALEONTOLOGY

The material described was collected by the authors in the last ten years and is housed at the Laboratorio de Paleontología y Biocronología, Universidad Nacional de Rosario (LPB), and Museo Prof. OLSACHER, Zapala (MOZPI). Casts, photographs and information about types and other specimens were kindly provided by E. PÉREZ D'A (Servicio Nacional de Geología y Minería de Chile, Santiago; SNGM), E.A. NESBITT and R.C. ENG (BURKE Museum, University of Washington, Seattle; BMS), H. JAHNKE and M. REICH (Institut für Geowissenschaften der Universität Göttingen; MGAU), and M. SANDER and N. STÖCKER (Bonn University, IPB). Body chamber is abbreviated with Bc and phragmocone with Ph; macroconch (female): [M], microconch (male): [m]. Measurements are indicated as follows: diameter (D), diameter at the last adult septum (D_{ls}), final adult diameter at peristome (D_p), umbilical width (U), whorl width (W), whorl height (H_1), and whorl ventral (or apertural) height (H_2), all given in millimeters [mm]; approximated or estimated values marked with (^{e}); length of body chamber (L_{Bc}) in degrees [°]. Number of primary (P) and ventral (V) ribs per half whorl. This form of counting ribs per half whorl is more sensitive for reflecting changes in ribbing density, and less exigent with quality of material, allowing to consider incomplete specimens for the obtention of more complete sets of measurements for ontogenetic trajectories. Nomenclature adopted for description of ribbing is shown in Fig. 4. Measurements of type and other selected specimens are given in Appendix 1. Other abbreviations used are HT: holotype, LT: lectotype, PT: paratype, TL: type locality, TH: type horizon, MT: monotypy, TS: type species, OD: original designation, SD: subsequent designation. The ontogeny of ribbing is the most important feature in the systematic taxonomy proposed in this paper for the Andean Ataxioceratidae, so that for clarity the adopted nomenclature is depicted in Fig. 4. Innermost whorls are especially considered for classification at the genus level, so that when possible this part of the ammonite is figured in double size.

Taking advantage that all the samples studied were collected bed-by-bed, the taxonomic approach followed is based on the assumption that the slowly evolving lineages are seen in the stratigraphic record as incomplete successions of more or less variable transients. This approach of horizontal classification is useful for the identification of species from the morphotypes available. Lineages are, if convenient and possible, divided into successive segments (groups of transients) in order to reflect relative age and morphological differences (see DIETZE *et al.,* 2005 for further details).

The biostratigraphic and chronostratigraphic units cited for the distribution and occurrence of the different species are defined below in the chapter Biostratigraphy and time-correlation.

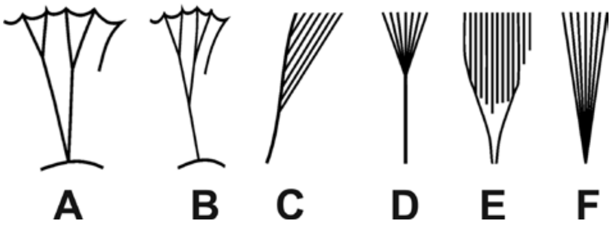


Fig. 4: Schematic representation and nomenclature adopted for the main types of rib polyfurcation in the Ataxioceratidae of the studied fauna. Orientation is adoral or peristomatic to the right. **A-B**: Polyzchizotomic rib-complex, the first bifurcation may be at the umbilical shoulder (**A**) or upper on the flank (**B**); typical of *Catutosphinctes* and less commonly in some *Choicensisphinctes*. **C**: Virgatotomic (s.s.) arrange, several (three or more) secondary ribs branching at different heights from the front of the primary; occurs saltuary in *Choicensisphintes* and more consistently in Andean "*Lithacoceras*". **D**: Palm-like bundle of secondaries branching from about a single point of a thicker primary, typical of adult bodychamber of Andean "*Lithacoceras*". **E**: Extreme palm-like bundle of secondaries branching from a wide and short primary; typical of the adult phragmocone and beginning of the body chamber of macroconch *Choicensisphinctes*. **F**: Fasciculate, multibranching at umbilical shoulder; rare and isolate occurrence in some *Choicensisphinctes* .

Superfamily Perisphinctoidea STEINMANN, 1891

Family Ataxioceratidae BUCKMAN, 1921

Remarks: Subdivision of the family follows DONOVAN *et al.* (1981) but includes the subfamily Torquatisphinctinae TAVERA, 1985 as prompted by OLÓRIZ & TINTORI (1991) and further discussed in PARENT (2003a) and below.

In describing the perisphinctids of the Andean Tithonian we have elaborated a classification which considers the morphological, temporal and spatial dimensions of the fauna, based on the consideration of the sexually dimorphic ontogeny of samples collected bed-by-bed through a well delimited paleogeographic setting. The resultant systematic taxonomy allows to describe simply and naturally most, if not all known ataxioceratids of the Tithonian of the NB. Thus, the model seems to be adequate for new taxonomic and biostratigraphic developments and refinement of the current knowledge.

The classification proposed for the Andean lower-middle Tithonian Ataxioceratidae includes three genera: two phyletic lineages, *Choicensisphinctes* Leanza, 1980 (Lithacoceratinae) and *Catutosphinctes* Leanza & Zeiss, 1992 (Torquatisphinctinae), and "*Lithacoceras*" Hyatt, 1900 represented by apparently two species in the lower Tithonian, about which persists little doubt on its generic assignment. Each one of these three genera is rather well characterized by its different ontogeny of sculpture, shell shape and coiling and, moreover, their sexual dimorphism is different, especially by the morphology of the microconchs. Both phyletic lineages include, all throughout the area of the NB, successions showing progressive differentiation, mainly in their spectrum of variation and novel morphologic variants, showing their own, independent evolutionary trends.

Under this classification it is not necessary to use the following conflictive genera to which are often assigned certain Andean ammonites: (1) *Virgatosphinctes* [M] / *Aulacosphinctoides* [m] (pars) have already been restricted to the group of the type species and the closest ones (Enay, 1972; see Enay, 2009 for a detailed revision) which are late Tithonian in age, probably originated in *Choicensisphinctes* (Enay & Cariou, 1999; Yin & Enay, 2004); (2) *Pseudinvoluticeras* Spath, 1925 was originally defined on the basis of a single poorly preserved specimen of which there has never been clear the stratigraphic position in the type locality in Somaliland; (3) *Torquatisphinctes, Pachysphinctes* and *Katroliceras* conform an Indo-Madagascan lineage discussed below; (4) *Subdichotomoceras* Spath, 1925 and (5) *Parapallasiceras* Spath, 1925, both discussed below.

Subfamily Lithacoceratinae Zeiss, 1968

Remarks: The subfamily has been recently reviewed by Zeiss *et al*. (1996) where can be seen the large number of nominal genera, most of them sexually dimorphic, which are commonly included.

Genus *Lithacoceras* Hyatt, 1900

Type species: *Ammonites ulmensis* Oppel, 1858; by OD.

Remarks: We assign two species tentatively to this genus based on that typical Tethyan Submediterranean species are the closest resembling. In morphological terms the Andean forms may be easily attributed to *Lithacoceras*, but, according to the restricted stratigraphic and geographic records currently available we have preferred to await for new collections from northern South America and the Carribbean region for a safer classification. Moreover, some specimens show transitional features between *Lithacoceras* and *Virgataxioceras* (see discussion below), both typical Submediterranean genera closely related in the same phyletic line. *Lithacoceras* is a broadly distributed genus (see Schweigert & Zeiss, 1999). Specimens attributable to *Lithacoceras* or *Virgataxioceras* are known from Mexico (Burckhardt, 1906; Callomon, 1992; Olóriz *et al.,* 1993) and western Canada (Poulton *et al.,* 1988) as already discussed in previous papers (Parent, 2003a; Parent *et al.,* 2006), and also occur in Antarctica (Witham & Doyle, 1989). Considering the discussion in the mentioned papers and the noted distribution of the genus, it seems highly probable that the "*Lithacoceras*" of the NB reached the region from Europe via the Hispanic Corridor.

"*Lithacoceras*" *picunleufuense* n. sp.
Figs. 5E-H, 6-12

1999. *Lithacoceras (Virgalithacoceras)* cf. *acricostatum* Ohmert & Zeiss.- Parent & Capello, p. 349.
2001. *Euvirgalithacoceras malarguense* (Spath).- Gründel & Parent, p. 14; fig. 2.
2003a. *Euvirgalithacoceras malarguense* (Spath, 1931).- Parent, p. 147; figs. 6A, 6D, 7B, 7E.
2006. "*Lithacoceras*" n. sp. aff. *malarguense* (Spath, 1931).- Parent *et al*., p. 257; figs. 2, 3A-3B.

Material: 37 macroconchs, 9 microconchs and several fragmentary specimens, all from beds PL-5 and PL-6.

Type series: Holotype [M]: Fig. 6 (LPB 1098) and three paratypes: PT-1 [M], Fig. 7A (MOZPI 7281); PT-2 [m], Fig. 7B (MOZPI 7305); PT-3 [m], Fig. 9B (MOZPI 7319/4); all from the type horizon.

Type locality and horizon.- Picún Leufú (Fig. 1); bed PL-5, *picunleufuense* α horizon, Picunleufuense Standard Zone, Lower Tithonian.

Derivation of name: After the type locality.

Description: Macroconch: medium size for the genus; compressed, evolute, suboval to rounded subtrapezoidal whorl section. Ribbing on phragmocone moderately dense, mainly bifurcate with a short stage of virgatotome trifurcates, passing on adult body chamber to strong primaries divided, in the middle of upper third of flanks, in palmate sheaves of finer secondaries. Peristome simple. Adult body chamber about three quarters to a complete whorl long. Microconch: Small, about one third of the adult size of the macroconch. Phragmocone

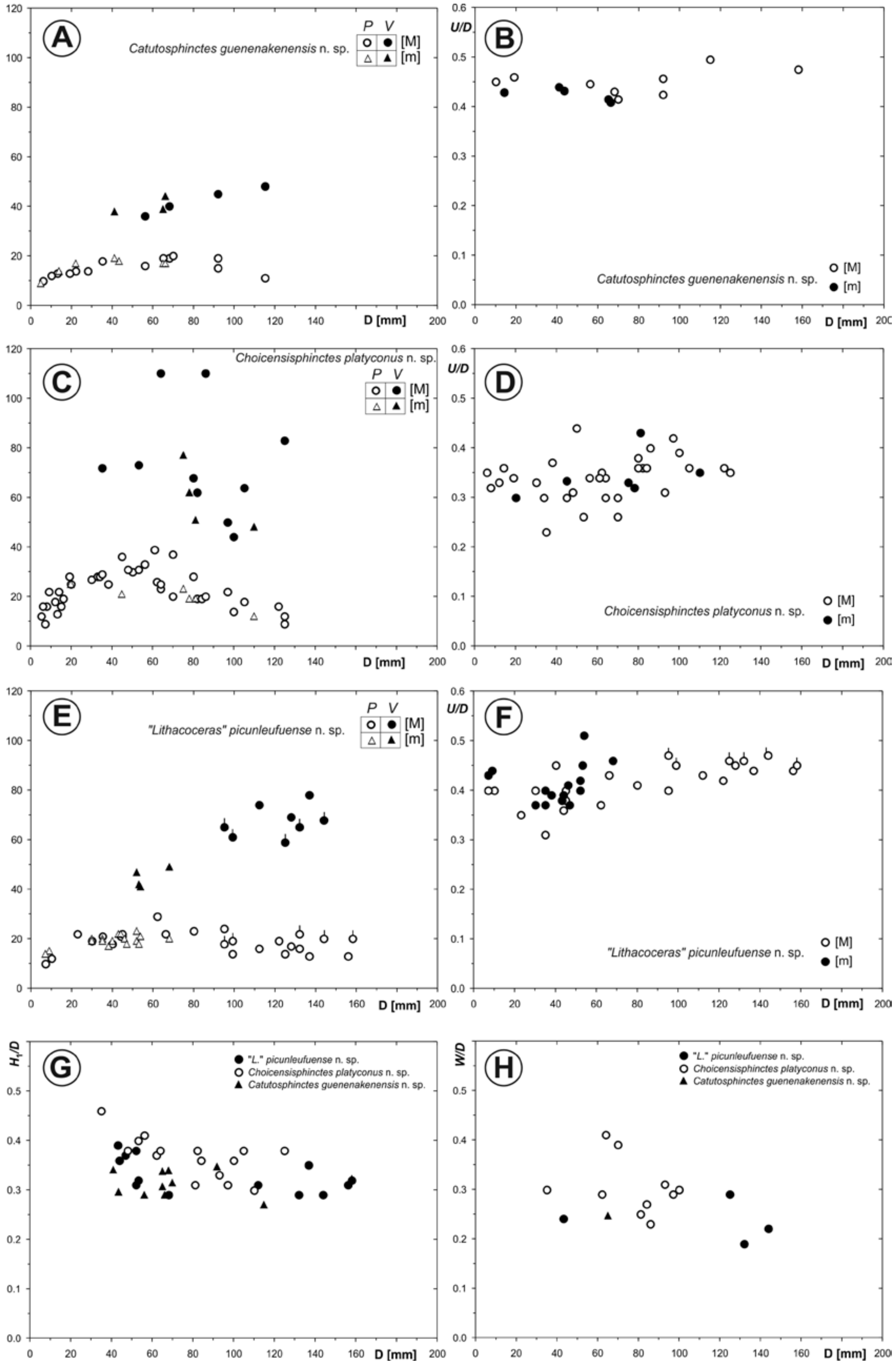


Fig. 5: Ontogenetic trajectories and variation of ribbing (*P*, *V* – *D*), relative umbilical diameter (*U*/*D* –*D*), relative whorl height (H_1/D – *D*) and relative whorl width (*W*/*D* –*D*) of "*Lithacoceras*" *picunleufuense* n.sp. [M&m] (points marked with a stick represent the transient β, those unmarked for transient α), *Choicensisphinctes platyconus* n.sp. [M&m] and *Catutosphinctes guenenakensis* n.sp. [M&m].

as in the macroconch at comparable diameter; adult body chamber slightly uncoiled, about half whorl long, compressed, densely ribbed by bifurcate primary or simple ribs and few intercalars and polyschizotomes. Peristome projected as a pair of spatulate lateral lappets.

The holotype (Fig. 6) is an adult macroconch with incomplete body chamber (estimated diameter at peristome about 170 mm), preserving remains of the shell in one of its sides. Diameter at last septum is 112 mm. Evolute, with a moderately open, shallow umbilicus. Compressed, suboval to rounded subrectangular whorl section on adult phragmocone and body chamber. Inner whorls evolute, with rounded whorl section. Ribbing of innermost whorls (D = 5-10 mm) composed of strong, acute prorsiradiate primary ribs which bifurcate on the upper flank (Fig. 6A_4). At about D = 4 mm occurs a strong

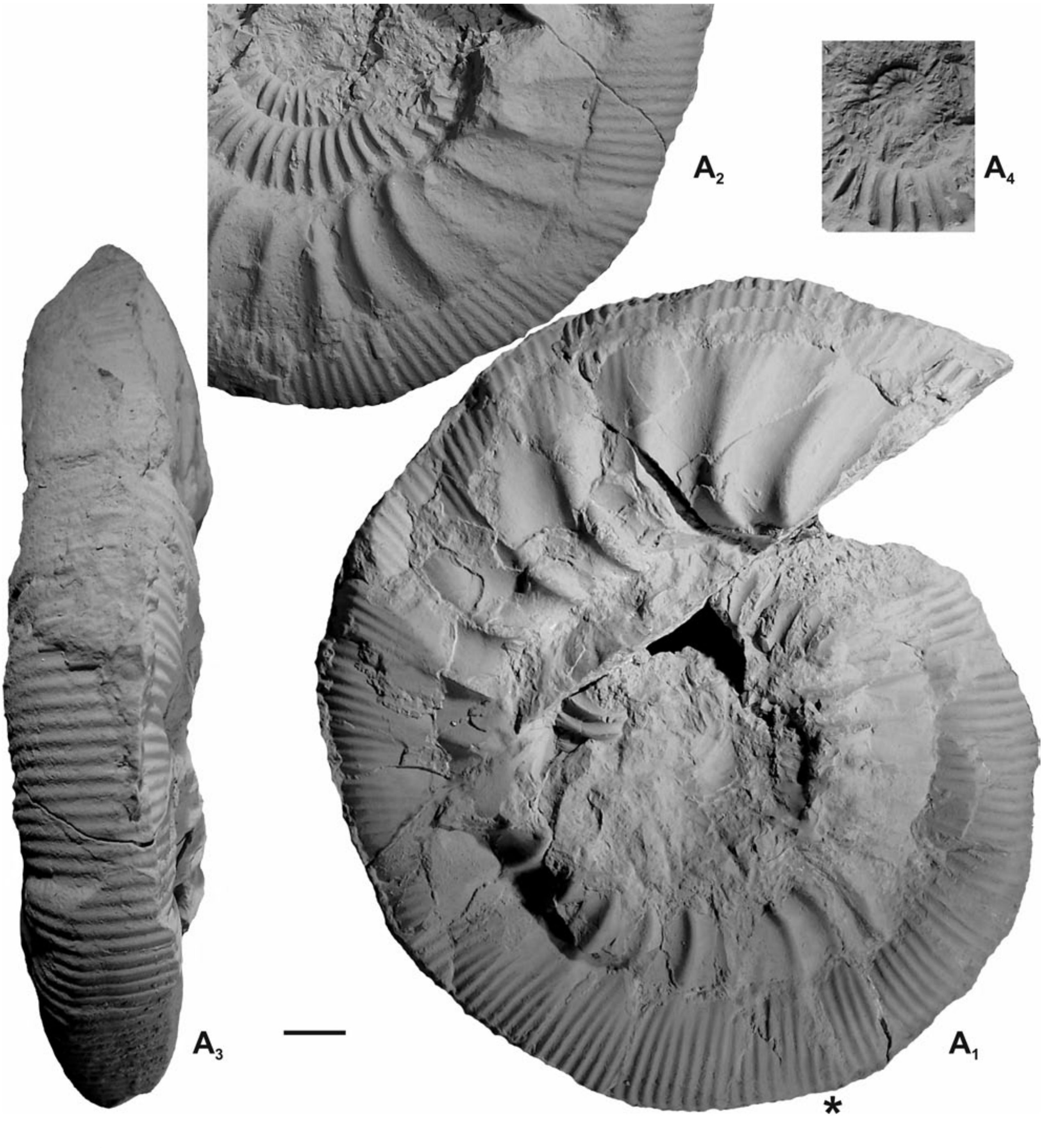


Fig. 6: *"Lithacoceras" picunleufuense* n. sp. (transient α). Holotype, adult [M] with incomplete body chamber (LPB 1098). **A_1-A_3**: Lateral and ventral views, **A_4**: innermost whorls enlarged (x2). Picún Leufú, bed PL-5, *picunleufuense* α horizon. In this and all subsequent Figures 7-36: (1) the scale bar is 10 mm length respect to figures in natural size (x1), (2) the asterisks indicate the onset of the body chamber, and (3) all ammonites are figured in natural size, otherwise indicated.

constriction bounded by strong primary ribs. Medium whorls are more densely ribbed with prosocline, acute primaries which born on the umbilical wall, bifurcate and later trifurcate in virgatotome style on the middle or upper half of the flank. From about 90-100 mm in diameter, after the short virgatotome stage, a distinctive variocostation occurs, primaries become stronger and more widely spaced; they born on the umbilical wall, cross the umbilical shoulder retroversely and cross the lower half of the flank directed forwardly; around the middle flank they divide profusely in sheaves of finer secondaries in polyschizotomic or subvirgatotome style; in the first half whorl of the body chamber the ribbing is palmate with ventral ribs crossing the venter unchanged and evenly spaced. At the end of the phragmocone can be seen frequent intercalatory ribs and one or two constrictions preceded by a primary divided in a polychizotomic style and a front primary which is acute and stronger, divided in two or three secondaries. Suture is not visible.

The macroconchs of bed PL-6 show some slight but consistent differences from those of the underlying type horizon bed PL-5. They are treated as type transient α (the oldest) and transient β:

- *Transient α (including the HT and paratypes).* Macroconchs are few variable, some specimens

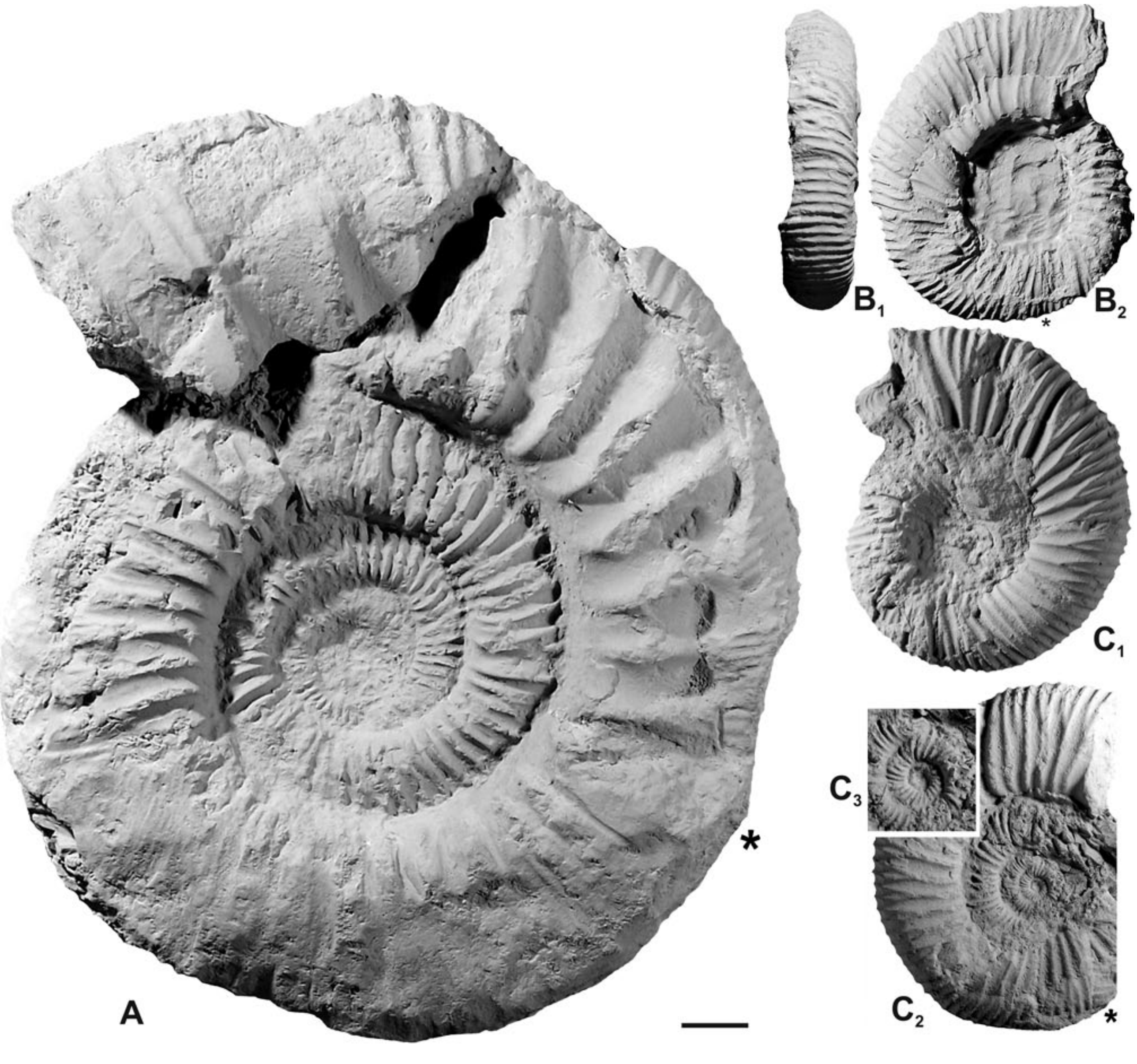


Fig. 7: *"Lithacoceras" picunleufuense* n. sp. (transient α). **A**: Paratype-1, adult [M] with incomplete body chamber (MOZPI 7281). **B**: Paratype-2, complete adult [m] with lappets (MOZPI 7305). **C**: complete [m] with lappets (MOZPI 7772) lateral views (C_1-C_2) and enlarged (x2) innermost whorls (C_3). Picún Leufú, bed PL-5, *picunleufuense* α horizon.

show denser ribbing on the phragmocone from the inner whorls respect to the holotype (Fig. 8B, 9D). A portion of body chamber of a large and compressed macroconch (estimated maximum diameter 200 mm) is sculptured by strong primaries, widely spaced and the typical, evenly spaced ventral ribbing vanishes towards peristome (Fig. 8A). This fragmentary specimen shows a conspicuous pair of closely-spaced, straight, undivided parallel primary ribs which occur irregularly in the species from the innermost whorls. A small adult macroconch (Fig. 9D) shows an atavic aspect recalling *Ataxioceras* FONTANNES, 1879 by the strongly ribbed body chamber with blade-like primaries unevenly spaced, unclearly furcate and separated by abundant short intercalatories.

Microconch adult size at peristome is moderately variable, ranging from 40 to 68 mm in diameter. The phragmocone is indistinguishable from the inner whorls of the macroconchs at comparable diameter. The adult body chamber is evolute, slightly uncoiled at the end, compressed subrectangular in whorl section. Ribbing is dense, irregular, composed by primaries and ventral ribs indistinct in strength, crossing the venter unchanged and evenly spaced. Primaries are somewhat

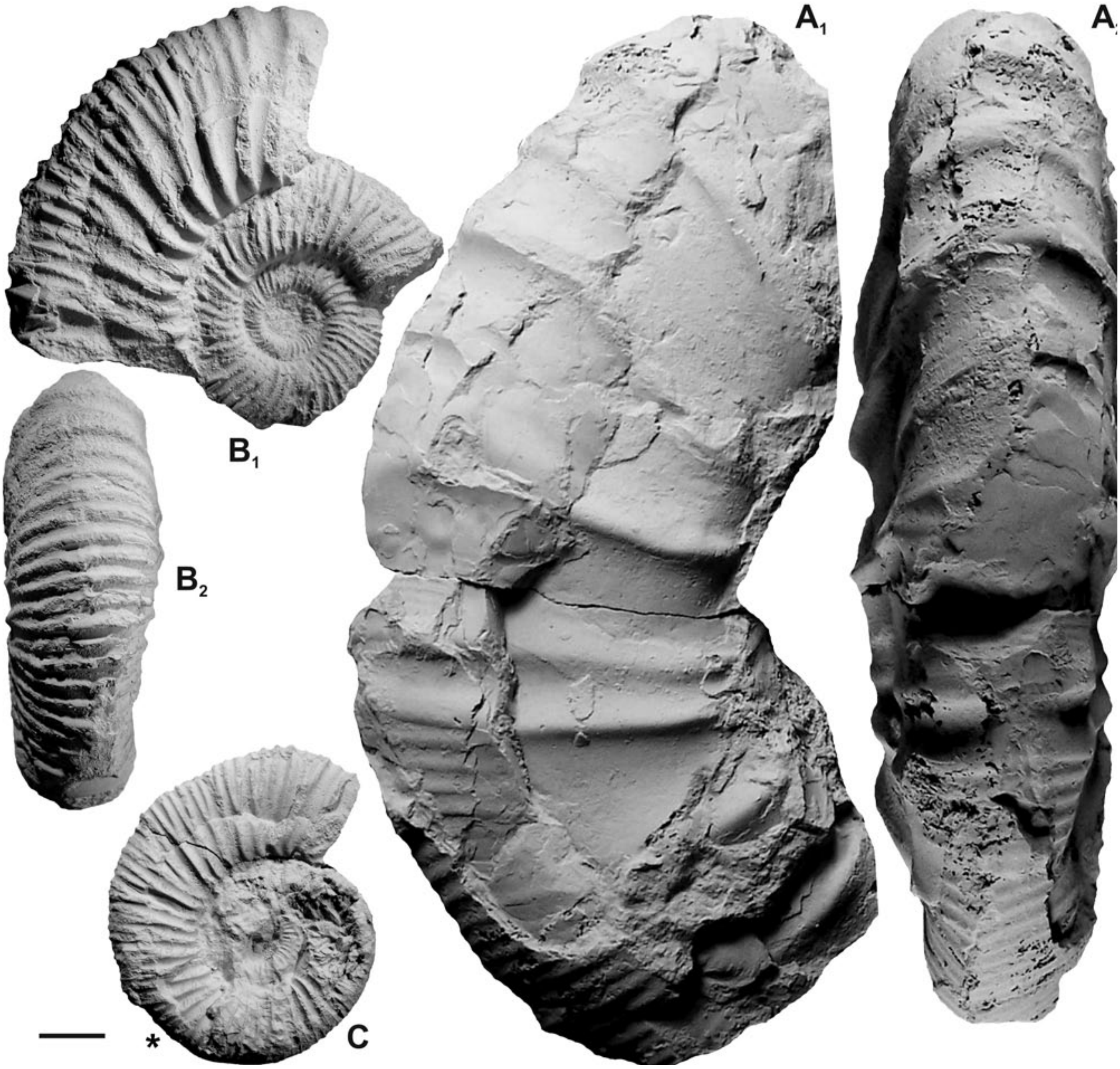


Fig. 8: *"Lithacoceras" picunleufuense* n. sp. (transient α). **A**: terminal portion of the body chamber of a large [M] (MOZPI 7765). **B**: adult [M] phragmocone (LPB 622). **C**: complete adult [m] with lappets (MOZPI 7479). Picún Leufú, bed PL-5, *picunleufuense* α horizon.

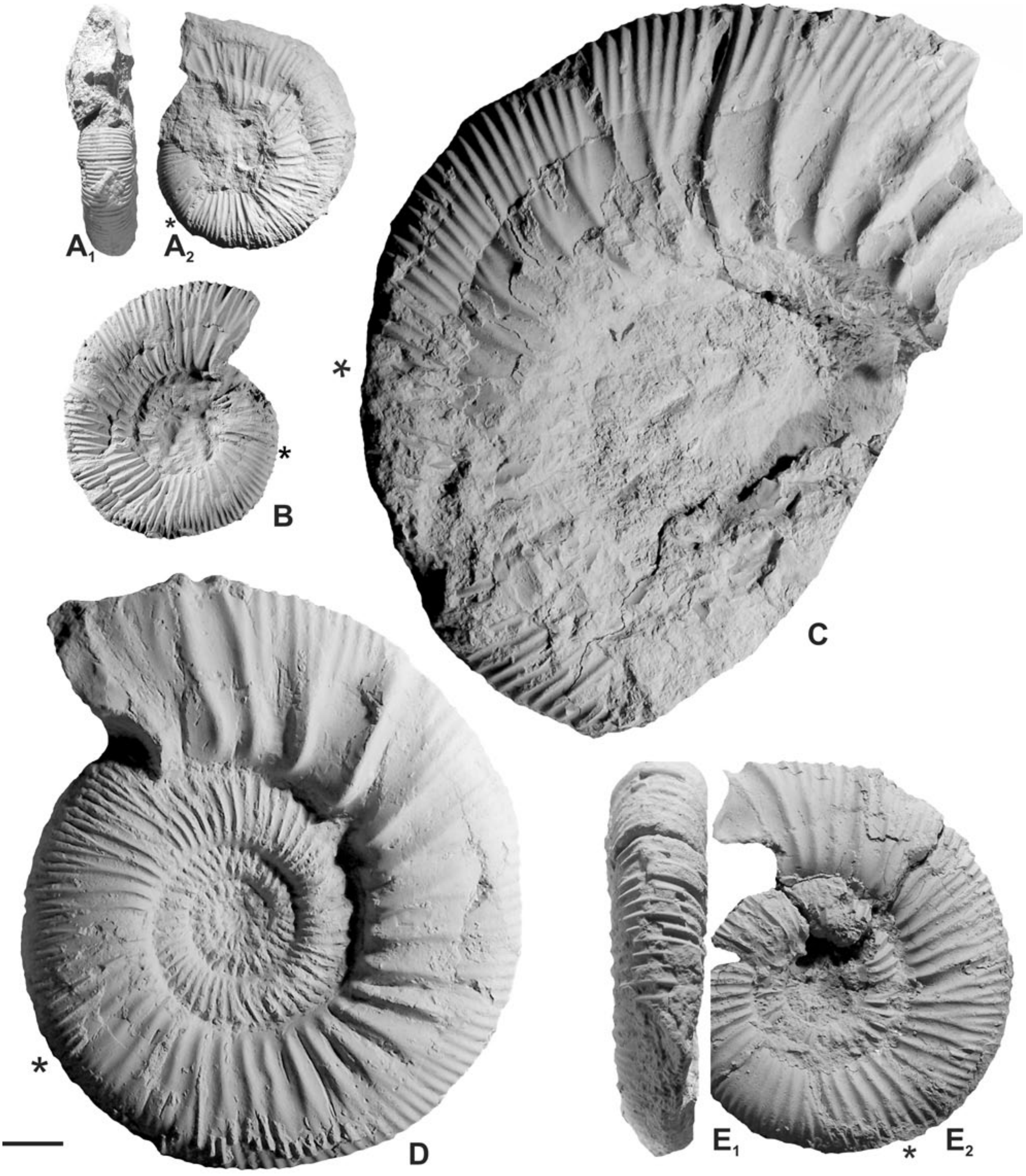


Fig. 9 : *"Lithacoceras" picunleufuense* n. sp. (transient α). **A** : complete adult [m] with lappets (MOZPI 7269/9). **B** : complete adult [m] (MOZPI 7319/4). **C** : incomplete adult [M] (MOZPI 7799) showing the typical ribbing and onset of variocostation from the beginning of the body chamber. **D** : complete small adult [M] (MOZPI 6459). **E** : complete large adult [m] with lappets (MOZPI 7473). Picún Leufú, bed PL-5, *picunleufuense* α horizon.

prosocline, bifurcate from the mid-flank; there are also some simple and intercalatory ribs occurring sporadically. The peristome in largest specimens is preceded by a strong constriction bounded by a polyschizotomic rib and an acute simple primary, and projected in a pair of long lappets. On the other hand, a pair of somewhat shorter lappets is preserved in the smaller and more densely ribbed specimens.

- *Transient β*. Only macroconchs available. Their general aspect is very similar to that of the transient α since the ranges of variation overlap, but some consistent differences may be pointed out: (1) most specimens tend to be more densely ribbed on the flanks of the phragmocone and the body chamber, but ventral ribbing on body chamber is less dense than in transient a (see Fig. 5E), (2) the onset of variocostation in most specimens appears later in ontogeny, at the beginning of the adult body chamber, (3) the adults are slightly more evolute (see Fig. 5F), (4) adult size is somewhat larger as indicated by two fragmentary specimens which are septate at 200 mm in estimated diameter, and (5) constrictions on adult phragmocone are well marked, wide and moderately deep, whereas in transient α they are mainly confined to the innermost whorls.

Remarks and comparison: The only species described for the Andean Tithonian which seems to be close to "*Lithacoceras*" *picunleufuense* n. sp. is *Subplanites malarguensis* SPATH, 1931. The latter species is known

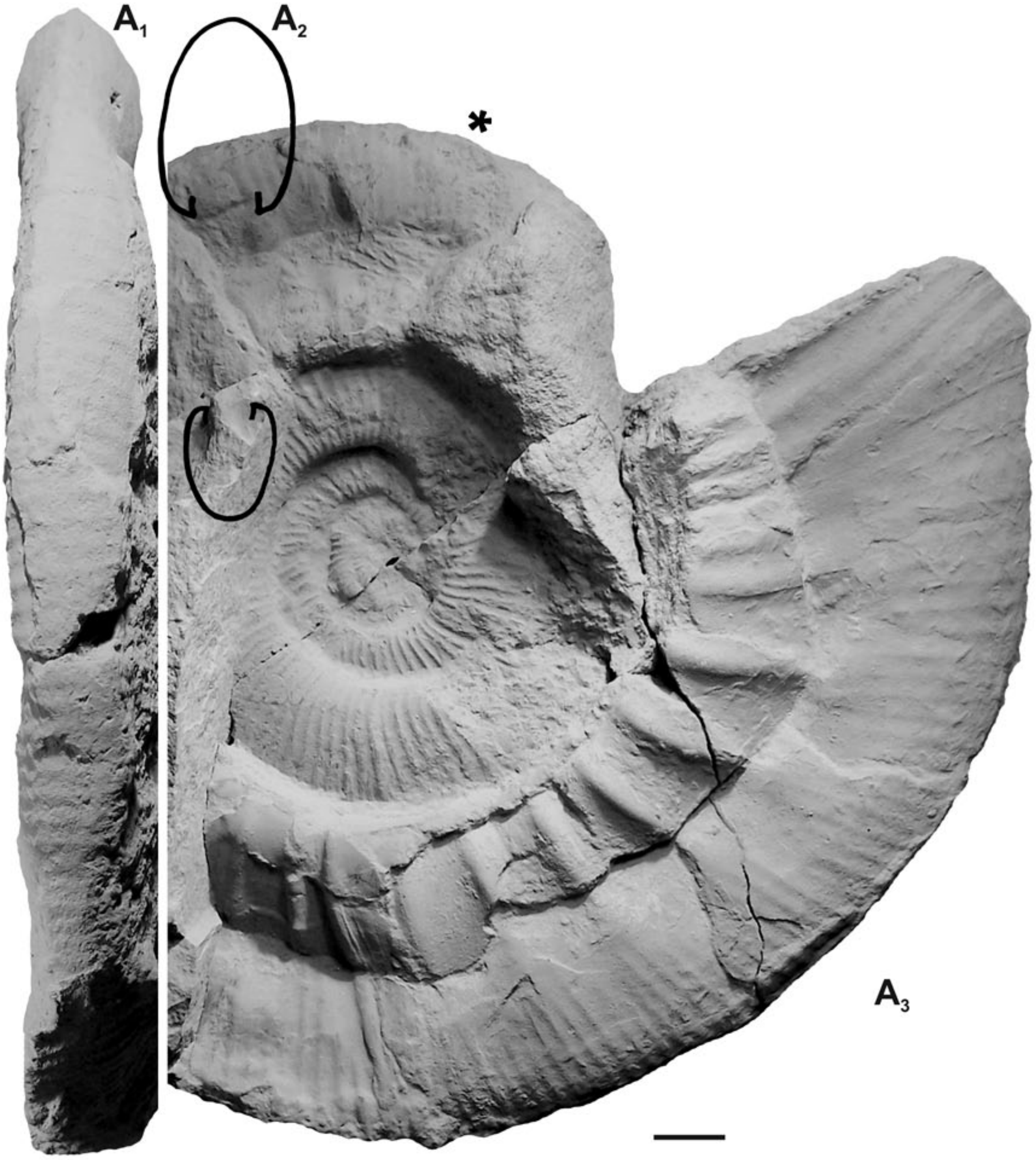


Fig. 10: *"Lithacoceras" picunleufuense* n. sp. (transient β). Complete adult [M] with peristome (MOZPI 7761). A_1, A_3: ventral and lateral views, A_2: whorl section of last whorl of phragmocone. Picún Leufú, bed PL-6, *picunleufuense* β horizon.

only by its holotype coming from Casa Pincheira, Mendoza, originally figured by BURCKHARDT (1900: pl. 24: 4) under *Perisphinctes* aff. *lictor* FONTANNES (*in* DUMORTIER & FONTANNES), 1876; later refigured by a hand-drawing (BURCKHARDT, 1903: pl. 4: 1-2) under *Perisphinctes* aff. *pseudolictor* CHOFFAT, 1893. Best resemblance of this specimen is with the more densely ribbed specimens of the transient β, but closer comparison is precluded for the holotype of *S. malaguensis* is an adult phragmocone with apparently only a short part of its body chamber which is important in the diagnosis of these ammonites. Significant differences, although not very strong, are the stouter whorl section from the inner whorls, the different aspect of the constrictions, and the lack of the diagnostic stage at the adult phragmocone of trifurcate virgatotome ribbing which, moreover, is more rigid and prosocline with abundant constrictions from the inner whorls in *"Lithacoceras" malarguense*.

Within the material described by INDANS (1954) from Southern Mendoza, there are several specimens which could be undoubtely assigned to "*Lithacoceras*" *picunleufuense* n. sp. Nevertheless, any comparison is useless for all that material has neither stratigraphic nor geographic information associated; the labels were unfortunately disconnected from the specimens prior to the study by INDANS.

S. malarguensis was frequently cited, sometimes as *Perisphinctes* aff. *pseudolictor*, for referring to ammonites from the base of the Tithonian of the NB, but neither a single specimen was ever figured (e.g., GROEBER, 1929, 1933; 1946, 1952; LEANZA & HUGO, 1977; LEANZA, 1980). It is very suggestive that some of these citations could have been references to specimens of *"L." picunleufuense* n. sp. since the type horizon of this species is a bed which has much horizontal continuity as widely recorded throughout the NB. The

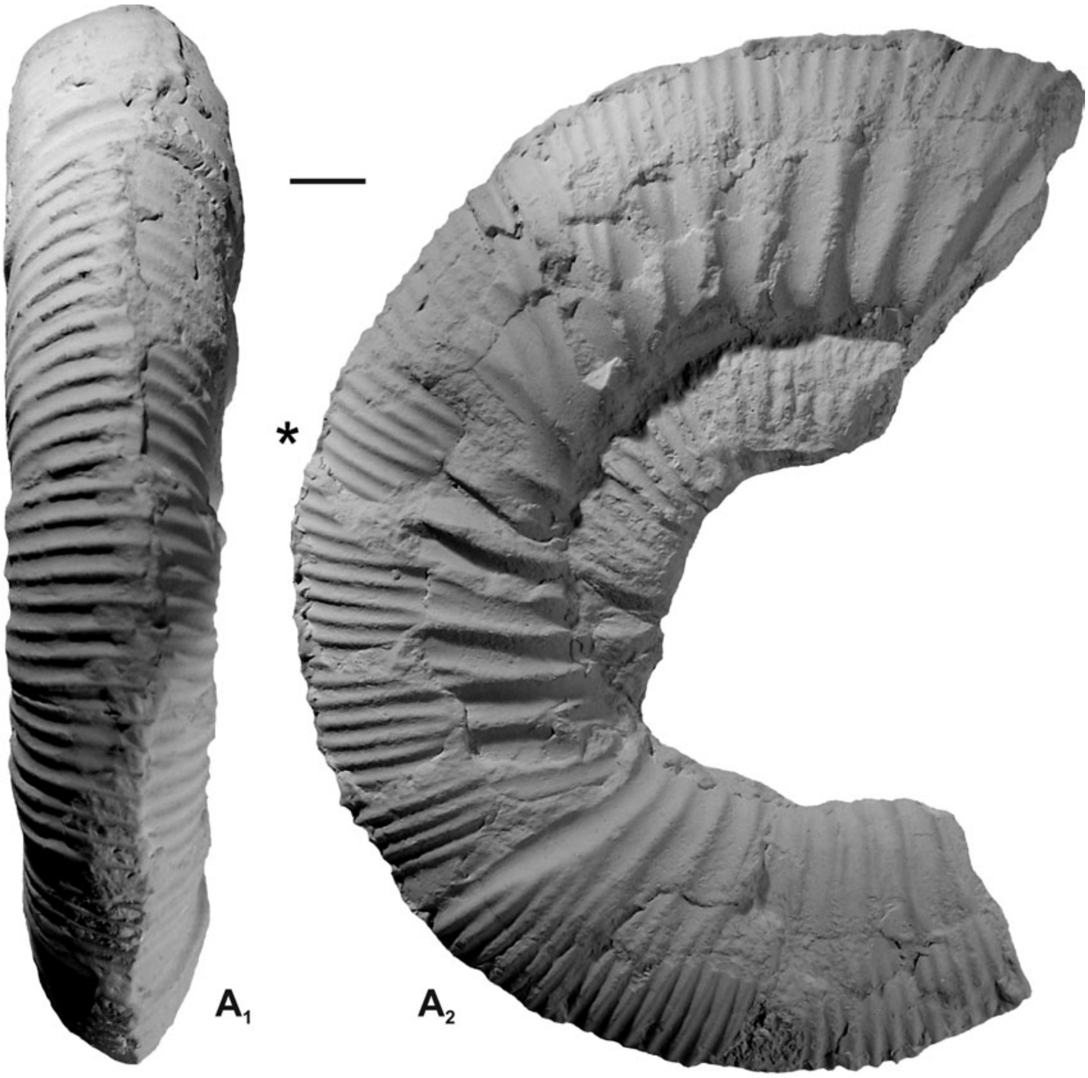


Fig. 11: *"Lithacoceras" picunleufuense* n. sp. (transient β). Terminal phragmocone and beginning of the body chamber of an adult [M] (LPB 836), showing the occurrence of marked constrictions and beginning of variocostation. Picún Leufú, bed PL-6, *picunleufuense* β horizon.

holotype of *S. malarguensis* was collected in the bed M6 of Casa Pincheira (BURCKHARDT, 1900, 1903) with other ammonites which conform an interesting assemblage (below called M6-assemblage). This assemblage is composed by ammonites which can be clearly assigned to genera of the systematic taxonomy used in the present paper for describing the whole ataxioceratid fauna of the lower and middle Tithonian of the NB. As figured by BURCKHARDT (1900) in his plate 24 the ammonites of the M6-assemblage are: (1) “*Lithacoceras*” *malarguense* (SPATH, 1931) in BURCKHARDT (1900: pl. 24: 4 - holotype -, and 8), (2) *Catutosphinctes windhauseni* (WEAVER, 1931) in BURCKHARDT (1900: pl. 24: 5-6), see below the discussion and refiguration of the type

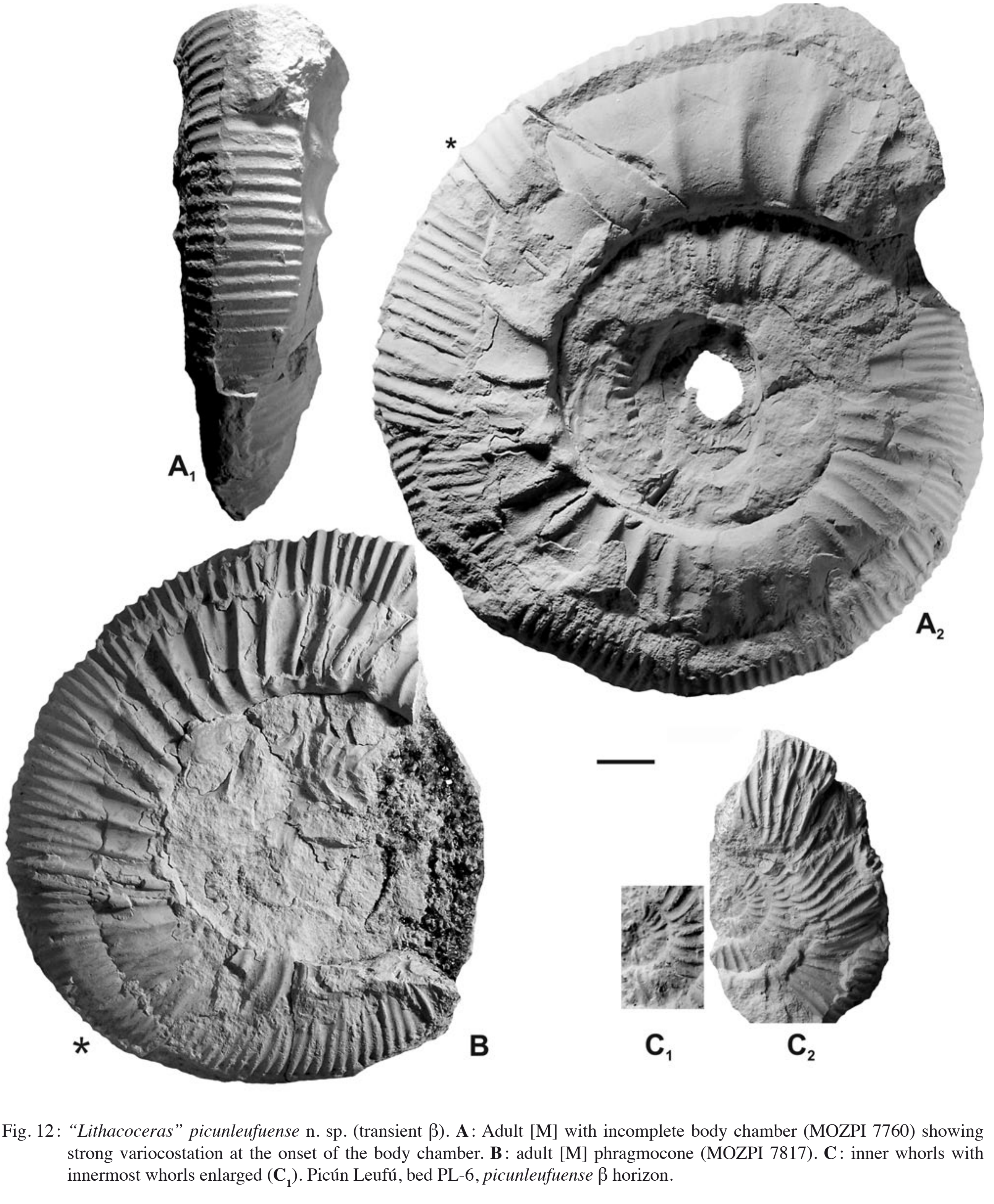


Fig. 12: *“Lithacoceras” picunleufuense* n. sp. (transient β). **A**: Adult [M] with incomplete body chamber (MOZPI 7760) showing strong variocostation at the onset of the body chamber. **B**: adult [M] phragmocone (MOZPI 7817). **C**: inner whorls with innermost whorls enlarged (**C$_1$**). Picún Leufú, bed PL-6, *picunleufuense* β horizon.

specimen, (3) *Catutosphinctes* cf. *guenenakenensis* n. sp. (BURCKHARDT, 1900: pl. 24: 1 and 2?), (4) *Choicensisphintes burckhardti* (DOUVILLÉ, 1910; see BURCKHARDT, 1900: pl. 24: 7, the HT by MT), and (5) "*Lithacoceras*" sp. (BURCKHARDT, 1900: pl. 24: 3). *Cat. windhauseni* has been recently collected in abundance in its type locality, La Amarga (short name for referring to the full name: La Amarga-Cerro Granito; PARENT *et al.*, 2008), from a horizon where the first representatives of *Pseudolissoceras zitteli* (BURCKHARDT, 1903) certainly occur. Direct evidence from Casa Pincheira is the fauna from the lowermost Tithonian bed G15 (GERTH, 1925) where *"L." picunleufuense* n. sp. transient β occurs abundantly (PARENT, 2003a: figs. 6A, 6D, 7B-7E) underlying the M6-assemblage. Thus, with the information available from the type locality of *S. malarguensis* and the occurrence of *Cat. windhauseni* with the other ammonites cited above, which are similar to those of the assemblage herein described from beds PL-5 and PL-6, indicate a stratigraphically younger horizon. Considering the moderate but significant morpho-ornamental differences and the younger age, *S. malarguensis* is considered as a representative of the "*Lithacoceras*" lineage of the NB, derived from "*L.*" *picunleufuense* n. sp.

Among the Submediterranean lithacoceratids, *Lithacoceras eigeltingense* OHMERT & ZEISS, 1980 and related forms from the earliest Tithonian of Europe is the closest species as discussed in PARENT *et al.* (2006). The resemblance is very close between both, the macro- and the microconchs (*Silicisphinctes* SCHWEIGERT & ZEISS, 1999), thus in addition to the close similarity of general shell shape and sculpture there is the form of sexual dimorphism, which is a crucial trait for resolving between close genetic relationships from homoeomorphic resemblance.

"Perisphinctes (Lithacoceras) albulus" (QUENSTEDT, 1887 in BERCKHEMER & HÖLDER, 1959: pl. 10: 51), most likely a representative of *Euvirgalithacoceras* ZEISS, SCHWEIGERT & SCHERZINGER, 1996, is identical in almost all respects with *"L." picunleufuense* n. sp. transient α. The differences are the lacking of the short stage of trifurcate virgatotome ribbing in the adult phragmocone (a diagnostic feature of "*L*". *picunleufuense* n. sp. [M]) and the larger adult size of the specimen figured by BERCKHEMER & HÖLDER (1959). Apart from these differences the HT of "*L.*" *picunleufuense* n. sp. looks identical.

The very close similarity of *"L." picunleufuense* n. sp., including the form of sexual dimorphism, with the cited diagnostic forms of latest Kimmeridgian (upper Beckeri Zone)-earliest Tithonian (Hybonotum Zone) Tethyan Lithacoceratinae, it is herein interpreted as close genetic relationships, strongly suggesting rather the same age for the Andean species, thus for the *picunleufuense* α and β horizons of the Picunleufuense Zone.

Occurrence and distribution: The described material was collected from the type horizon (transient α) and the next overlying horizon (transient β), Picunleufuense Zone. The species has been also recorded in La Amarga, Pampa Tril, Arroyo Cieneguita, and Casa Pincheira.

Genus *Choicensisphinctes* LEANZA, 1980

Type species: *Perisphinctes choicensis* BURCKHARDT, 1903; by OD.

Diagnosis: LEANZA (1980: 32): "Discoidal, somewhat inflated and rather evolute shell. Whorl section subtrapezoidal, with rounded borders, wider than high. Ornamentation of the internal whorls regularly biplicate. Outer whorls display strong, prominent and projected primary ribs. Periumbilical swellings originate from bundles of 4 to 10 fine equally spaced, somewhat projected secondary ribs which cross the venter without interruptions. No virgatotomic branching occurs. Constrictions are present. Suture line has trifid L lobe as deep as E, and E/L saddle wider and higher than E/U saddle. Two U lobes are present which are very simple and not oblique."

This original diagnosis needs emendation for the following reasons: (1) it was proposed for discriminating among the representatives of the Virgatosphinctinae SPATH, 1925; (2) virgatotome branching certainly occurs, shortly, on the phragmocone of certain species; (3) sexual dimorphism is not considered; and (4) the mature modifications of the adult body chambers are not included. However, reformulation might be based on the description of material from different localities and considering a longer stratigraphic range than that of Picún Leufú as described below.

Remarks: In his original definition of the genus LEANZA (1980: 32) indicated that *C. choicensis*, *C. erinoides* BURCKHARDT, 1903 and *Perisphinctes* aff. *erinus* (D'ORBIGNY, 1850 in BURCKHARDT, 1900; later renamed *Craspedites limitis* BURCKHARDT, 1930) form a "homogeneous stock" on which he based the genus. The HT by MT of the type species *Choicensisphinctes choicensis* is a phragmocone, probably adult, only known by a hand-drawing (BURCKHARDT, 1903: pl. 6: 10-12), which could not be traced for refiguration. The specimen seems to be a macroconch but this is hard to interpret from the available figures. TL: the area between Cajón del Burro and the valley of the Río Choicas at the beginning of the Río Grande, Mendoza (Fig. 1); TH: level M17 of BURCKHARDT (1900: 62). From this horizon come the type specimens of several systematically and biostratigraphically important morphospecies (hereafter called the M17-assemblage): *C. choicensis*, *C. erinoides*, *Perisphinctes involutus* QUENSTEDT, 1846 [later splitted as *Virgatites australis* BURCKHARDT, 1903 and *Virgatites* aff. *apertus* (VISCHNIAKOFF, 1882) in BURCKHARDT, 1903] and *Virgatites mendozanus* BURCKHARDT, 1911 (formerly described as *Perisphinctes* aff. *lothari* OPPEL in BURCKHARDT, 1900). The stratigraphic position and age of this horizon is discussed below. The HT by MT of *Choicensisphinctes erinoides* (figured by BURCKHARDT, 1900 : pl. 25 : 1 ; later refigured by BURCKHARDT, 1903 : pl. 8 : 1-2) is an adult macroconch phragmocone ; TL and TH as for *C. choicensis*. New material from Picún Leufú is described below. The HT by MT of *Choicensisphinctes limitis* (BURCKHARDT, 1930) was formerly illustrated as *Perisphinctes* aff. *erinus* D'ORBIGNY, 1850 by BURCKHARDT (1900 : pl. 26 : 3 ; later refigured in 1903 : pl. 9 : 1-2). It is a large adult macroconch phragmocone with incipient uncoiling and beginning of bodychamber ; TL : Portezuelo or Paso Montañés, Mendoza, TH : the bed 15 (BURCKHARDT, 1900 : 62), apparently belongs to the Zitteli Zone, middle Tithonian.

The holotypes of these three species are very similar to each other, gradually intergrading in involution and rib density whereas adult sizes seem to be similar. Moreover, there are several nominal species in literature dealing with the Andean Tithonian ammonite fauna which can be included in the genus. All of them share characteristic features of ribbing and shell shape that once arranged in stratigraphical succession show the record of a homogeneously evolving lineage of moderately variable species. Assuming a wide morphologic range by variation in involution, whorl section shape and adult size but showing stability in sculpture ontogeny, it can be delineated a wider conception of the genus *Choicensisphinctes*. The macroconchs are moderately stout serpenticonic to platyconic or compressed platyconic to suboxyconic, moderately involute, with a deep umbilicus formed by a relatively high, vertical umbilical wall. Inner(most) whorls covered by a simple sculpture of prosocline primaries bifurcated on the upper half or third of the flanks. Ribbing of outer whorls of phragmocone is rather fine and dense, slightly prosocline to flexuous, arising from the umbilical seam (but from the umbilical shoulder in the adult body chamber). Primary ribs bifurcate or polygyrate at about mid-flank and then follows a characteristic ontogenetic stage in which are developped isolated virgatotomes intercalated with trifurcates or bifurcates with intercalars ; some polygyrate and/or polyschizotomics profusely divided occur, especially behind constrictions. The adult body chamber may be strongly variocostate to completely smooth ; commonly primary ribs are strong and inflated, raising on the umbilical shoulder and profusely divided in sheaves of three up to thirteen or more secondaries, all of them crossing the venter or vanishing completely towards the peristome. In the microconchs the phragmocone is identical with that of the macroconchs at comparable diameters ; the adult body chamber is platyconic to inflate serpenticonic, more rarely suboxyconic, with a peristome possessing a pair of rather short and wide, subtriangular lappets.

It is worth to note that, as described below, most of the variations, even some of the morphotypes seen in the lineage throught the lower and middle Tithonian are already observable in the earliest species *Choicensisphinctes platyconus* n. sp. This is the most clear indication of the coherence of the lineage as interpreted herein. The species which can be included in *Choicensisphinctes* are the following :

Perisphinctes densistriatus STEUER, 1897. The HT by MT (figured by STEUER, 1897, transl. 1921 : pl. 15 : 9-11 ; refigured in PARENT, 2003a : fig. 3) is a phragmocone which could belong to a much larger specimen since uncoiling indicating the mature stage is not evident. TL : Arroyo Cieneguita, Mendoza ; TH : bed or level Cieneguita I of STEUER (1897, transl. 1921). The age of this bed was supposed to be late middle Tithonian (PARENT, 2003a), nevertheless new collections in this locality indicate an older age, most likely early middle Tithonian, lower Zitteli Zone. This conclusion is based on the recent collection of adult macroconchs (and the corresponding microconch) which match at comparable diameters with the HT of *C. densistriatus* in the lower Zitteli (or Mendozanus ?) Zone of Cerro Lotena and La Amarga, just below the type horizon of the oppeliid *Pasottia andina* PARENT, SCHWEIGERT, SCHERZINGER & ENAY, 2008. The HT shows an evolute form of *Choicensisphinctes*.

Virgatites australis BURCKHARDT, 1903. The HT by MT is the specimen figured as *Perisphinctes involutus* QUENSTEDT by BURCKHARDT (1900 : pl. 25 : 3), later refigured (BURCKHARDT,1903 : pl. 6 : 5, pl. 7 : 9). The specimen consists of a phragmocone with the beginning of the body chamber with no signs of uncoiling or variocostation, indicating it could have reached more than 100 mm in *D* at peristome. TL and TH as for *C. choicensis*. New material of *Choicensisphinctes australis* from the Zitteli Zone of Picún Leufú is described below.

The specimen figured by DOUVILLÉ (1910 : pl. 1 : 5) has a very different ornamentation with respect to the HT, including varices in the last preserved whorl. However, this latter specimen comes from an unknown locality and horizon ; DOUVILLÉ (1910 : 5) indicated that all the ammonites described in his paper were collected by M. RECOPÉ in some place between Rio Agrio and Arroyo Picún Leufú, a very wide area in east-central Neuquén where rocks of all the Mesozoic crop out.

Virgatites aff. *apertus* (VISCHNIAKOFF, 1882) in BURCKHARDT (1903 : pl. 7 : 12 ; formerly figured as *Perisphinctes involutus* QUENSTEDT in BURCKHARDT, 1900 : pl. 25 : 4). This specimen belongs to the M17-assemblage and, out of a slightly earlier variocostation, it is indistinguishable from the HT of *V. australis*.

Virgatites buckhardti DOUVILLÉ, 1910. The HT by MT is the specimen figured by BURCKHARDT (1900 : pl. 24 : 7) as *Perisphinctes* aff. *densistriatus* STEUER, 1897. This specimen was later refigured under the name *Virgatites* aff. *quenstedti* ROUILLIER by BURCKHARDT (1903: pl. 6: 1-4), apparently after preparation of the umbilicus. TL: Casa Pincheira, Mendoza; TH: bed M6 of BURCKHARDT (1900, 1903) in which occurs the M6-assemblage discussed above; *malarguense* horizon (see below).

Holcodiscus wilfridi DOUVILLÉ, 1910. The HT by MT is the specimen figured by DOUVILLÉ (1910: pl. 2: 6). TL and TH unknown (see above). This specimen is a small nucleus which could belong to *Choicensisphinctes*, but considering the lack of geographic and stratigraphic information it is a completely useless nominal species and thus considered as a nomen nudum.

(?) *Virgatosphinctes andesensis* DOUVILLÉ, 1910. The HT, designated by DOUVILLÉ (1910: pl. 1: 4), and the paratype (DOUVILLÉ, 1910: pl. 1: 3) are microconchs with lappets. TL and TH unknown (see above). This is another useless nominal species (probably nomen nudum) which, moreover, is based on two rather different ammonites. On the other hand it is very difficult to decide a generic attribution for the holotype since some *Catutosphinctes* from the lower Zitteli Zone of Cerro Lotena, La Amarga and Pampa Tril are very similar.

Virgatosphinctes mexicanus BURCKHARDT, 1906 in DOUVILLÉ (1910: pl. 1: 1-2). DOUVILLÉ figured two specimens which differ from *Lithacoceras mexicanum* by their finely ribbed phragmocone and the complex ribbing of the body chambers, including the characteristic features of *Choicensisphinctes* with pseudovirgatotomic, polyzchizotomic and simple ribs in front of conspicuous constrictions. Moreover, both specimens, coming from an unknown locality and stratigraphic position, are lappeted microconchs, morphologically very close to *Choicensisphinctes mendozanus* but the phragmocone is more densely ribbed.

Virgatites mendozanus BURCKHARDT, 1911. The complex nomenclatural history of this species has been summarized by LEANZA (1980: 13). It seems that a type specimen has never been designated. BURCKHARDT (1911) apparently based the species on two specimens figured by himself (BURCKHARDT, 1900: pl. 25: 6-7; the figure 8 could belong to one of these specimens), later refigured as hand drawings (BURCKHARDT, 1903: pl. 7: 1-8). The larger and more informative specimen (BURCKHARDT, 1900: pl. 25: 7) is herein designated as the lectotype; TL and TH as for *C. choicensis*. The stratigraphic position of the type material and the implications in the Andean scale of the Tithonian are discussed below, because of the importance of this species has being the index of the Mendozanus Zone.

The paralectotype is a complete phragmocone with part of the body chamber showing clearly adult features of variocostation and uncoiling; the variocostation is developed in the form of an irregular ribbing of polyschizotomic ribs alternating with widely spaced simple and bifurcates with low points of furcation. It seems to be a microconch with few doubts. The LT is also a complete phragmocone with part of its body chamber. In this latter specimen there is evidence of incipient uncoiling and variocostation which seems to be more gradual than that of the paralectotype, most likely as a part of the changes that the larger macroconchs develop during the ontogeny – as well illustrated by the HT of *C. erinoides* (BURCKHARDT, 1900: pl. 25: 1). The generic assignation to *Choicensisphinctes* has much importance and implications for it has been commonly assigned to *Virgatosphinctes*. Both type specimens show only few isolated virgatotome ribs intercalated with conspicuous polyzchizotomic, simple and bi- or trifurcate ribs irregularly arranged. This kind of sculpture is unknown from *Virgatosphinctes* (see ENAY & CARIOU, 1997, 1999; YIN & ENAY, 2004), but characteristic for *Choicensisphinctes*.

Pseudinvoluticeras decipiens SPATH, 1925 (HT by MT: DOUVILLÉ, 1910: pl. 3: 3) and *Pseudinvoluticeras douvillei* SPATH, 1925 (HT by MT: DOUVILLÉ, 1910: pl. 3: 4) are based on two almost identical specimens belonging beyond any doubt to *Choicensisphinctes*. Nevertheless, both nominal species have unknown type horizons and localities, probably both might be considered as nomen nudum.

Virgatosphinctes windhauseni WEAVER, 1931. WEAVER (1931: 426) based the species on two specimens cited as “syntypes”, indicating they come from his locality 809, 1.5 km west of Cerro Granito. Nevertheless, the outcrops of Tithonian rocks are known only as a belt located around 1 to 2 km East and Southest of Cerro Granito; the type locality is then the locality area currently named La Amarga, or La Amarga-Cerro Granito (see Fig. 1). Both specimens were collected in a bed described as “calcareous shales near the base of the Tithonian”. The most complete specimen figured by WEAVER (1931: pl. 48: 325) is designated herein as the lectotype and refigured in Fig. 13A; the paralectotype (WEAVER, 1931: pl. 48: 324) is refigured in Fig. 13B. The LT is an adult phragmocone showing incipient uncoiling and crushed remains of the body chamber on the first half of the last whorl of the phragmocone. The paralectotype is an uncoiled adult phragmocone with, apparently, part of its body chamber. This is the most compressed, involute and finely, densely ribbed among the nominal species of the genus *Choicensisphinctes*. In the TL we have recently collected very similar specimens from a bed where occur *Pseudolissoceras zitteli* associated with *Catutosphinctes windhauseni* (WEAVER, 1931; discussed below) in abundance and other forms of *Choicensisphinctes* (including specimens whose phragmocone are comparable with *C. densistriatus*). This horizon (Fauna

B in Parent *et al.,* 2006) underlies the type horizon of the oppeliid *Pasottia andina*. New material from Picún Leufú, although fragmentary, is described below.

Virgatosphinctes lotenoensis Weaver, 1931. The species is based on two specimens: the HT originally designated (Weaver, 1931: 425, pl. 48: 322) collected in Cerro Lotena in "lower Tithonian" beds; and the paratype (not figured originally), probably from the same locality and horizon as suggested by the same lithology of the matrix and the labelling with consecutive field numbers. Both specimens, herein refigured as Fig. 13C-D, are phragmocones with no evident uncoiling and very similar each other – only differing in that the HT shows the beginning of a faint variocostation in the form of widening of primary ribs on the umbilical shoulder which divide below the middle of the flank. These two specimens are similar to the HT of *C. burckhardti* and their stratigraphic position is roughly the same.

Virgatosphinctes andesensis (Douvillé, 1910) in Weaver (1931). The specimen from Cerro Lotena described and figured by Weaver (1931: pl. 48: 318-320) is a complete adult microconch with lappets identical with the lectotype of *Choicensisphinctes mendozanus*. The other specimen figured by Weaver (1931: pl. 48: 321) is also similar but incomplete. Both specimens are said to be topotypes, but this is erroneous

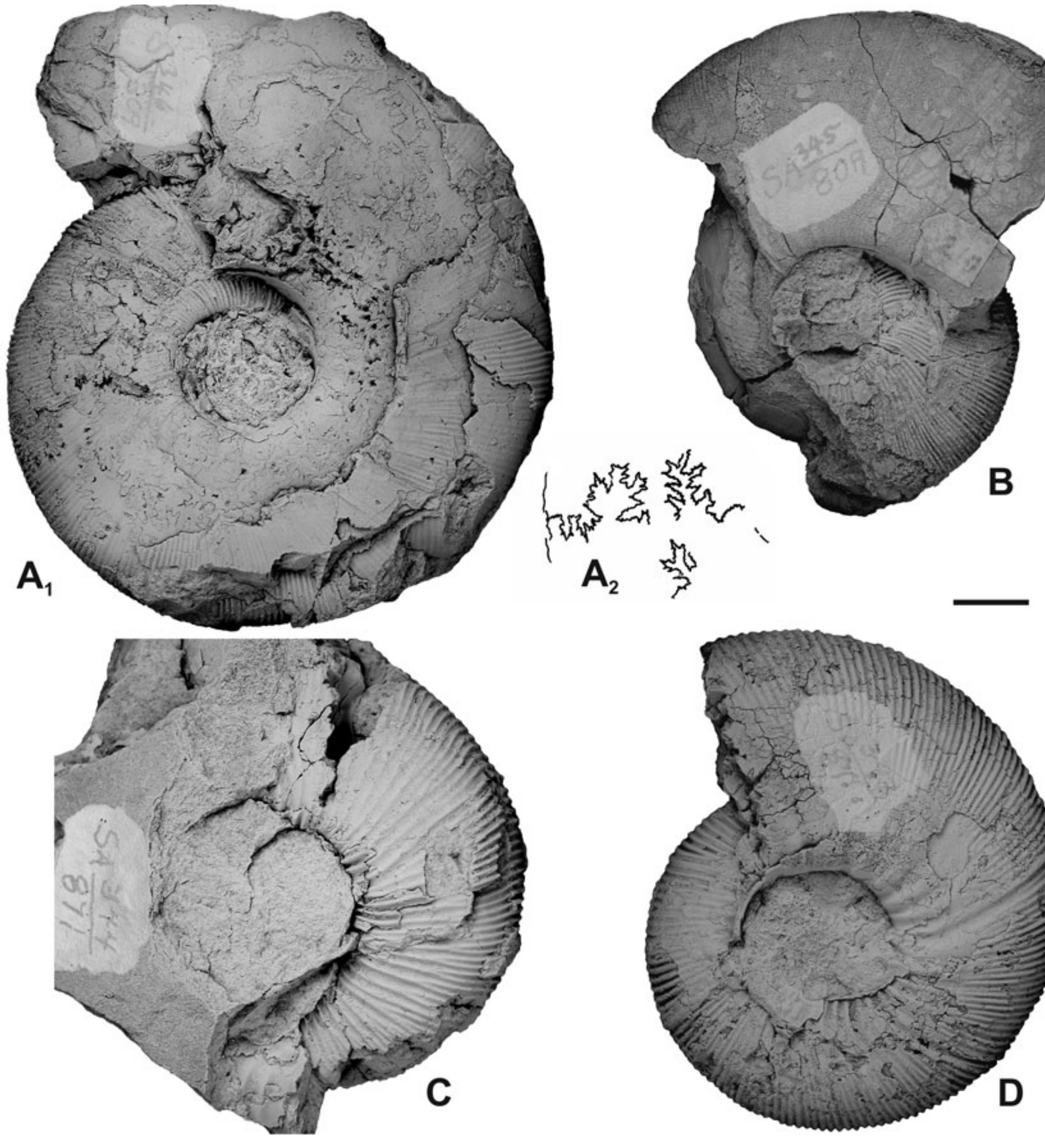


Fig. 13: **A-B**: *Choicensisphinctes windhauseni* (Weaver, 1931), lower-middle Tithonian of La Amarga. **A**: Lateral view (**A$_1$**) and septal suture line (**A$_2$**) of the lectotype (BMS 346) designated herein; adult [M] phragmocone with remains of body chamber on the first half of the last whorl preserved. **B**: Paralectotype (BMS 345); adult [M] phragmocone with beginning of the body chamber. **C-D**: *Choicensisphinctes lotenoensis* (Weaver, 1931), lower-middle Tithonian of Cerro Lotena. **C**: Paratype (BMS 344); [M] phragmocone. **D**: Holotype (BMS 343); [M] phragmocone.

because the type locality and horizon of the type material are unknown (see above). WEAVER (1931) has insistently pointed out that *Choicensisphinctes mendozanus* is the most abundant ammonite of his "lower Tithonian", below beds with *P. zitteli*. Nevertheless, as already remarked by LEANZA (1980: 13), WEAVER neither described nor figured a single specimen of *C. mendozanus*. It seems that he could have been referring to the specimens figured by himself under *V. andesensis*.

LEANZA (1980: pl. 2: 5) figured as *V. andesensis* a specimen from the so-called Mendozanus Zone of Cerro Lotena. This specimens is very similar to the lectotype of *Choicensisphinctes mendozanus*.

Virgatosphinctes evolutus LEANZA, 1980. This species is only known by its holotype (LEANZA, 1980: pl. 5: 4), collected in the so-called Mendozanus Zone of Cerro Lotena. This specimen shows the characteristic features of *Choicensisphinctes* and, on the other hand, is almost identical with the above mentioned specimen of *V. andesensis* from Cerro Lotena, only differing in being somewhat more inflated. The ribbing pattern is the typical of the microconchs and inner whorls of the large macroconchs of *Choicensisphinctes* of the M17-assemblage as well illustrated by the holotype and paralectotype of *C. mendozanus*.

As can be seen the number of nominal species which can be attributed to *Choicensisphinctes* is rather large and most, if not all, of them were defined on the basis of poorly preserved or incomplete specimens, difficulting the assertion of relationships between them and between the adult morphology of the macro- and microconchs. Under this framework the representatives of *Choicensisphinctes* collected in Picún Leufú are mainly described in morphotypic terms. The only exception is the new species *C. platyconus* described below in terms of a widely variable, sexually dimorphic species since it occurs in abundance in a well defined stratigraphic position from which, apparently, none of the type specimens of the existing nominal species has been collected.

Choicensisphinctes platyconus n. sp.

Figs. 5C-D, 5G-H, 14-20, 21A.

2003a. *Euvirgalithacoceras malarguense* (SPATH).- PARENT, p. 147, figs. 6B-C, 7A.

2006. *Choicensisphinctes* cf. *windhauseni* (WEAVER, 1931).- PARENT *et al.*, p. 254, fig. 5A-B.

Material: 29 macroconchs, 5 microconchs and abundant fragmentary specimens, all from beds PL-5 and PL-6.

Type series: Holotype [M]: Fig. 14A (MOZPI 6431) and three paratypes: PT-1 [M], Fig. 15D (LPB 1096); PT-2 [m], Fig. 15A (MOZPI 7474); PT-3 [m], Fig. 15B (MOZPI 7497); all from the type horizon.

Type locality and horizon: Picún Leufú (Fig. 1); bed PL-5, *picunleufuense* α horizon, Picunleufuense Zone, lower Tithonian.

Derivation of name: After the platyconic shape of the shell.

Diagnosis: Macroconch: medium to small adult size, involute platyconic, whorl section higher than wide, flat to slightly rounded flanks, umbilicus narrow to moderately open. Phragmocone densely ribbed by slightly flexuous trifurcate, polygyrate and frequent polyschizotomic ribs which on last whorl of phragmocone become more prominent on the umbilical shoulder and profusely divided in sheaves of finer secondaries. Body chamber ornamented with undivided primaries, strong on lower flank and vanishing towards the venter. Microconch: adult size about one third to one half the adult size of the macroconch; phragmocone indistinguishable from inner whorls of the macroconch; adult body chamber compressed platyconic, uncoiled, densely and finely ribbed by primaries which bifurcate or trifurcate nearby the middle of the flank. Lappets moderately wide subtriangular. Length of body chamber about half a whorl.

Description: The holotype is a macroconch with complete phragmocone and half whorl of body chamber. The inner whorls ($5 < D < 10$ mm) are evolute, somewhat depressed, widely umbilicate, covered by subradial primaries, passing to a dense and fine ribbing which persists up to the end of the phragmocone. In juvernile and adult phragmocones ($D > 12$-15 mm) the primaries start on the upper umbilical wall, cross the shoulder backwardly directed and become prosocline on flanks where bifurcate and trifurcate almost indistinctly but becoming stronger towards the body chamber; intercalatory ribs are frequent but their occurrence is uneven. The whorl section is rounded subtriangular to oval, higher than wide, passing through a rounded umbilical shoulder to a rather high subvertical umbilical wall. The body chamber is rounded subrectangular to oval in whorl section, higher than wide and uncoiled since the first half. Only rounded and widely spaced primary ribs occur, showing a tendency to weaken towards venter which is almost smooth. The peristome is not preserved and the suture is not visible.

Within available material, mainly from the lower level PL-5, there can be distinguished at least four main morphotypes mainly based on macroconchs of a highly polyphenic (non "polymorphic" auctt.) species. Variation is mainly concerned on variations in the degree of involution and strength and density of ribbing. They can be arranged in a rather continuous spectrum: (1) morph A: the macroconchs (Fig. 17A-B) are relatively more evolute and strongly ribbed from the last part of the adult phragmocone than the holotype, and the microconchs (Fig. 18A) are more evolute and strongly ribbed than the paratype microconchs; (2) morph B: the typical macroconchs (Fig. 14A-B) and microconchs

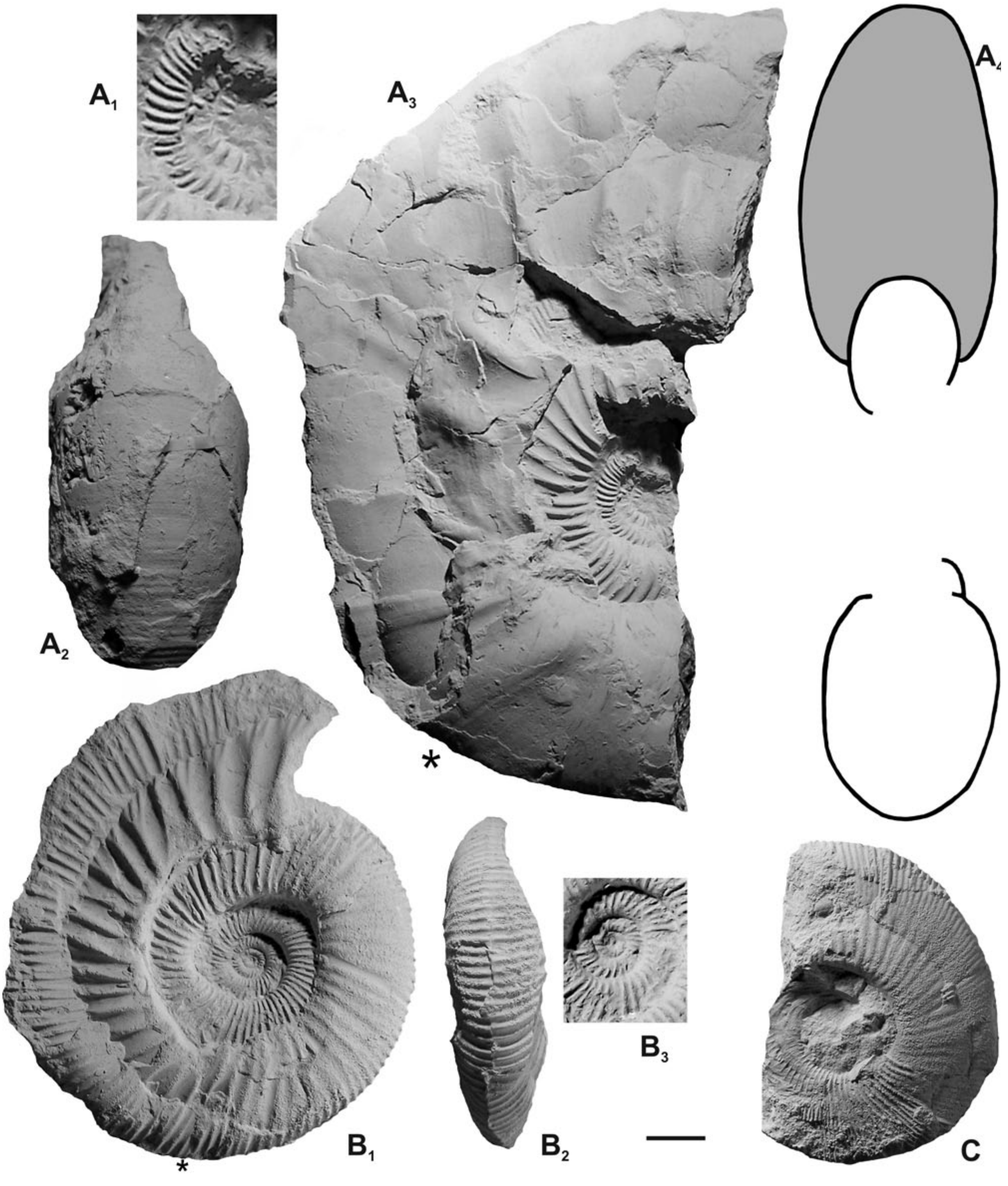


Fig. 14: *Choicensisphinctes platyconus* n. sp. **A**: Holotype, adult [M] with incomplete body chamber (MOZPI 6431), ventral and lateral views (**A**$_2$-**A**$_3$), innermost whorls enlarged (x2) (**A**$_1$) and natural size whorl section of the body chamber (**A**$_4$). **B**: Juvenile [M] with incomplete body chamber (LPB 1099), lateral and ventral views (**B**$_1$-**B**$_2$) and enlarged (x2) innermost whorls (**B**$_3$). **C**: juvenile [M] with beginning of the body chamber (LPB 1100). Picún Leufú, bed PL-5, *picunleufuense* α horizon.

(Fig. 15A-B), as characterized by the holotype and paratype microconchs; (3) morph C (Figs. 14C, 15C-D, 16A-F): macroconchs somewhat smaller, more involute and densely and finely ribbed, the primaries divide in sheaves of very fine secondaries at about the middle of the flanks; and (4) morph D (Fig. 20A-B): macroconchs involute since the innermost whorls, with finely ribbed phragmocone and short segments covered only by growth lines. The body chamber is very distinctive respect to the other morphs, strongly ribbed by gross, tumid primaries unevenly spaced and divided in sheaves of very fine secondaries; towards the peristome they remain wide and rounded, undivided or irregularly bifurcate with intercalatories. Some very well preserved specimens (morphs B and C) show their first whorls, about D = 3-4 mm, globose and involute, with faint prosocline primary ribs on flanks and completely smooth venter which is broad and rounded (Fig. 16B). There is a large adult microconch (Fig. 18B) with well preserved lappets whose last whorl of phragmocone is exactly identical to the adult body chamber of the adult microconchs of morph B shown in Fig. 15A-B. The body chamber of this large microconch shows the morphology and sculpture of the beginning of the body chamber of the normal adult macroconchs.

The specimens of morph A could be separated as a different species, but as they co-occur with the other morphotypes in the same horizon, the inner whorls

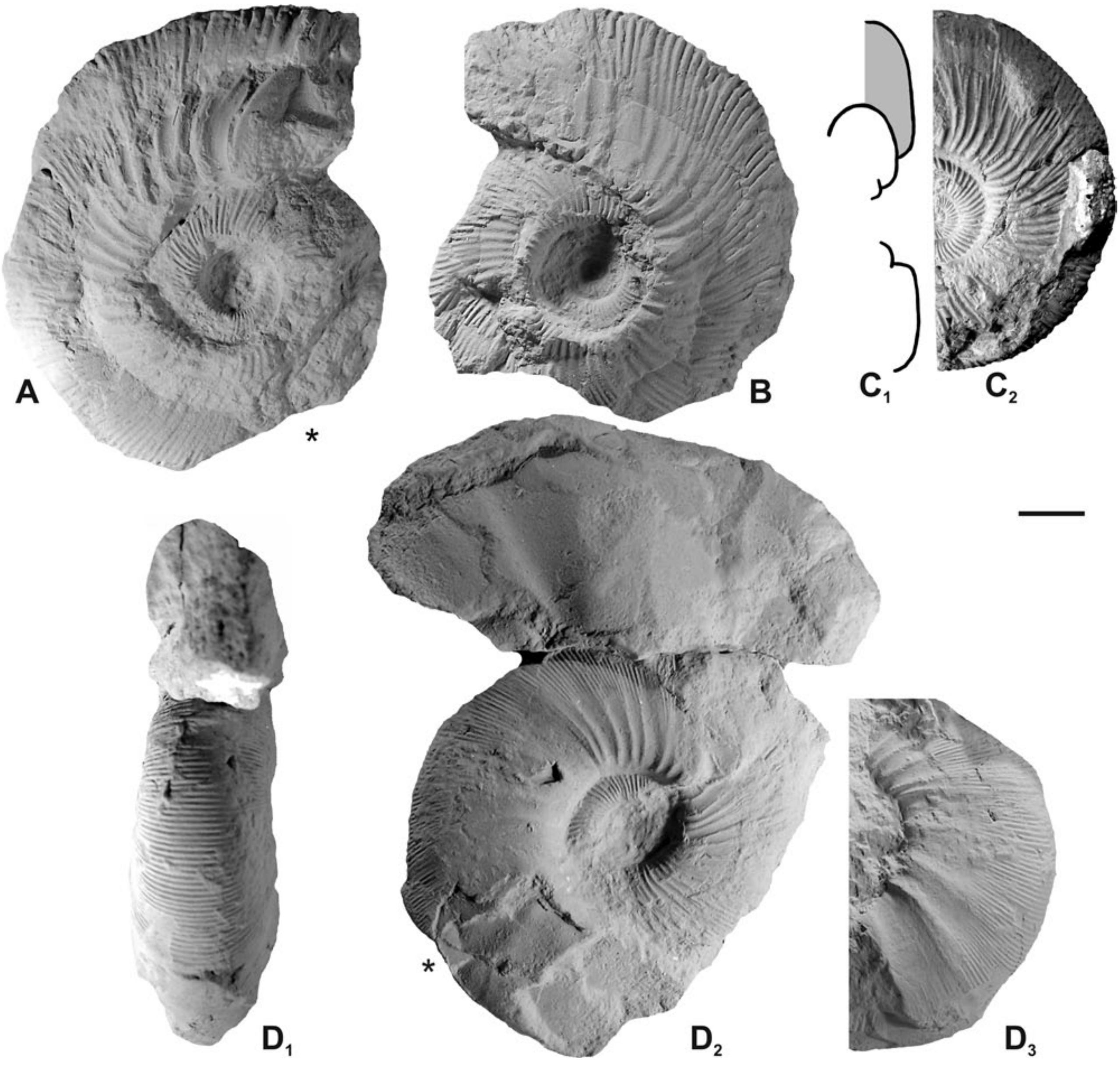


Fig. 15: *Choicensisphinctes platyconus* n. sp. **A**: Complete adult [m] with lappets (MOZPI 7474). **B**: Complete adult [m] with lappets (MOZPI 7497). **C**: Inner whorls of a ? macroconch (MOZPI 6395). **D**: Complete small-sized adult [M] (LPB 1096). Picún Leufú, bed PL-5, *picunleufuense* α horizon.

are identical and the ribbing style is the same as in the holotype, it is more convenient to retain them as extreme variants.

Remarks and comparison: Comparison with other species of the genus represented in Picún Leufú is given below, under the respective species. Among other species of the genus, there is a close resemblance with *C. burckhardti*, but the holotype of this latter comes from an upper stratigraphic position and bears abundant well marked, narrow constrictions in the last whorl. Specimens of the morph C of *C. platyconus* n. sp. are similar but they are smaller, more compressed platyconic and with finer secondaries well differentiated from stronger primaries. Within the range of variation of the new species there are some specimens which are very similar to different morphotypes of the lineage as represented in upper levels in P. Leufú and, however, other localities. The specimen in Fig. 16G shows the characteristic fine and dense ribbing with strong constrictions bounded by collared ribs seen in the poorly recorded *C.* cf./aff. *platyconus* n. sp. of levels PL-7b and PL-7e (Fig. 23C-F). The specimen from bed PL-6 (Fig. 21A) is strongly similar to that of *C. australis* of bed PL-11 (Fig. 21B).

The conception of *C. platyconus* n. sp., including a very wide spectrum of morphotypes, may be compared with the adopted for other authors for other Ataxioceratidae.

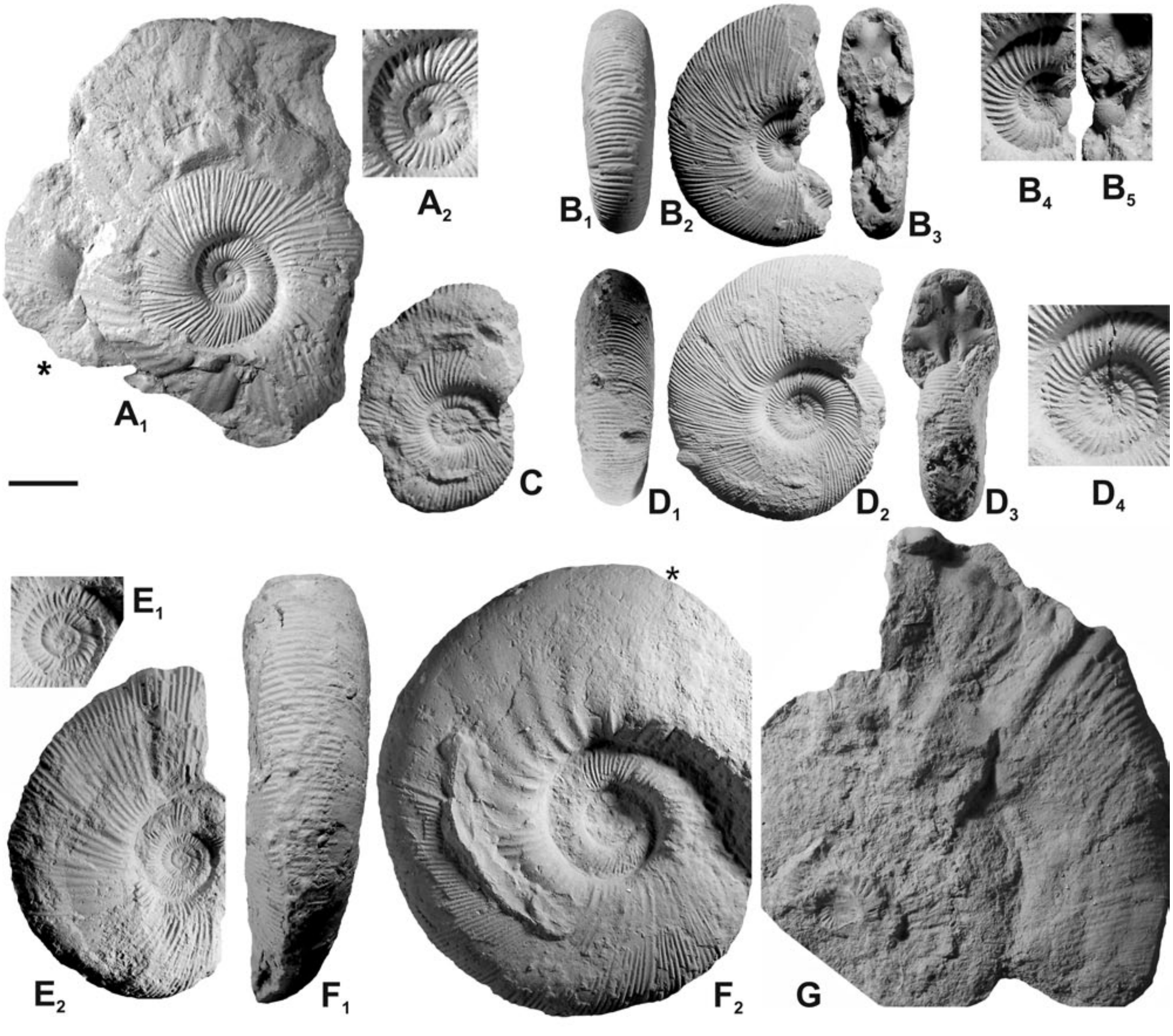


Fig. 16: *Choicensisphinctes platyconus* n. sp. **A**: Small-sized adult [M] with incomplete body chamber (MOZPI 7354), lateral view (**A**$_1$) and enlarged (x2) innermost whorls (**A**$_2$). **B**: Phragmocone (MOZPI 7352) showing whorl section and innermost whorls (**B**$_4$-**B**$_5$) enlarged (x2). **C**: ? Macroconch phragmocone (MOZPI 7388) showing an abrupt change of whorl section on the last whorl. **D**: Phragmocone (MOZPI 7346) showing whorl section and innermost whorls (**D**$_4$) enlarged (x2). **E**: Phragmocone (LPB 1101), innermost whorls (**E**$_2$) enlarged (x2). **F**: Small-sized adult [M] with beginning of the body chamber (LPB 1095). **G**: Small-sized adult [M], poorly preserved inner whorls and last portion of the body chamber (MOZPI 7294) showing the same sculpture pattern as in *Choicensisphinctes* cf./aff. *platyconus*. Picún Leufú, bed PL-5, *picunleufuense* α horizon.

An illustrative comparison is with some examples taken from the detailed description of the Early Kimmeridgian Ataxioceratinae by ATROPS (1982). The most striking variant in *C. platyconus* n. sp. is the morph D (Fig. 20A-D). This is comparable with the variation in *Ataxioceras hypselocyclum* FONTANNES as illustrated by ATROPS (1982: pl. 40: 1-2): two macroconchs with similar shell shape but differing in the sculpture of the adult body chamber in the way that the specimens of *C. platyconus* n. sp. morph D differ from those of morph B, showing normal ataxioceratid ribbing respect to strongly ribbed by gross, tumid primaries unevenly spaced and divided in sheaves of very fine secondaries and including strong constrictions.

Occurrence and distribution: Lower Picunleufuense Zone, *picunleufuense* α and β horizons. Out of Picún Leufu this species has been recorded in La Amarga, Cerro Lotena (poor material), Pampa Tril, Arroyo Cieneguita and Casa Pincheira, consistently in the same horizons or stratigraphic position as the material described.

Origin of *Choicensisphinctes*: Direct phyletic relationships between "*Lithacoceras*" and *Choicensisphinctes* have been suggested from material of Casa Pincheira (PARENT, 2003a). The new material described in the present paper, the additional specimens discussed from older and younger horizons, and the more abundant material showing the wide ranges of morphologic variability gives additional support to that hypothesis. Indeed, the close morphological similarity in significant features like sculpture ontogeny and sexual dimorphism and the widely recorded co-occurrence of *"L." picunleufuense* n. sp. and *C. platyconus* n. sp. suggest that the genus *Choicensisphinctes* could have been originated in *Lithacoceras* being *C. platyconus* n. sp. the earliest species of the lineage. Moreover, there are specimens which show hybrid morphology, like hybrid forms mixed in the populations. These specimens have a typical phragmocone of *C. platyconus* n. sp. but the body chamber has the typical morphology and sculpture of *"L." picunleufuense* n. sp. (Fig. 19A). Under this interpretation the fauna of the *picunleufuense* a horizon could be considered as the record of a time-interval in which the differentiation of *C. platyconcus* n. sp. is still not complete.

Another possible ancestor of *Choicensisphinctes* is the Mexican late Kimmeridgian - earliest Tithonian lithacoceratid *Procraspedites* SPATH, 1930 (TS: *Craspedites praecursor* BURCKHARDT, 1906) which is closely comparable, especially with the more suboxyconic forms like *C. platyconus* n. sp. or *C. limitis*. OLÓRIZ *et al.* (1998) have described the ontogeny of some moderately well preserved specimens after which it is clear that the Late Kimmeridgian forms differ from *Choicensisphinctes* by its weaker sculpture on the flanks

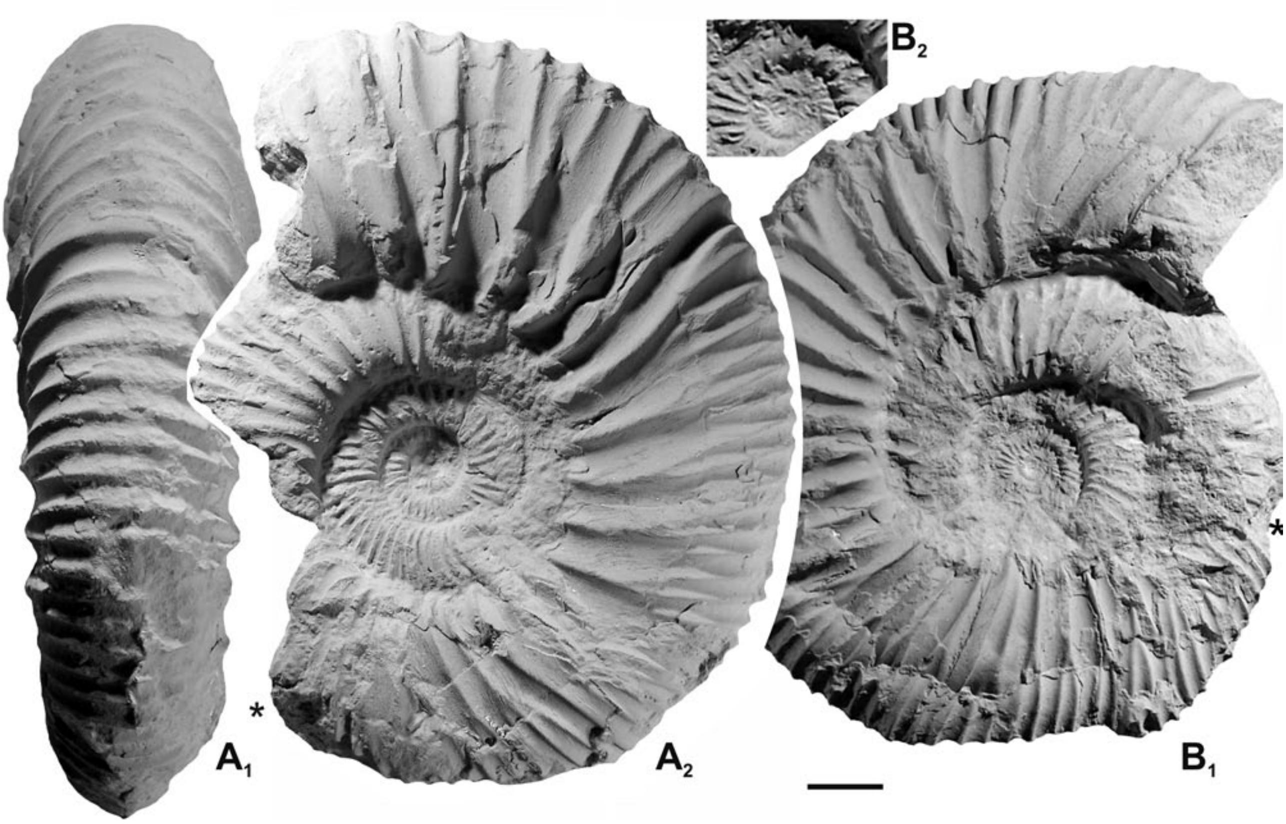


Fig. 17: *Choicensisphinctes platyconus* n. sp. **A**: Adult [M] with incomplete body chamber (MOZPI 6397). **B**: Complete small-sized adult [M] (MOZPI 7469); **B$_2$**: innermost whorls enlarged (x2). Picún Leufú, bed PL-5, *picunleufuense* α horizon.

from the inner or middle whorls, the absence of complex polyschizotomic ribs, the occurrence of parabolic structures and the more compressed whorl section with narrower umbilicus. This combination of differences seems to be significant enough for differentiation of both genera although they could surely be closely related. The septal suture lines show the slight differences typically observed between closely related ammonites with different degrees of inflation and involution of the shell. For instance the partial suture of the compressed and involute *C. australis* illustrated by BURCKHARDT (1900: pl. 29: 9) is almost identical with that of *P. praecursor*

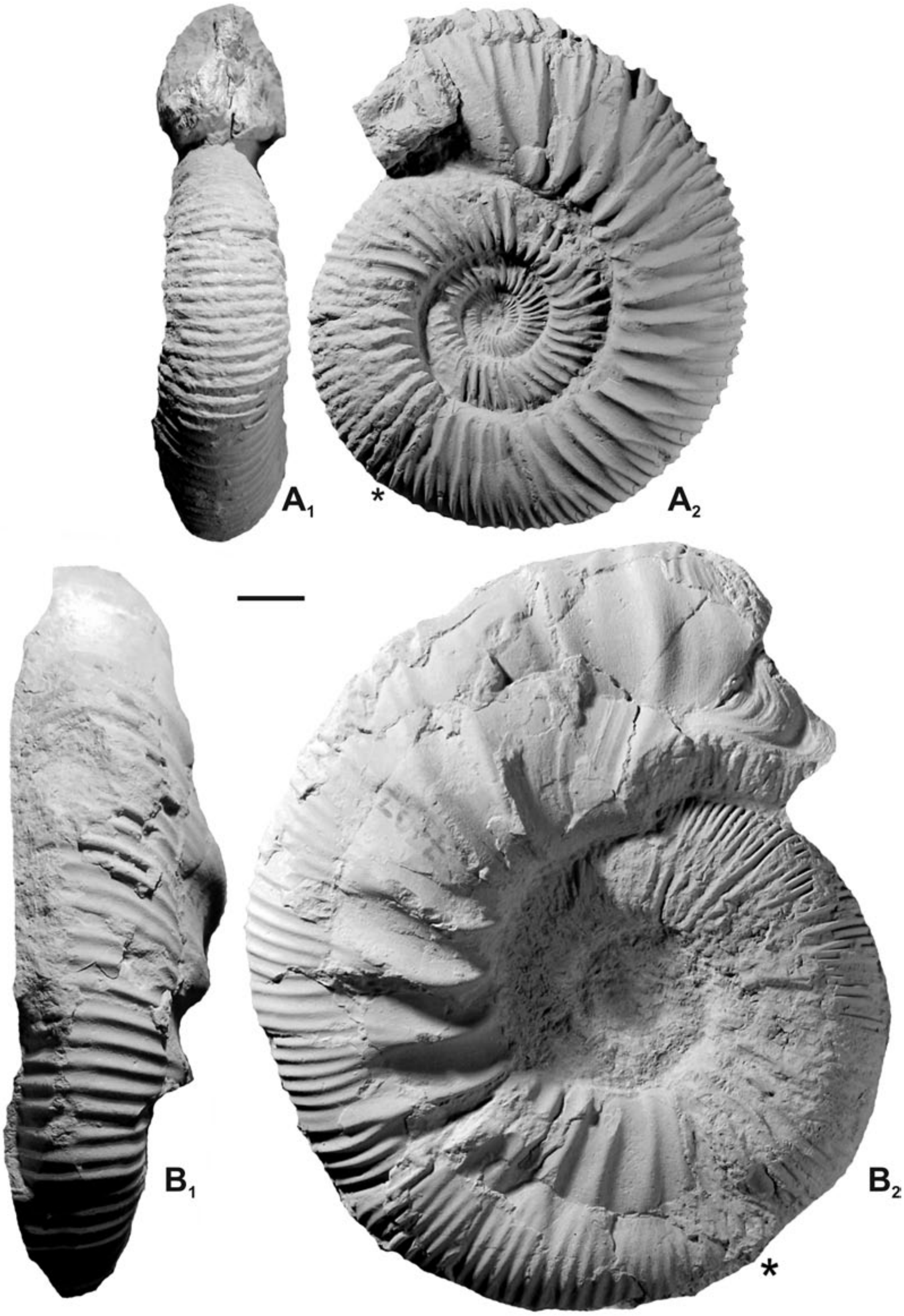


Fig. 18: *Choicensisphinctes platyconus* n. sp. **A**: Complete adult [m] with lappets (MOZPI 7766), extremely evolute variant. **B**: Complete large-sized adult [m] with lappets (MOZPI 7797); the phragmocone is identical in shape and size with the complete adult microconchs with body chamber figured in Fig. 15A-B. Picún Leufú, bed PL-5, *picunleufuense* α horizon.

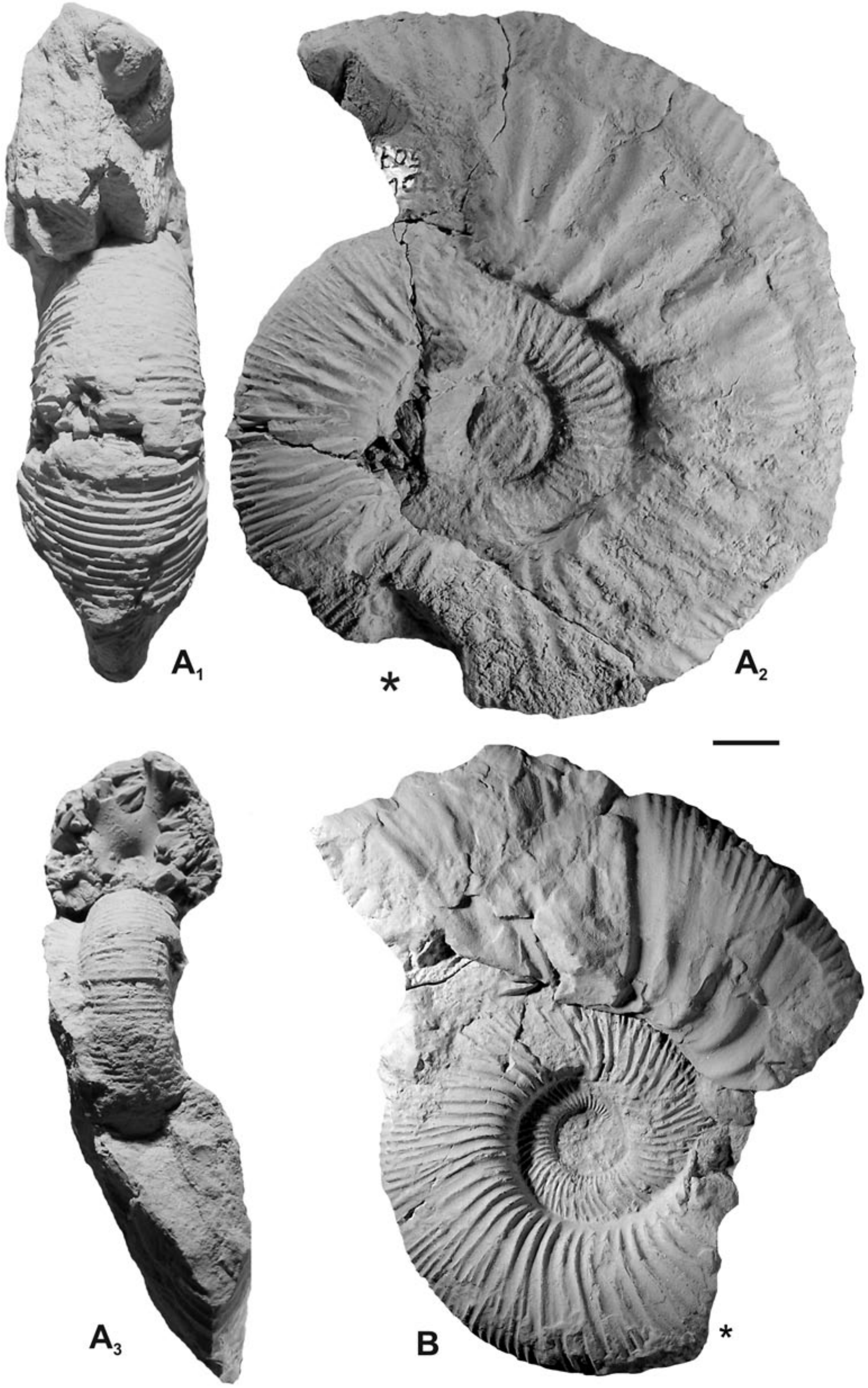


Fig. 19 : *Choicensisphinctes platyconus* n. sp. **A** : Adult [M] with incomplete body chamber (MOZPI 7507) ; **A$_1$** : apertural view, **A$_2$** : lateral view, **A$_3$** : ventral view with the beginning of the body chamber removed showing the fine ventral ribbing of the inner whorls. **B** : Adult [M] with incomplete body chamber (MOZPI 7318/3). Picún Leufú, bed PL-5, *picunleufuense* α horizon.

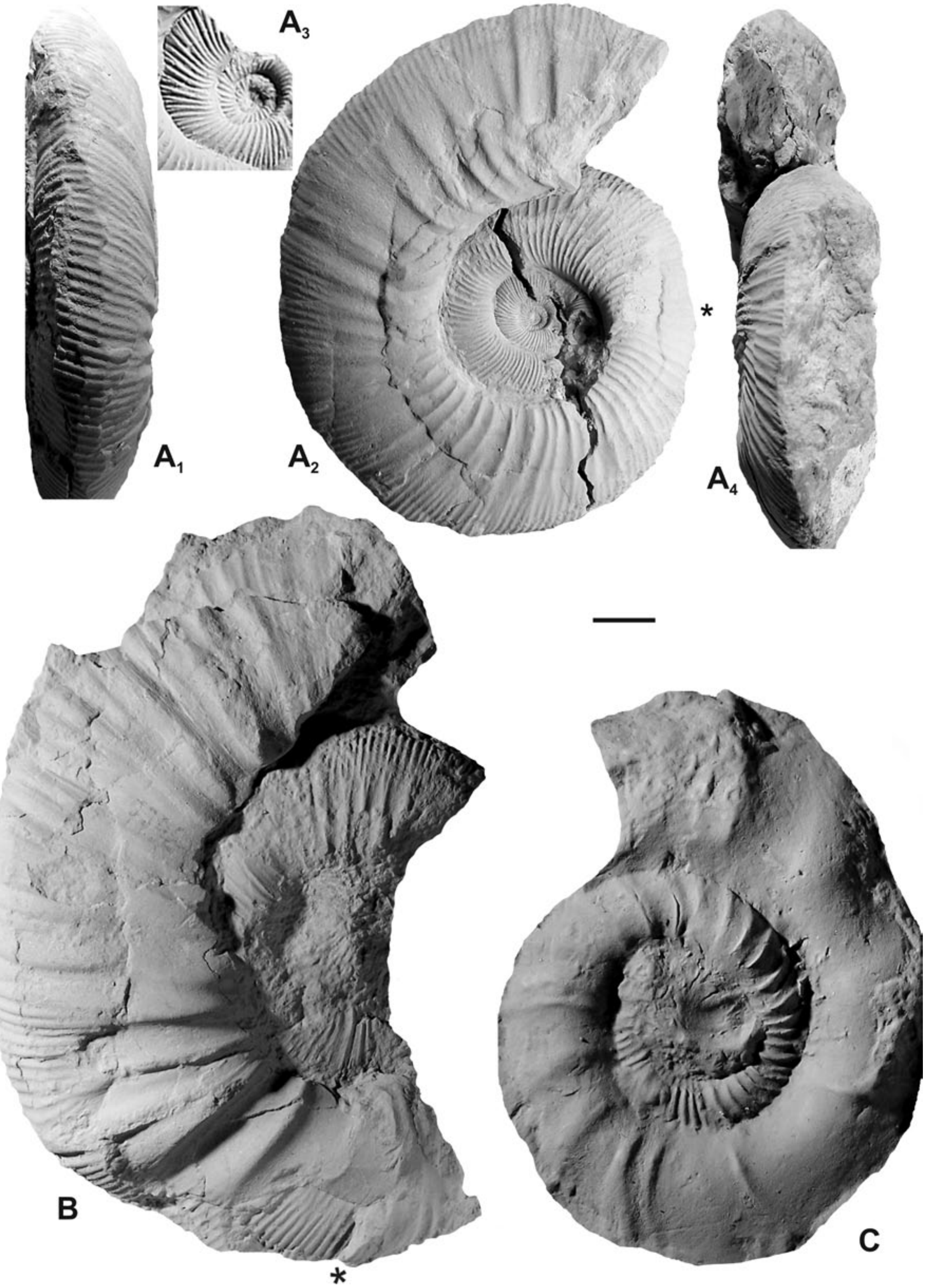


Fig. 20: *Choicensisphinctes platyconus* n. sp. **A**: Adult [M] with almost complete body chamber (LPB 1094); ventral ($\mathbf{A_1}$), lateral ($\mathbf{A_2}$) and apertural ($\mathbf{A_4}$) views, $\mathbf{A_3}$: innermost whorls enlarged (x2). **B**: Adult [M] with incomplete body chamber (LPB 1097). **C**: Cast (LPB-M 123) of an adult [M] with incomplete body chamber (MOZPI 7301), variant with beginning of the body chamber covered by gross, wide-spaced cuneiform primary ribs. Picún Leufú, bed PL-5, *picunleufuense* α horizon.

illustrated by Olóriz *et al*. (1998 : fig. 2), whereas that of the robust *C. erinoides* and *C. limitis* (in Burckhardt, 1900 : pl. 29 : 12-13) have comparatively wider saddles.

Choicensisphinctes cf./aff. *platyconus* n. sp.
Fig. 23B-E

2003a. *Choicensisphinctes choicensis* (Burckhardt, 1903).- Parent, p. 154, fig. 8A-C.
2007. *Choicensisphinctes* cf. *windhauseni* (Weaver, 1931).- Parent & Cocca, p. 26 (pars).

Material : Abundant fragmentary material from beds PL-7b and PL-7e.

Remarks and comparison : This form is very abundant throughout its stratigraphic range where specimens occur crushed or as impressions. This is an evolute form of *Choicensisphinctes*, finely and densely ribbed on adult phragmocone and body chamber, where there are marked prosocline constrictions bounded by strong collared ribs. The primary rib behind the constriction is polyschyzotomic-subvirgatotome. Primary ribs are profusely divided in sheaves in a style very similar to *C. australis* (cf. Fig. 21B). Nevertheless, this latter species is more involute. As noted above, the specimen of *C. platyconus* n. sp. shown in Fig. 16G is very similar, showing that similar morphotypes are already present in older populations.

The specimen from the lower Tithonian of Casa Pincheira described as *C. choicensis* by Parent (2003 : fig. 8), clearly belongs to *C.* cf./aff. *platyconus* n. sp. It is a rather complete macroconch, evolute from the innermost whorls, with subtrapezoidal whorl section ($W/H_1 = 0.98$), and preserving a half whorl of bodychamber which is robust and has a characteristic venter which is wide and densely ribbed. The phragmocone is also densely ribbed with sharp, slightly prosocline ribs, passing on the bodychamber to strong blade-like primaries which divide in sheaves with many intercalars. The lateral ribbing of the bodychamber is very significant and allows to distinguish this evolute chronospecies from *C. erinoides*, *C. australis* and *C. limitis*.

In Portada Covunco, in the upper part of bed PC-1 and in bed PC-2 (Parent & Cocca, 2007 : fig. 2), occurs the present species in the form of well preserved but crushed specimens or as impressions.

Choicensisphinctes windhauseni (Weaver, 1931)
Figs. 13A-B, 23A

Material : A single poorly preserved specimen (MOZPI 7271), loose from the upper part of bed PL-7.

Description and remarks : Compressed platycone moderately involute phragmocone preserving only the beginning of the body chamber. Flanks nearly flat, venter narrow and rounded. Phragmocone and body chamber very finely and densely ribbed. On the body chamber primaries are wide on the lower third of flank where they divide in sheaves of 4-5 very fine secondaries which cross the venter unchanged.

Occurrence and distribution : The specimen described comes from the lower Zitteli (or Mendozanus ? Zone). Specimens identical to the holotype have been collected in the same stratigraphic position at La Amarga (Fauna B of Parent *et al.,* 2006) where it is abundantly represented, showing a moderately variable morphology and strength of sculpture.

Choicensisphinctes australis (Burckhardt, 1903)
Fig. 21B

Material : A complete specimen (LPB 1102/1) from bed PL-11.

Description : Suboxycone shell, compressed, involute with moderately wide umbilicus. Whorl section rounded subtriangular to suboval with rounded venter ; the maximum width is nearby the umbilical shoulder. Ribbing on phragmocone is fine and dense reaching the maximum behind the beginning of the body chamber. Primaries start on the umbilical seam and run on the flanks slightly prorsiradiate, bifurcating or trifurcating on the middle of the flank or lower ; no intercalatories are observed ; the secondaries cross evenly spaced the venter without changes. The body chamber is slightly uncoiled and extends along some 300°. On the first half the primaries become wider and rounded from the uppermost umbilical wall adopting a wedge-like shape, and on the lower half of the flank they divide in sheaves of 8 to 10 secondaries which, together scarce intercalars, cross the venter with no changes. On the last half the secondaries fade off, and the primaries, remaining wide and rounded on the lower third of the flank, weaken towards the venter as undulations.

Remarks and comparison : Among the available nominal species the specimen described is identical to the parts of the shell preserved in the HT of *C. australis* and the conespecific specimen described by Burckhardt (1900 : pl. 25 : 4) as *Perisphinctes involutus* (Quenstedt), both forming part of the M-17 assemblage (see above). It seems to be a species which, at least in these levels, is rather small in adult size. Indeed the specimen described is an adult as indicated by the uncoiled and strongly variocostate body chamber with smooth venter and gross umbilical swellings.

The specimen described is very similar to some variants of the late representatives of *C. platyconus* n. sp. of bed PL-6, *e.g.* the macroconch in Fig. 21A which differs slightly by the ribbing of the body chamber which is not so profusely divided and the primaries are more acute. There is a continuous morphological transition between *C. platyconus* n. sp. of bed PL-5, those of PL-6 and the present specimens of *C. australis* which are representing part of the early evolutionary changes of the lineage in the Andean Tithonian.

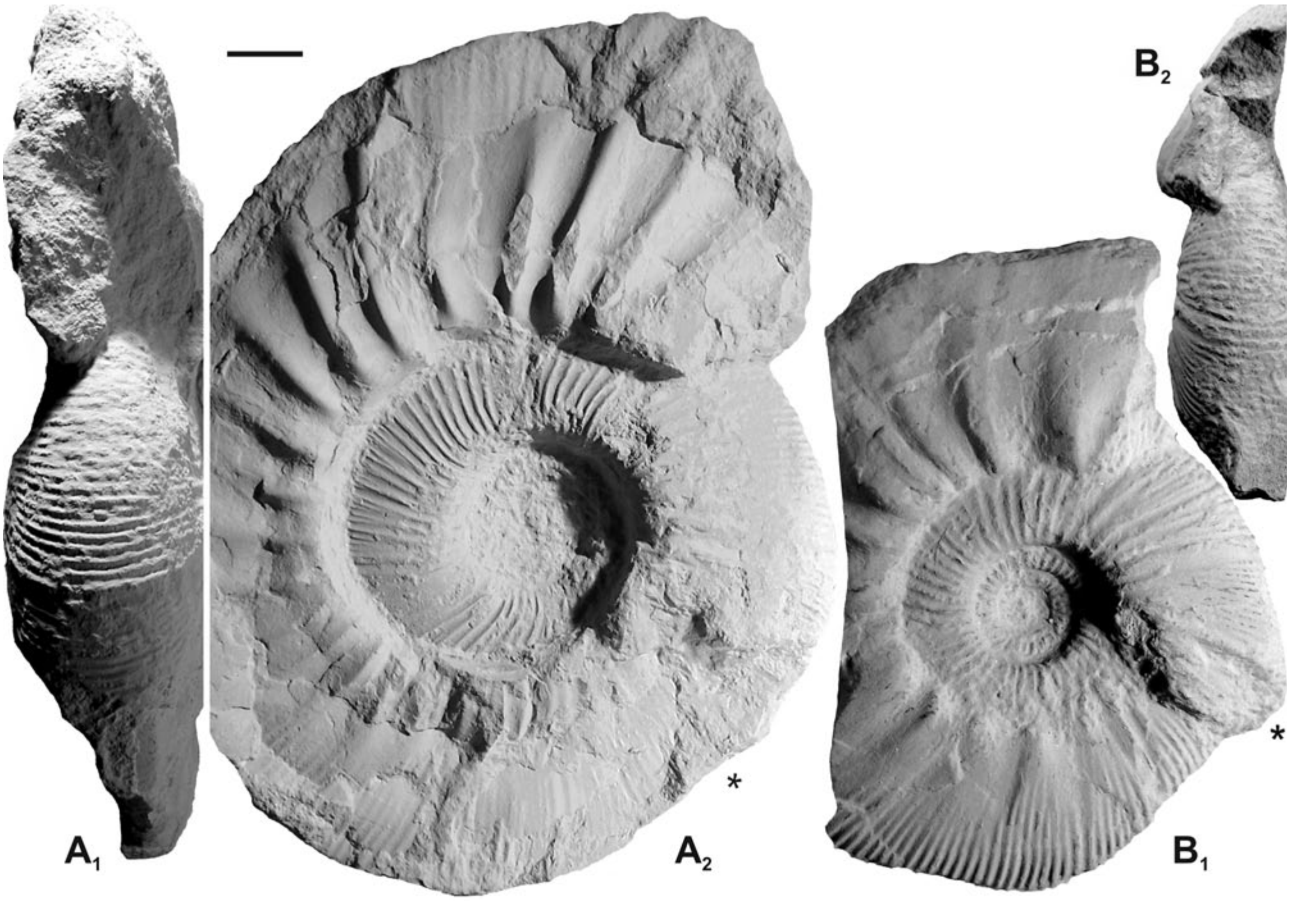


Fig. 21 : **A** : *Choicensisphinctes platyconus* n. sp., adult [M] with almost complete body chamber (MOZPI 7762), Picún Leufú, bed PL-6, *picunleufuense* β horizon. **B** : *Choicensisphinctes australis* (BURCKHARDT, 1903), adult [M] with almost complete body chamber (LPB 1102/1), Picún Leufú, bed PL-11, Zitteli Zone.

Choicensisphinctes erinoides (BURCKHARDT, 1903)
Fig. 22

Material : Three incomplete macroconchs from bed PL-12. Much fragmentary material from the same level observed in the field but not collected.

Description : The best preserved specimen available is a stout suboxycone phragmocone (D = 200 mm) with narrow umbilicus (U/D = 0.25) and well rounded venter. Ribbing is composed by well spaced, short, strong primaries (P = 7) which divide in sheaves of several fine secondaries on the lower third of the flank. The fine secondaries with indistinct intercalatories cross the venter without changes, producing a dense ventral ribbing. On the middle of the flanks the ribbing is rather weak. Other unfigured fragmentary specimen show that the phragmocone reaches at least 250 mm in diameter, other ones with body chamber and fragments of large body chambers indicate adult sizes of about 700 mm. Among the larger specimens, some of them are more evolute with strong bullae-like periumbilical primary ribs on the last whorl of the phragmocone (about 200 mm in diameter) ; its body chamber (D > 300 mm) is moderately uncoiled and completely smooth with a trend to become subtriangular in whorl section.

Remarks and comparison : Considering all the available material it can be seen that there are two morphotypes. The more involute specimens can be easily compared to *C. limitis* and the more evolute ones to *C. erinoides*. The differences between the holotypes of these species are the degree of involution with covariation in rib density and strength, exactly as seen in our samples, and also in the older *C. platyconus* n. sp. However, the inner whorls cannot be compared since the holotype of *C. limitis* has the umbilical window obscured by matrix. In this form they could likely belong to a single species with a range of variation as typical in perisphinctids, but for the time being it must be awaited for new collections at the type locality. Material from the upper Zitteli Zone in La Amarga, Cerro Lotena and Arroyo Cieneguita includes different macroconchs closely matching the discussed holotypes which are also macroconchs. Moreover, *C. erinoides*, *C. choicensis*, *C. limitis* and *C. australis* seem to form a continuous spectrum of morphological and sculptural variation as discussed above. The inner whorls of these macroconchs are indistinguishable

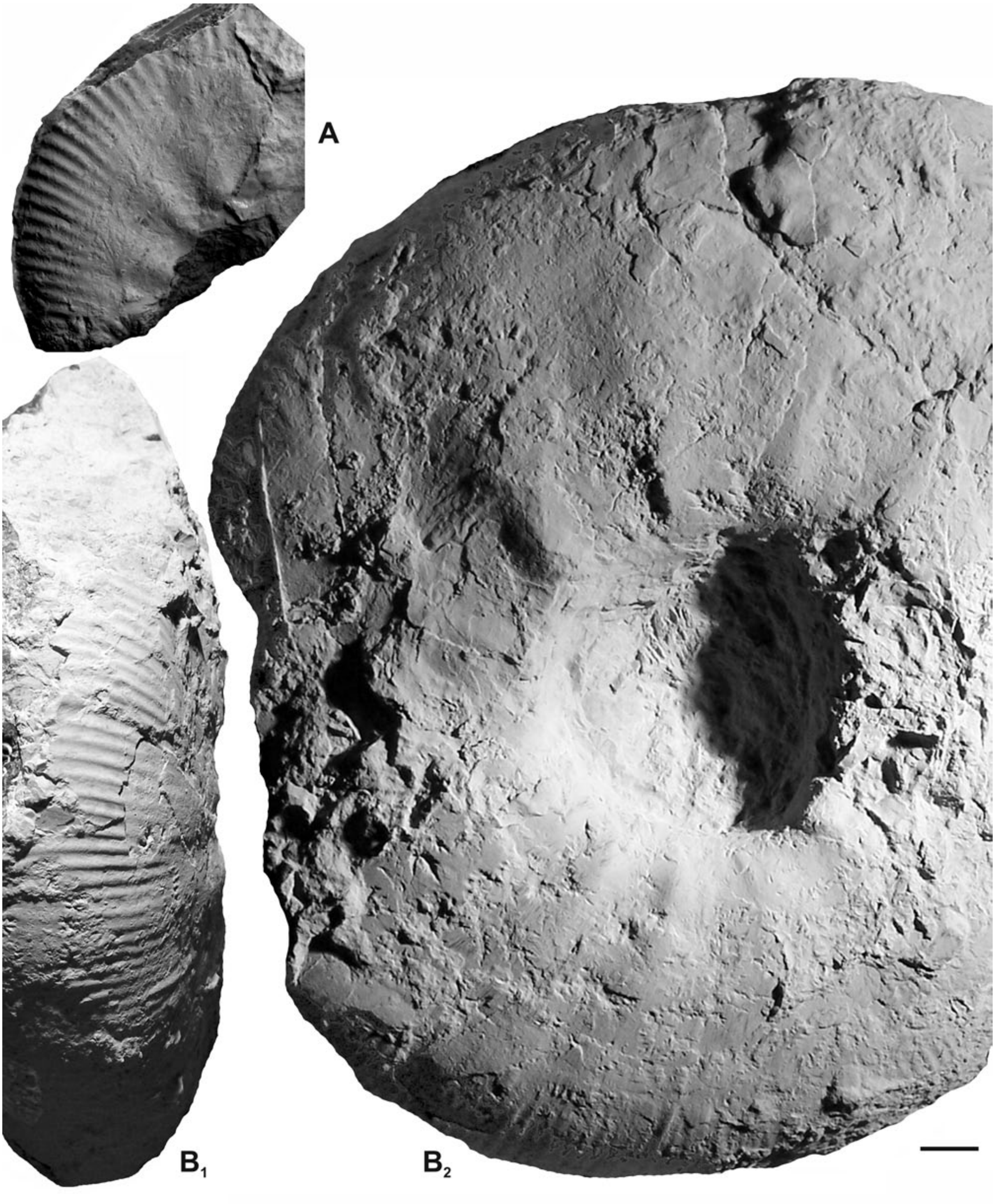


Fig. 22: **A**: *Choicensisphinctes* cf. *erinoides* (BURCKHARDT, 1903), phragmocone (LPB 856); Picún Leufú, bed PL-8. **B**: *Choicensisphinctes erinoides* (BURCKHARDT, 1903), adult [M] phragmocone (MOZPI 7806) with no apparent signs of uncoiling; Picún Leufú, bed PL-12 (Zitteli Zone).

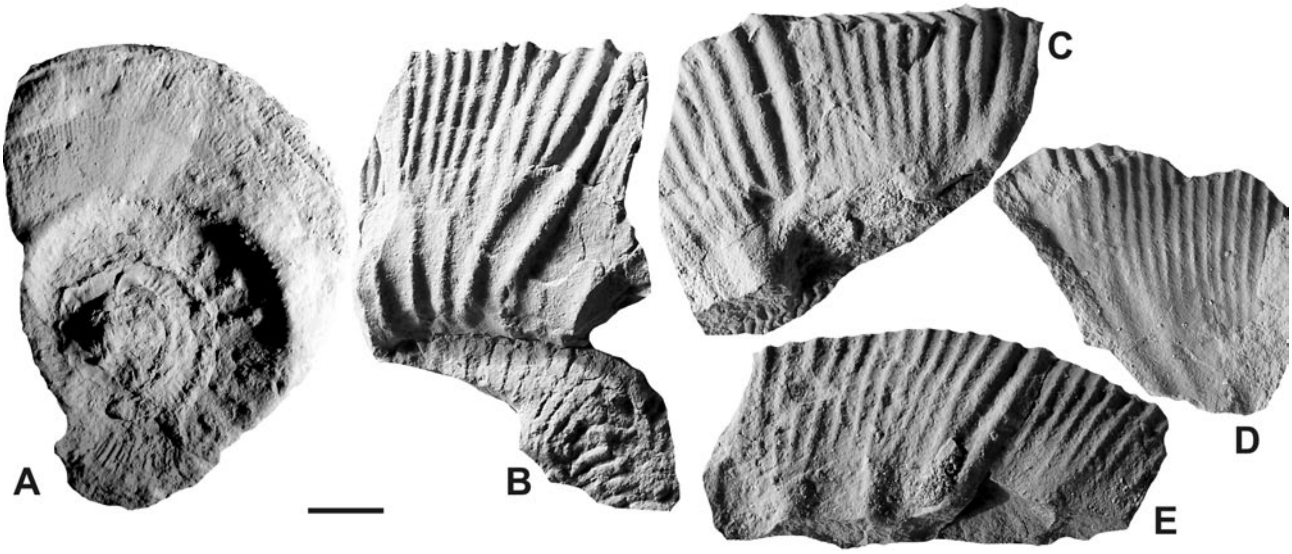


Fig. 23: **A**: *Choicensisphinctes windhauseni* (WEAVER, 1931), adult [M] with incomplete body chamber, Picún Leufú, bed PL-7f, ? Mendozanus Zone or Zitteli Zone. **B-E**: *Choicensisphinctes* cf./aff. *platyconus* n. sp., fragments of body chambers (MOZPI 7084/1, 7084/3), Picún Leufú, beds PL-7b – PL-7e, Picunleufuense Zone.

from those of *C. mendozanus*. Thus considering the co-occurrence of the type specimens it is very likely that they are sexual dimorphic partners. The type specimens of *C. mendozanus* seem to be adults in which the body chambers are somewhat uncoiled and remain ribbed on flanks and venter with slight or incipient variocostation, what is different in comparison with the macroconchs of the genus which become smooth on the venter with wide-spaced primaries on the flanks. This hypothesis of dimorphic correspondence is supported by the form of sexual dimorphism described for *C. platyconus* n. sp., in which some large microconchs of the more evolute variants (Fig. 18A-B) retain the inflated serpenticonic aspect of the inner whorls up to the body chamber, closely resembling the type specimens of *C. mendozanus*.

For the time being it can only be drawn a morphotypic classification from the material available, thus we assign our specimens to a single species, but separated from *C. australis*, which seems to be much smaller in adult size and more compressed, and in Picún Leufú it was recorded in a slightly deeper stratigraphic position.

A specimen likely belonging to *C. erinoides*, and very similar to the HT but smaller, was described and figured by LEANZA (1980: pl. 4: 1) indicating that the specimen occurs below the first occurrences of *P. zitteli*. Nevertheless, the material described by LEANZA was collected without detailed stratigraphic control by A. WINDHAUSEN in 1912 (LEANZA, 1980: 6). Other specimens from that collection were described under different genera (LEANZA, 1980: pl. 2: 2-4, pl. 3: 1, 3, 5, pl. 4: 2, pl. 5: 2-3). All these latter specimens are very similar – sometimes identical – to each other, mainly consisting of phragmocones closely matching with the holotype of *C. choicensis*. They are robust and moderately involute specimens between 45 and 95 mm in diameter, with dense prosocline ribbing on the inner whorls and at $D > 60$ mm covered with strong, well spaced primaries divided in sheaves on mid-flank, giving origin to finer secondaries which, with some intercalar ribs, cross evenly spaced the widely rounded venter.

C. platyconus n. sp., from a deeper stratigraphic level, differs from *C. erinoides* as described above by (1) the smaller adult size, (2) the finer and denser ribbing of the inner whorls and (3) the sculpture of the adult phragmocone and the body chamber develop less marked sheaves of secondaries arised from short, inflated calyx-like primaries as also well seen in *C. australis*.

The fragmentary specimen shown in Fig. 22A as *C.* cf. *erinoides* (bed PL-8) is comparable with the material of *C. erinoides* described from bed PL-12.

Occurrence and distribution: *C. erinoides* (and the discussed group of associated nominal species) has been recorded, besides Picún Leufú, in La Amarga and Cerro Lotena, and with cf.-specimens in Arroyo Cieneguita (associated with *P. zitteli*).

Choicensisphinctes cf. *mendozanus*
(BURCKHARDT, 1911)
Fig. 24

Remarks: The available specimen (MOZPI 7440) is an adult microconch with remains of lappets. It was collected several years ago in Picún Leufú but has no accurate stratigraphical information associated. However, it can be deduced from the museum label, the matrix and by comparison with other fragmentary material known from

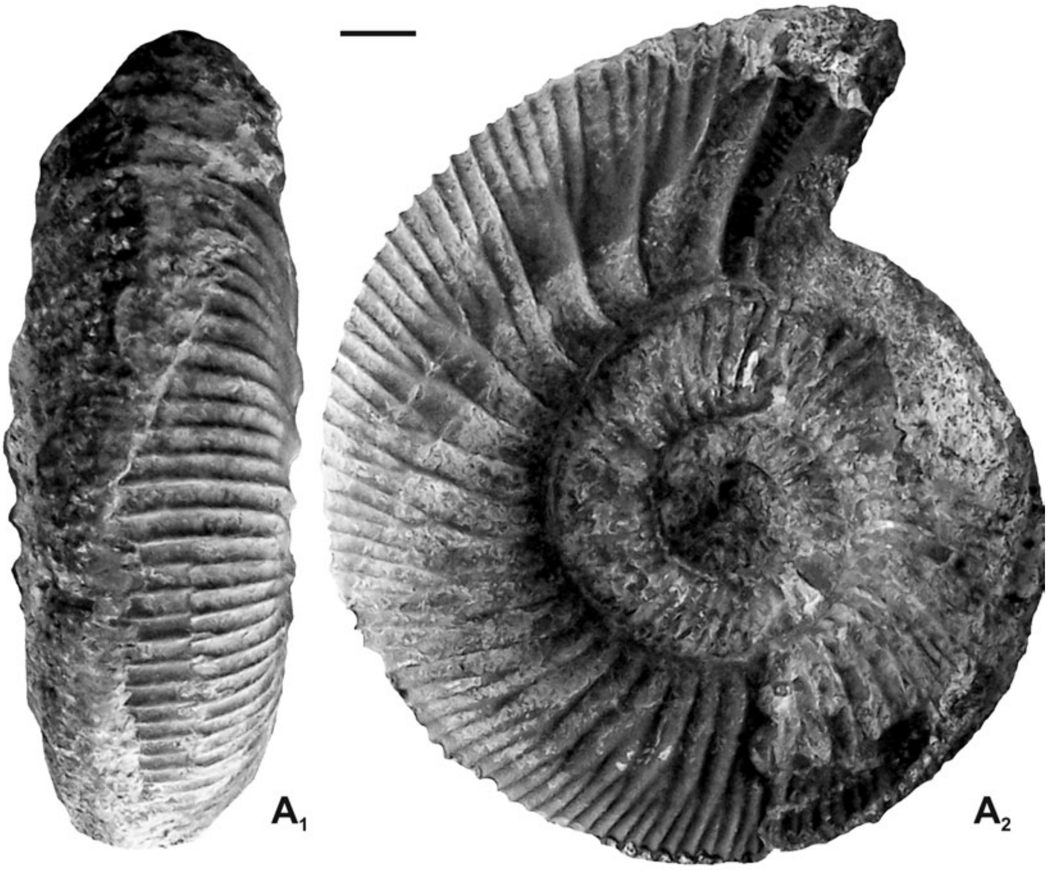


Fig. 24: *Choicensisphinctes* cf. *mendozanus* (BURCKHARDT, 1911). Adult [m] from Picún Leufú, old collection (MOZPI 7440), from an undefined horizon within the interval of beds PL-7f to PL-10, Zitteli Zone.

the locality that it comes from a horizon somewhere in the interval of the beds PL-7f to PL-10. It is herein figured because it matches closely with the lectotype of *C. mendozanus* and, interestingly, it was collected from beds of the Zitteli Zone

Subfamily Torquatisphinctinae TAVERA, 1985

Remarks: The subfamily is mainly conformed by the Indo-Madagascan lineage *Torquatisphinctes* SPATH, 1924 - *Pachysphinctes* DIETRICH, 1925 - *Katroliceras* SPATH, 1924, and can be added with confidence the genus *Catutosphinctes* LEANZA & ZEISS, 1992, as a separate Andean lineage (see PARENT, 2003a). Most of the widely cited European (Submediterranean) "*Torquatisphinctes*" belong to another genera, which are most likely even phyletically unrelated. Besides *Torquatisphinctes, Katroliceras* and *Pachysphinctes* the original composition of the subfamily as envisaged by TAVERA (1985) included several more genera: *Subdichotomoceras* SPATH, 1925, *Parapallasiceras*, *Danubisphinctes* ZEISS, 1968, *Biplisphinctes* and *Burckhardticeras* OLÓRIZ, 1978. *Subdichotomoceras* (?= *Propectinatites* COPE, 1968a) is based on a Subboreal species (*S. lamplughi* SPATH, 1925) within the subfamily Pectinatitinae (BIRKELUND *et al.,* 1983). *Parapallasiceras* and *Danubisphinctes* form a sexual dimorphic pair as recently shown by SCHERZINGER & SCHWEIGERT (1999) and belong clearly to the subfamily Lithacoceratinae. *Burckhardticeras* OLÓRIZ, 1978 (name preoccupied by *Burckhardticeras* ERBEN, 1956) seems to be the earliest representative of the Himalayitidae in Europe in the Ponti Zone as pointed out by OLÓRIZ (1978), and was suggested (PARENT, 2001) to originate from the Torquatisphinctinae, although the relationships are not yet clear. *Biplisphinctes* is based on *Perisphinctes cimbricus* NEUMAYR, 1873 from the Beckeri Zone of the late Kimmeridgian. This form could be at the origin of the Torquatisphinctinae (OLÓRIZ, 1978; CALLOMON, 1992: 267).

Information about the stratigraphic distribution of the Torquatisphinctinae in the southern Tethysian Indo-Madagascan area, is scarce. The most recent revisions are those by KRISHNA *et al*. (1996a, b) for Kachchh and by HOWARTH (1998) for Yemen, where full lists of references may be found. The revision by HOWARTH (1998) shows, after reinterpretation of some of the Yemeni assemblages, that the lineage *Torquatisphinctes*

- *Pachysphinctes* - *Katroliceras* evolved mainly in the late Kimmeridgian Acanthicum to Beckeri zones, what is in accord with the ranges indicated by KRISHNA *et al.* (1996a, b).

Torquatisphinctes naifaensis HOWARTH, *Pachysphinctes bathyplocus* (WAAGEN), *Pachysphinctes major* SPATH and *Pachysphinctes mahokondobeyrichi* (DIETRICH) occur in a set of beds that HOWARTH (1998) labelled as Fauna 7. The illustrated taramelliceratids and the fragmentary lithacoceratids of this level do not contribute very much for time-correlation. The occurrence of *Nebrodites hospes* (NEUMAYR), an early morph of *Orthaspidoceras*, *Idoceras* cf. *balderum* (OPPEL) and the specimen described as *Sutneria wiedmanni* ZEISS, which shows a clear early Kimmeridgian aspect, are altogether significant for an early Kimmeridgian age, around the Divisum/Acanthicum zones.

Katroliceras formosum SPATH, *Katroliceras pottingeri* (SOWERBY), *P. bathyplocus* and *P. major* occur in the Fauna 8 which HOWARTH attributed to the Hybonotum Zone. Nevertheless, *Hybonoticeras ornatum* (SPATH), illustrated with a typical specimen by HOWARTH (1998: pl. 15: 1) from his Fauna 8, is diagnostic for a late Kimmeridgian age (see SCHWEIGERT *et al.*, 1996). In Germany it occurs in the Setatum Subzone, *ornatum* horizon, of the Beckeri Zone. Furthermore, an additional specimen of *H. ornatum* was discovered in a collection from Yemen (kept by V. MITTA, Borissjak Paleontological Institute of Russian Academy of Sciences, PIN RAS) by one of the authors (AS), together with representatives of *Sutneria* which are very close or even identical with *Sutneria casimiriana* (FONTANNES). The later species is also characteristic of the *ornatum* horizon. The fragmentary specimen (HOWARTH, 1998: pl. 15: 4) described under *Hybonoticeras* cf. *hybonotum* (OPPEL) shows a dense radial ribbing and a smooth venter lacking spines. This specimen best matches with *Hybonoticeras kachhense* SPATH (synonym: *Hybonoticeras ciliatum* BERCKHEMER & HÖLDER, 1959), another species from the late Kimmeridgian. However, very similar forms appear in the uppermost Kimmeridgian. Therefore, the beds from where the Fauna 8 comes, including the latest *Katroliceras* and *Pachysphinctes* in Yemen, may be confidently dated as late Kimmeridgian Beckeri Zone.

Extensions into the earliest Tithonian Hybonotum Zone may be represented by (1) *K. pottingeri* cited by KRISHNA *et al.* (1996b) and supported by SCHWEIGERT *et al.* (1996) based on a comparison of the *Hybonoticeras* fauna of Europe and India, and (2) the Ethiopian specimens figured by ZEISS (1994: fig. 5 and pl. 4) as *K.* aff. *pottingeri*. The specimen in ZEISS (1994: pl. 4), is one of the largest and rather complete adult macroconchs illustrated of the genus. The inner whorls match completely with the specimens figured by HOWARTH (1998: pl. 4: 5-6). On the last whorl of the phragmocone it develops a first variocostation, passing from trifurcate primaries to widely splayed, collared ribs. On the last part of the body chamber a final additional variocostate stage is characterized by coarse, widely spaced unbranched primary ribs which tend to vanish on the venter. The intermediate stage of variocostation is better preserved in the other specimen (ZEISS, 1994: fig. 5) from the same locality and stratigraphic position. Interestingly, this latter specimen is very similar to some morphotypes from the Mendozanus and Zitteli zones of Cerro Lotena, La Amarga and Portada Covunco which could be included in *Catutosphinctes windhauseni* (WEAVER).

The striking morphological resemblance, including diagnostic combinations of features uncommon in other similar perisphinctids, and the temporal continuity between *Catutosphinctes* and the Indo-Madagascan genera, strongly suggest that this genus originates from the late Kimmeridgian *Katroliceras*. The apparent biogeographic disjunction between these ammonite groups could indicate that *Catutosphinctes* is an Andean branch of the Indo-Madagascan lineage that became eudemic in the NB. The widely accepted trans-Gondwanian marine connection between the Andean and the Indo-Madagascan (or Sub-Austral) biogeographic domains, through the Mozambique Corridor (ENAY & CARIOU, 1997, 1999 and references therein) via the Weddell Sea well developed for the Tithonian times (GOLONKA, 2007; MCDONALD *et al.*, 2003 and references therein), support this hypothesis.

Genus *Catutosphinctes* LEANZA & ZEISS, 1992

Type species: *Catutosphinctes rafaeli* LEANZA & ZEISS, 1992; by OD.

Diagnosis: See LEANZA & ZEISS (1992: 1847). A conspicuous and diagnostic feature is the raising of the primary ribs in the point of furcation where can be formed even a lamellar tubercle; this process occurs typically on inner and middle whorls. It can be added that the members of the lineage are evolute serpenticones with subrectangular to rounded whorl section. The microconchs are smaller, bear lappets and their body chambers are shorter than in the macroconchs.

Remarks: *Catutosphinctes* includes the Andean Tithonian succession of species listed in PARENT (2003a: 58), formerly under *Torquatisphinctes, Pachysphinctes* and *Katroliceras*. This lineage has been confirmed after bed-by-bed collections during last years throughout the Neuquén-Mendoza Basin, showing a dense succession of chronospecies evolving from the early Tithonian (or late Kimmeridgian) *Catutosphinctes guenenakenensis* n. sp. [M&m] described below. There are other several species described in the literature which conform to the lineage, expanding the list as follows:

Catutosphinctes windhauseni (WEAVER, 1931) [M&m]. HT by monotypy: the specimen figured by WEAVER (1931: pl. 44: 300) herein refigured as Fig. 25A,

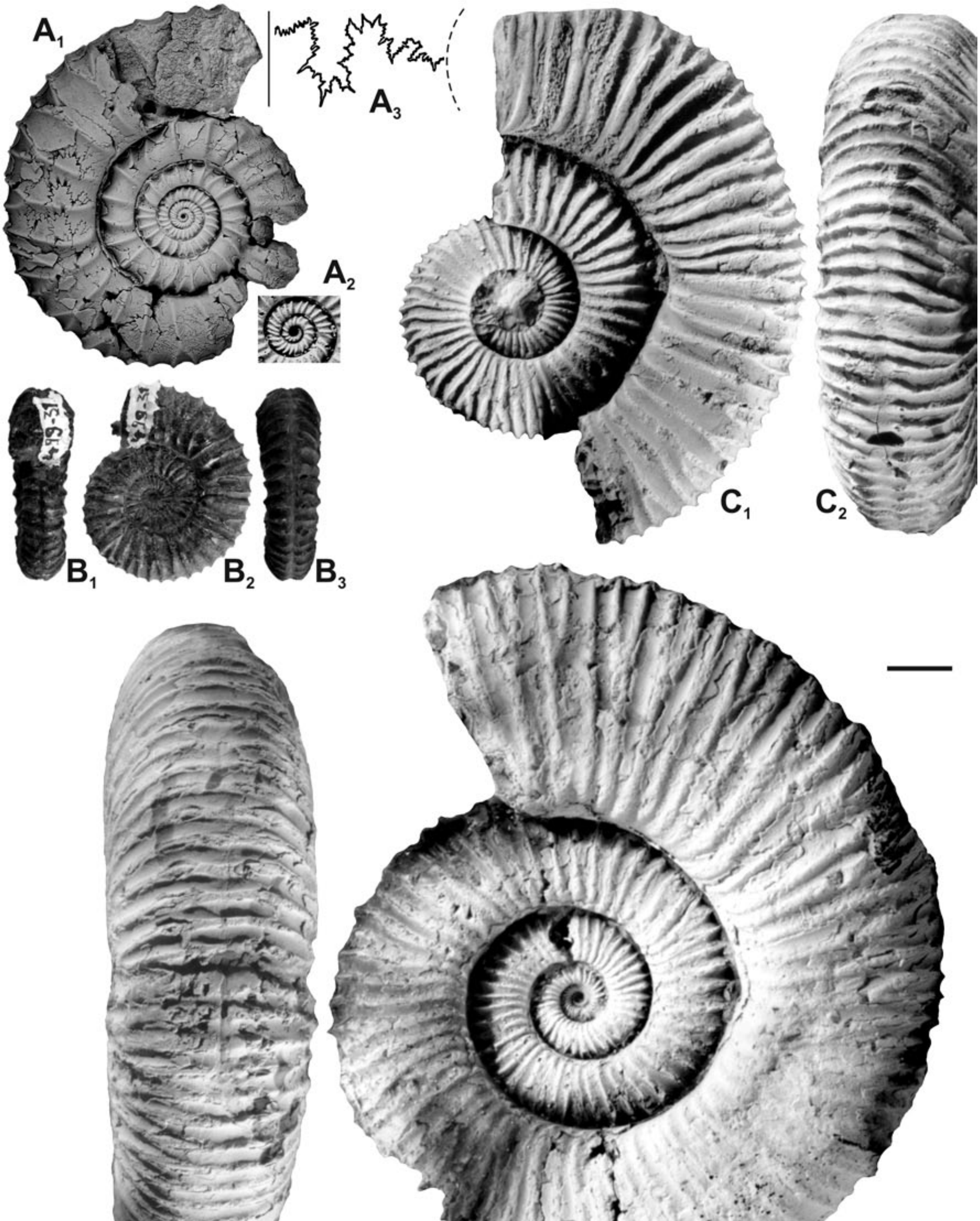


Fig. 25: **A**: *Catutosphinctes windhauseni* (WEAVER, 1931), holotype, macroconch phragmocone (BMS 323). **A$_1$**: Lateral view, **A$_2$**: enlarged (x2) innermost whorls, **A$_3$**: septal suture line; 6 km west of Cerro Lotena, lower middle Tithonian. **B**: *Catutosphinctes proximus* (STEUER, 1897), paralectotype, phragmocone (MGAU 499-31), Arroyo Cieneguita, bed/level Cieneguita II, middle Tithonian. **C**: *Reineckeia pawlowi* STEUER, 1897, holotype; adult phragmocone with incomplete body chamber (MGAU 499-22B), figured by STEUER (1897, transl. 1921: pl. 7: 6-8). Arroyo de La Manga, unknown horizon within the Tithonian. **D**: *Reineckeia fraudans* STEUER, 1897, holotype; phragmocone with beginning of the body chamber (MGAU 499-33), figured by STEUER (1897, transl. 1921: pl. 9: 4-5). Arroyo de La Manga, unknown horizon within the Tithonian.

completely septated; TL: 6 km west of the Cerro Lotena; TH: middle Tithonian (sic). In La Amarga the species occurs in abundance in the beds where was collected part of the Fauna B (PARENT *et al.*, 2006) which could be still early Tithonian. Morphologically is similar to *C. guenenakenensis* n. sp. but with significant differences as explained below. Specimens which could be attributed to *Cat. windhauseni* occur in Portada Covunco, Casa Pincheira (as part of the M6-assemblage of BURCKHARDT, 1900: pl. 24: 5-6). The stratigraphic position in La Amarga, P. Covunco and Casa Pincheira is consistently the same as in the Cerro Lotena, above the Fauna A and below the upper beds of the Zitteli Zone.

Catutosphinctes proximus (STEUER, 1897) [M&m]. This species was recently reviewed and the lectotype refigured (PARENT, 2003a: fig. 9I-J). Recent collections in Cerro Lotena, Cañadón de los Alazanes, Pampa Tril, Casa Pincheira and Arroyo Cieneguita have shown that this morphospecies has a long stratigraphical range figured in the form of two transients (PARENT, 2001, 2003a): the older or transient α illustrated by the adult specimen from Arroyo Cieneguita figured by STEUER (1897, transl. 1921: pl. 15: 11) and the transient β typified by the lectotype (STEUER, 1897, transl. 1921: pl. 8: 7-8).
The paralectotype figured by STEUER (1897, transl. 1921: pl. 8: 10-11), herein refigured photographically as Fig. 25B, is a small phragmocone with himalayitid aspect including strong, distant, mostly bifurcate primaries, which rise on the furcation point, as typical in *Catutosphinctes*. All ribs are interrupted on the venter, forming a deep narrow groove much resembling the type species of *Aulacosphinctes* UHLIG, 1910, *Ammonites moerikeanus* OPPEL, 1863. Nevertheless, *Aulacosphinctes* and their macroconchs (*Micracanthoceras* SPATH, 1925) have small tubercules at least in the inner whorls (ENAY in VERMA & WESTERMANN, 1973; see GEYSSANT, 1997: pl. 26: 1, cast of the LT of *Micracanthoceras microcanthum*, the type species of *Micracanthoceras*).

Catutosphinctes rafaeli LEANZA & ZEISS [M&m]. Unfortunately the HT, from the middle Tithonian of Los Catutos, is a crushed and incomplete adult macroconch. In Portada Covunco and Cerro Lotena occurs in a similar or slightlydeeper stratigraphic position as the TH very big and complete macroconchs which are larger than 400 mm in diameter, with the body chamber uncoiled and strongly ornamented by simple rounded blade-like primaries.

Catutosphinctes araucanensis (LEANZA, 1980) [M&m]. The HT (LEANZA, 1980: pl. 6: 3) is a microconch with lappets from the middle Tithonian of Cerro Lotena. Macroconchs from the TH in Cerro Lotena have about twice the size, with the body chamber bearing an identical sculpture to that of the HT of *C. rafaeli*.

Catutosphinctes catutosensis (LEANZA & ZEISS, 1990) [M] and *Catutosphinctes americanensis* (LEANZA, 1980) [M&m]. Both species are very similar and their stratigraphic positions seems to be the same or very close. In Cerro Lotena and Los Catutos both taxa occur above *C. rafaeli*.

Catutosphinctes australis (LEANZA, 1945). LEANZA described a rather heterogeneous series of ammonites as *Berriasella australis* n. sp. without designating holotype. The figured specimens (LEANZA, 1945: pl. 2: 6, 10-11, 14) can not be assigned to *Berriasella* UHLIG, 1905 (TS: *Ammonites privasensis* PICTET, 1867) because their very different morphology and ornamentation respect the species of this genus; nevertheless they all show the diagnostic features of inner whorls of *Catutosphinctes*, especially the widely splayed bifurcations on the very evolute and rounded whorls. It is herein designated as lectotype the specimen figured by LEANZA (1945: pl. 2: 6, 11) from the Alternans Zone of Arroyo del Yeso, Mendoza (Fig. 1). It is apparently an adult microconch with an incomplete body chamber, almost indistinguishable from the microconchs of *C. rafaeli* from the Internispinosum Zone of Portada Covunco illustrated by PARENT & COCCA (2007). The only difference is the slightly more densely ribbed inner whorls of the LT of *C. australis*.

Catutosphinctes azulensis (LEANZA, 1945) [M]. The HT by monotypy is the specimen figured by LEANZA (1945: pl. 1: 6-7), a phragmoconce which is nearly complete according to a complete large macroconch of the species collected in Pampa Tril which is at least 140 mm in diameter at the peristome.

Catutosphinctes inflatus (LEANZA, 1945). The HT by monotypy is the macroconch specimen figured by LEANZA (1945: pl. 1: 1) under "*Berriasella fraudans* (STEUER, 1897) var. inflata n. var.". The HT (by monotypy) of *Reineckeia fraudans* STEUER (1897, transl. 1921: pl. 9: 4-6), refigured photographically herein as Fig. 25D, is a completely different ammonite: evolute, subplatyconic with subrectangular whorl section; the sculpture is composed mainly by simple ribs with some bifurcate which become more frequent in the last whorl; the ribs, from the innermost whorls, rise on the ventro-lateral shoulder forming a small lamellar tubercle. The type locality is Arroyo de la Manga, but unfortunately the type horizon is unknown since STEUER did not indicate a stratigraphic subdivision of the fauna described from this locality. From the same locality comes the HT (by monotypy) of *Reineckeia pawlowi* STEUER (1897, transl. 1921: pl. 7: 6-9) which is very similar to *R. fraudans*, showing the same distinctive pattern of himalayitid sculpture, although there seems to be some differences in the septal suture lines. The HT by monotypy of *R.pawlowi* is herein refigured photographically as Fig. 25C.

In the lower Tithonian there are specimens of *Catutosphinctes* which can be hard to distinguish from the contemporaneous forms of *Choicensisphinctes*, and in some cases also from "*Lithacoceras*". This phenomenon of homeomorphy may be solved by considering the complete ontogeny, especially ribbing, and the sexual dimorphism.

- The inner whorls of *Catutosphinctes* are serpenticonic, very evolute, the whorl section tends to be subrectangular to sub-rounded; the ribbing is coarse, widely splayed after bifurcation where is commonly observed this portion raised, even forming a lamellar tubercle. Inner whorls of *Choicensisphinctes* are somewhat more inflated and involute, with a widely rounded venter; the ribbing is denser and finer with narrowly splayed secondaries with a trend to be somewhat stronger on the lower half of the flank (in later forms primaries are inflated in the lower part of the flank). Inner whorls of *Lithacoceras* tend to be more compressed; the ribbing is evenly spaced and bifurcate, with no intercalars, evenly running the flank and bifurcating on the upper third of the flank.
- Adult phragmocones can be very similar but there are characteristic/diagnostic features in each genus. *Catutosphinctes* is evolute, serpenticonic with sharp ribbing, mainly bifurcate and with polyschizotome ribs associated with constrictions. *Choicensisphinctes* tends to be more inflated with high vertical umbilical wall; ribbing is finer and denser with polyschizotome and virgatotome ribs occurring sporadically, frequently associated with constrictions. "*Lithacoceras"* is more compressed with regular bifurcate ribbing, moderately sharp and dense; at the end of the adult phragmocone or beginning of the bodychamber there is a short stage of trifurcate ribs in a well defined virgatotome style.
- The adult bodychamber of macroconch *Catutosphinctes* is serpenticonic, sometimes robust and inflated, but there is always a wide umbilicus; ribbing is strong, well spaced and widely splayed after bifurcation. The adult microconchs are smaller and not variocostate with a pair of lappets moderately long and narrow.

  The adult bodychamber of macroconch *Choicensisphinctes* is commonly higher than wide, suboval; ribbing well differentiated in strong primaries divided in sheaves from the lower part of the flank and then vanishing almost completely towards the aperture. There is a marked tendency to become stout suboxycones. The adult microconchs are smaller and apparently very variable, from serpenticone to suboxycone, densely to moderately densely ribbed and with short, subtriangular lappets most frequently.

  The adult bodychamber of macroconch "*Lithacoceras*" is rather compressed, subrectangular to subtrapezoidal, evolute; ribbing is composed by wide prosocline primaries which divide in sheaves on the mid-flank or, in some cases, upper. The adult microconchs are slender ammonites with compressed whorl section, ribbing is few variocostate respect the phragmocone, becoming irregularly arranged but preserving strength. They have spatulated lappets.

Catutosphinctes guenenakenensis n. sp.
Figs. 5A-B, 5G-H, 26-30.

2006. "*Torquatisphinctes*" cf. *mendozanus* (Burckhardt, 1911).- Parent *et al.*, p. 259, fig. 3C-3D (the latter herein refigured as Fig. 25A).

Material: 60 macroconchs, 10 microconchs and several fragmentary specimens, all from beds PL-5 and PL-6.
Type series: Holotype [M]: Fig. 26A (MOZPI 7768) and three paratypes: PT-1 [M], Fig 28B (MOZPI 7764); PT-2 [m], Fig. 26B (MOZPI 7471); PT-3 [m], Fig. 28C (LPB 1104); all from the type horizon.
Type locality and horizon: Picún Leufú (Fig. 1); bed PL-5, *picunleufuense* α horizon, Picunleufuense Standard Zone, lower Tithonian.
Derivation of name: After Guénena-kéne, the name of one of the main groups of original inhabitants of Argentina.
Diagnosis: Macroconch: evolute serpenticone; inner whorls suboval depressed in whorl section, outer whorls rounded subrectangular, and body chamber suboval. Ribbing strong with polyschizotomics at constrictions; on the phragmocone primaries are prosocline, bi- or trifurcated widely splayed, raised in the point of furcation; adult phragmocone with strong blade-like primaries polyfurcate in 3-5 secondaries with intercalars unevenly distributed; adult body chamber with strong to collared ribs. Body chamber occupies about three quarters of a whorl. Microconch: one to two quarters the size of the macroconch. Phragmocone indistinguishable from the inner whorls of the macroconch at comparable diameter. Body chamber more or less densely ribbed with bifurcate and few simple ribs. Lappets narrow, moderately long. Body chamber about half a whorl long.
Description: Macroconchs: Innermost whorls ($2.5 < D < 6$ mm) very evolute with depressed, rounded whorl section, covered by acute, strong and well spaced primaries of which one each two or three bifurcates near the ventro-lateral shoulder. The next whorls of phragmocone ($6 < D < 60$-70 mm) are somewhat more involute with subrectangular to suboval whorl section, commonly as wide as high. The ribbing is composed by acute primaries which start on the umbilical wall, cross indistinctly the umbilical shoulder and the lower half of the flank slightly prosocline. On the middle to the upper third of the flank most primaries bifurcate or trifurcate, some few remain undivided or simple. All ribs cross the venter orthogonally and evenly spaced, becoming weak and so forming a groove that can be observed but inconsistently at different diameters in different specimens, the more regular groove is observed between 20-40 mm in diameter. There are about two

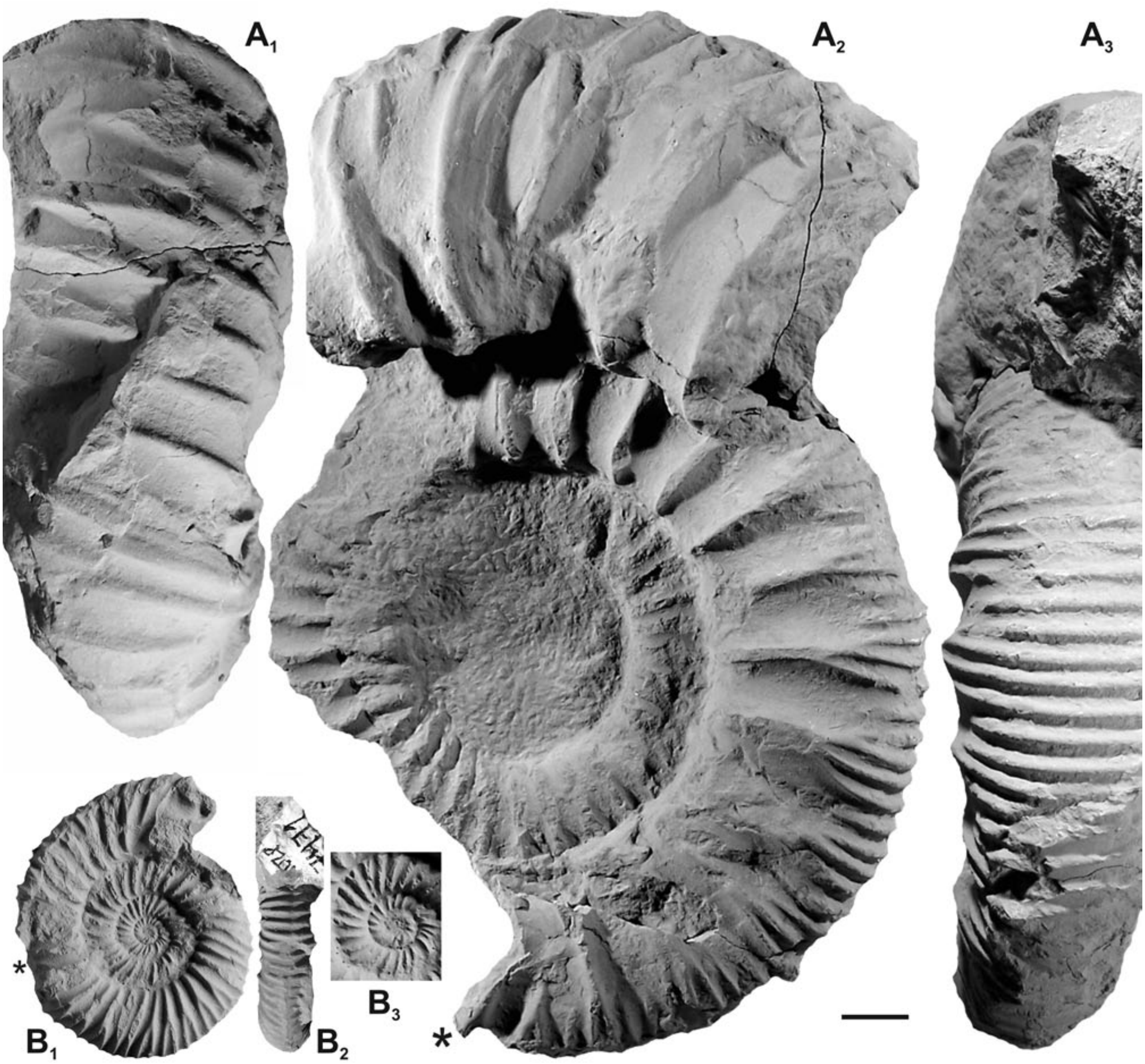


Fig. 26: *Catutosphinctes guenenakenensis* n. sp. **A**: Holotype, adult [M] with incomplete body chamber (MOZPI 7768). **B**: Paratype 2. Adult [m] with lappets (MOZPI 7471); innermost whorls (**B**$_3$) enlarged (x2). Picún Leufú, bed PL-5, *picunleufuense* α horizon.

wide shallow constrictions per whorl that are preceded by a polyschizotomic or a virgatotome triplicate rib, and in its front there is a reinforced and undivided primary. The last whorl of the phragmocone is more depressed and subquadratic; ribbing changes to strong blade-like primaries which divide in 3 to 5 finer secondaries which together occasional intercalatories, all cross evenly spaced the venter without changes in strength. The phragmocone ends at 80-110 mm in diameter in different specimens. The body chamber becomes somewhat compressed and uncoiled. The adult size shows some variation, the HT has a max diameter of about 150 mm close to the peristome but other specimens are smaller, ranging from 80 to 100 mm close to peristome (e.g., Fig. 28A). Ribbing is composed by strong blade-like primaries with collared aspect; all of them are simple or irregularly divided on the upper part of the flanks; some sparse intercalars confined to the upper part of the flanks are irregularly distributed on the adult body chamber.

Microconchs: smaller than the macroconchs and indistinguishable at comparable diameters. Differentiation arises at the onset of the adult body chamber. It is shorter and bears at the peristome moderately long lappets of about a half long as the height of the whorl section. There

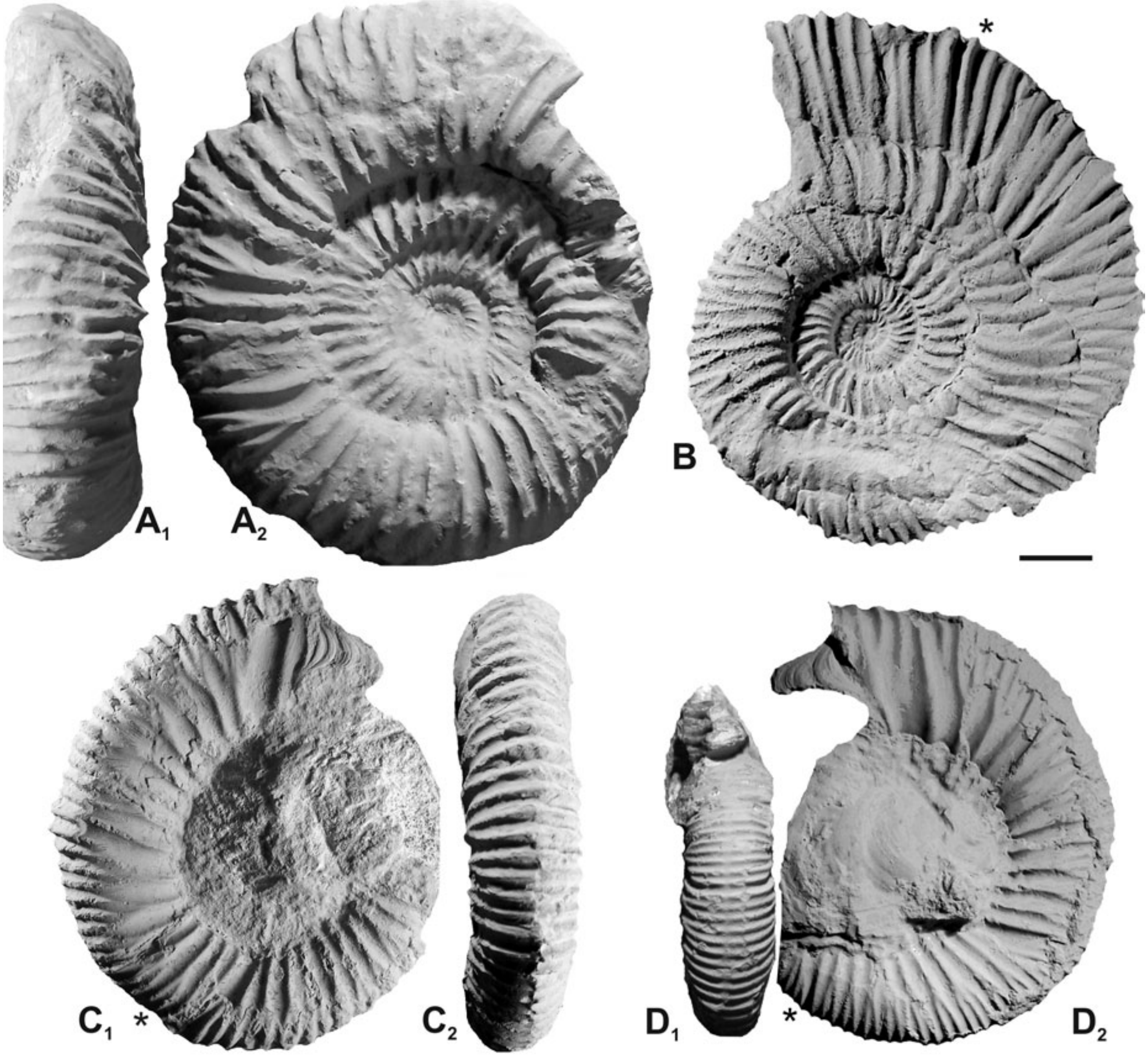


Fig. 27: *Catutosphinctes guenenakenensis* n. sp. **A**: Adult [M] phragmocone with beginning of the body chamber (LPB 623). **B**: Adult [M] phragmocone with beginning of the body chamber (MOZPI 7769). **C**: Complete large-sized adult [m] with lappets (MOZPI 7487). **D**: Complete large-sized adult [m] with lappets (LPB 1103); the attached oyster covering the umbilicus is frequent in bed PL-5. Picún Leufú, bed PL-5, *picunleufuense* α horizon.

is some variation in the adult size ranging from $D = 42$ to 65 mm.

Remarks and comparison: *C.* cf./aff. *guenenakenensis* (described below) is more densely ribbed in the inner whorls (see Fig. 31A) but the adult phragmocone and body chamber of this poorly known species seem to differ little. *Cat. windhauseni* differs in being more evolute throughout the ontogeny and the middle, and by the outer whorls of the phragmocone which are covered by more widely spaced primary ribs which bifurcate splaying more widely although the style of ribbing is the same in both species.

The fragmentary ammonite from the Península de Paraguana, Venezuela, figured under *Virgatosphinctes* sp. by MACDONALD (1968: fig. 5b; determination by R.W. IMLAY) resembles the body chamber of small adult macroconchs of *C. guenenakenensis* n. sp., but the ribbing is more prorsiradiate.

C. guenenakenensis n. sp. is the earliest species of the Andean lineage recorded from the NB which is supposed to be a direct derivative of Late Kimmeridgian (? earliest Tithonian) southern Tethyan representatives of the Torquatisphinctinae (see discussion above). The specimens of *K. formosum* figured by HOWARTH (1998: pl. 2: 3, 6, pl. 4: 1-3, 5) are very similar to *C. guenenakenensis* n. sp. in sculpture and shell shape. Differences are the more evolute with flattish flanks middle whorls and the more densely ribbed inner whorls of *K. formosum*, but the most significant difference is in the larger microconchs of this latter in comparison

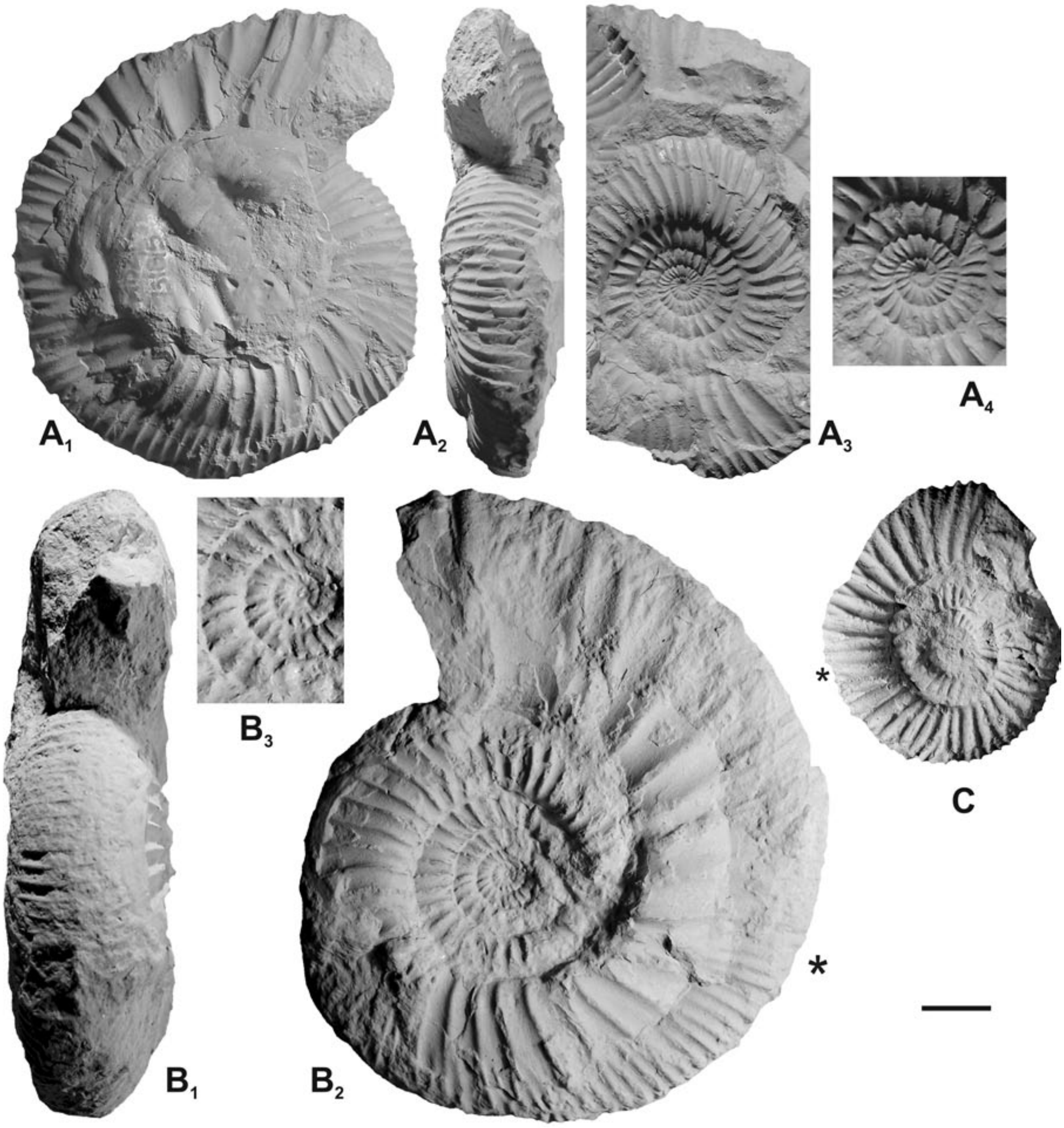


Fig. 28: *Catutosphinctes guenenakenensis* n. sp. **A**: Small-sized adult [M] with almost complete body chamber (MOZPI 7318/5); innermost whorls ($\mathbf{A}_4$) enlarged (x2). **B**: Adult [M] with incomplete body chamber (MOZPI 7764); innermost whorls ($\mathbf{B}_3$) enlarged (x2). **C**: adult [m] with lappets (LPB 1104). Picún Leufú, bed PL-5, *picunleufuense* α horizon.

with the smaller ones of *C. guenenakenensis* n. sp. However, we have not observed segmental growth after constrictions as described by Howarth (1998: 46) for the Yemeni *Torquatisphinctes*.

Occurrence: In Picún Leufú *C. guenenakenensis* n. sp. occurs in the *picunleufuense* α and β horizons of the Picunleufuense Zone, early Tithonian; in roughly equivalent horizons the species also occurs in several other localites of the basin: Cerro Lotena, La Amarga, Pampa Tril, Arroyo Cieneguita, and Casa Pincheira.

The specimen from Casa Pincheira figured in Parent (2003a: fig. 7C) under *Euvirgalithacoceras malarguense* actually belongs to the conspicuous morphotype of *C. guenenakenensis* n. sp. of the *picunleufuense* β hz. illustrated in Fig. 29C. Interesting for time-correlation, this specimens from Casa Pincheira is part of the assemblage which also includes a fine representative of "*L.*" *picunleufuense* transient β (Parent, 2003a: fig. 6A) which is identical to the specimen from the *picunleufuense* β hz. shown in Fig. 10.

Catutosphinctes cf./aff. *guenenakenensis* n. sp.
Fig. 31A-E

Material: Several incomplete and fragmentary specimens from beds PL-7a – PL-7e.

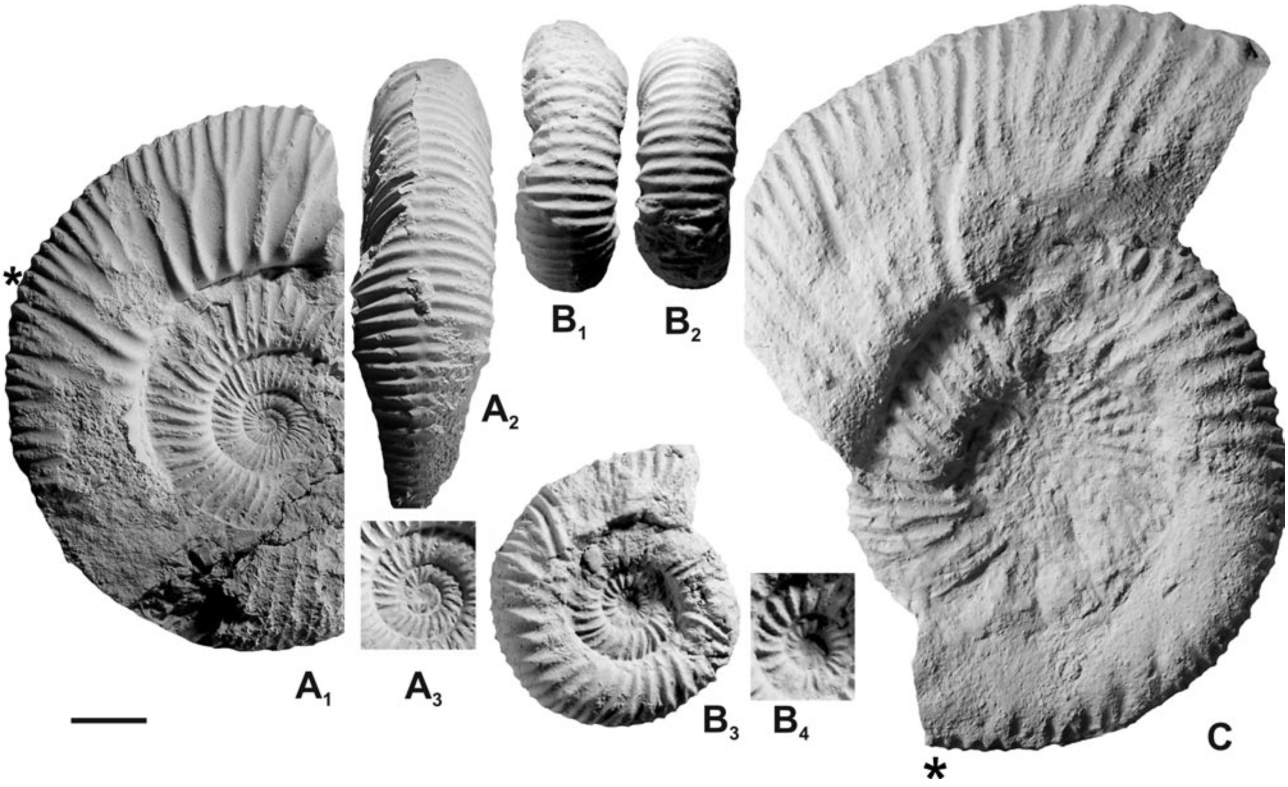


Fig. 29 : *Catutosphinctes guenenakenensis* n. sp. **A** : Adult [M] with beginning of the body chamber (LPB 1105) ; innermost whorls (**A**$_3$) enlarged (x2) ; Picún Leufú, bed PL-5, *picunleufuense* α horizon. **B** : Phragmocone (MOZPI 7496) ; innermost whorls (**B**$_4$) enlarged (x2) ; Picún Leufú, bed PL-5, *picunleufuense* α horizon. **C** : Adult [M] with the beginning of the body chamber (LPB 830) ; Picún Leufú, bed PL-6, *picunleufuense* β horizon.

Description : Fragmentary body chambers of adult macroconchs are rather compressed, covered by strong blade-like primaries divided, on the upper third of the flanks, in 3 to 5 secondaries which together some intercalars cross orthogonally and evenly spaced the venter without changes.

Smaller specimens, only phragmocones, are evolute from the innermost whorls with subrectangular to subquadratic whorl section. Ribbing on inner whorls is fine and dense, slightly prosocline, bifurcating on the upper part of the flanks. On subadult whorls, between 30 and 60 mm in diameter, the typical ribbing of the genus is well evident : mainly bifurcate primaries and less frequent trifurcates and few constrictions preceded by a polygyrate and with a simple primary in the front ; all ribs cross the venter evenly spaced and with a median weakening, especially about 30-40 mm in diameter.

Remarks and comparison : Sculpture and shell shape indicate these specimens belong to *Catutosphinctes*. The body chamber is identical to the outermost whorl of phragmocone and beginning of the body chamber of *C. guenenakenensis* n. sp. Nevertheless, the inner whorls are somewhat different in the finer and denser ribbing on flanks. It could be considered a transient of the species, but more complete material is necessary for assessing the patterns of variation and the significance of the differences.

Occurrence : This form ranges from bed PL-7c to PL.7e, the upper part of the Picunleufuense Zone (unnamed horizon), associated with *C.* cf./aff. *platyconus*.

Family Aspidoceratidae ZITTEL, 1895

Aspidoceratidae indet. A [Laevaptychus]
Fig. 32A

Material : Two single valves, more or less well preserved (MOZPI 7343/1 – 7343/2) from bed PL-5, *picunleufuense* α horizon, Picunleufuense Standard Zone, lower Tithonian.

Remarks : The specimens belong to a rather large aspidoceratid with a relatively narrow whorl section.

Aspidoceratidae indet. B [Laevaptychus]
Fig. 32B

Material : A single moderately well preserved, bivalved specimen (MOZPI 7778/3) from bed PL-9, *perlaevis* horizon, Zitteli Zone.

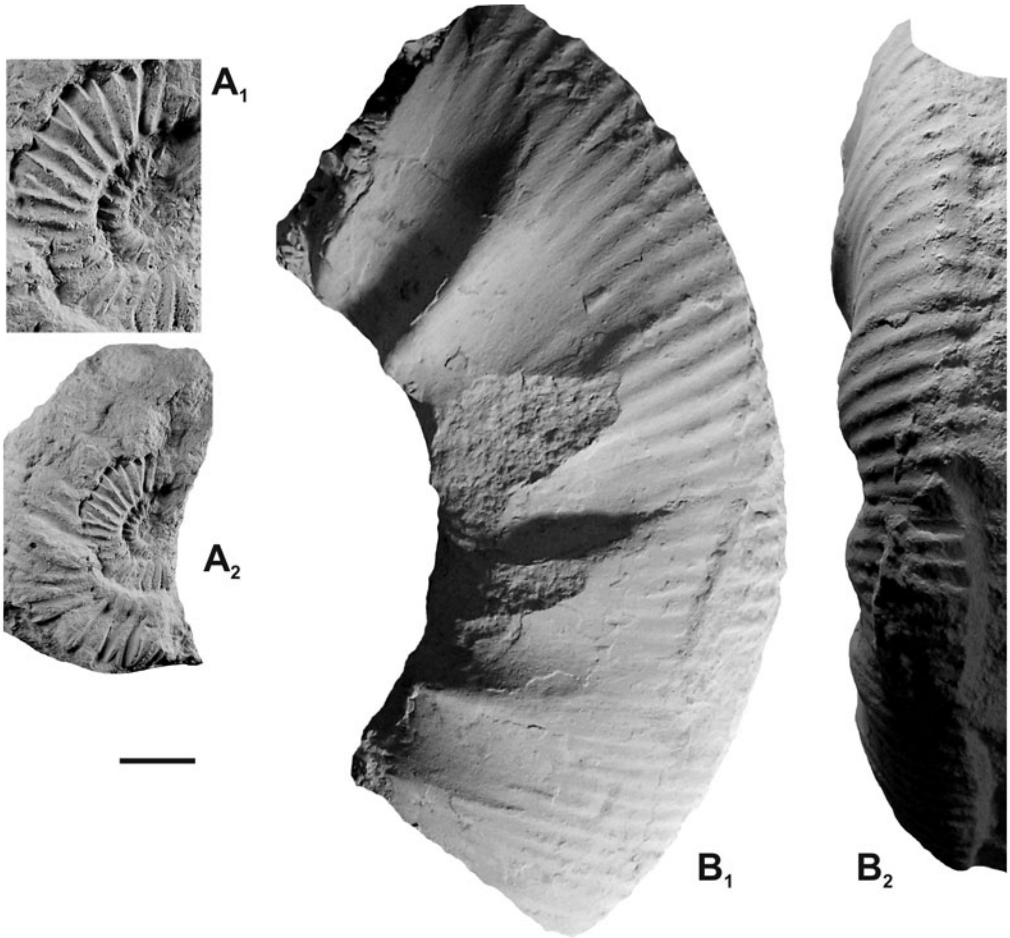


Fig. 30: *Catutosphinctes guenenakenensis* n. sp. **A**: Inner whorls (LPB 829); enlarged (x2) view (**A$_1$**). **B**: portion of adult [M] body chamber (MOZPI 7821) showing the bundles of secondary ribs with intercalars and the strong blade-like primaries typical of the body chamber in the species. Picún Leufú, bed PL-6, *picunleufuense* β horizon.

Remarks: The specimen belongs to an aspidoceratid with narrow whorl section. Similar isolated forms are known from the lower Kimmeridgian of Europe and *Hybonoticeras* from the Solnhofen Limestones (southern Germany) has a similar narrow outline. The specimen was collected within an assemblage which includes *Physodoceras* sp. A and *Sutneria* sp. A. The compressed whorl section of the juvenile specimen of *Physodoceras* sp. A has a narrow whorl section but more material is needed for analyzing a probable correspondence.

Genus *Sutneria* ZITTEL, 1884

Type species: *Nautilus platynotus* REINECKE, 1818; SD MUNIER-CHALMAS, 1892.

Remarks: *Sutneria* has been suggested to belong to the family Aspidoceratidae by ENAY (1977: 109) what was later proved by SCHWEIGERT (1998). Moreover, this genus consists merely of the microconchs of different macroconch aspidoceratids of which the dimorphic correspondence has been established in few cases. The studied fauna of Picún Leufú includes microconch aspidoceratids which are described under *Sutneria* since the corresponding macroconchs are not yet identified.

The holotype of *Hildoglochiceras wiedmanni* LEANZA (1980: pl. 1: 4) from the Zitteli Zone of Cerro Lotena is a microconch aspidoceratid almost indistinguishable from *Sutneria parabolistriatum* (KRANTZ, 1926) collected from an undefined horizon of Arroyo Loncoche, Mendoza Province. The HT by MT of this latter species is herein refigured photographically (Fig. 33).

Sutneria? sp. A
Fig. 32D-E$_2$

Material: Two crushed but rather completely preserved (microconch) specimens (MOZPI 7773, 7776) from the very top of bed PL-8 and bed PL-9.

Description: Compressed, moderately involute platyconic shell. Phragmocone smooth with rounded umbilical shoulder, flattish flanks and rather narrow, rounded venter. The body chamber is preserved but mostly crushed in both specimens; slightly uncoiled with

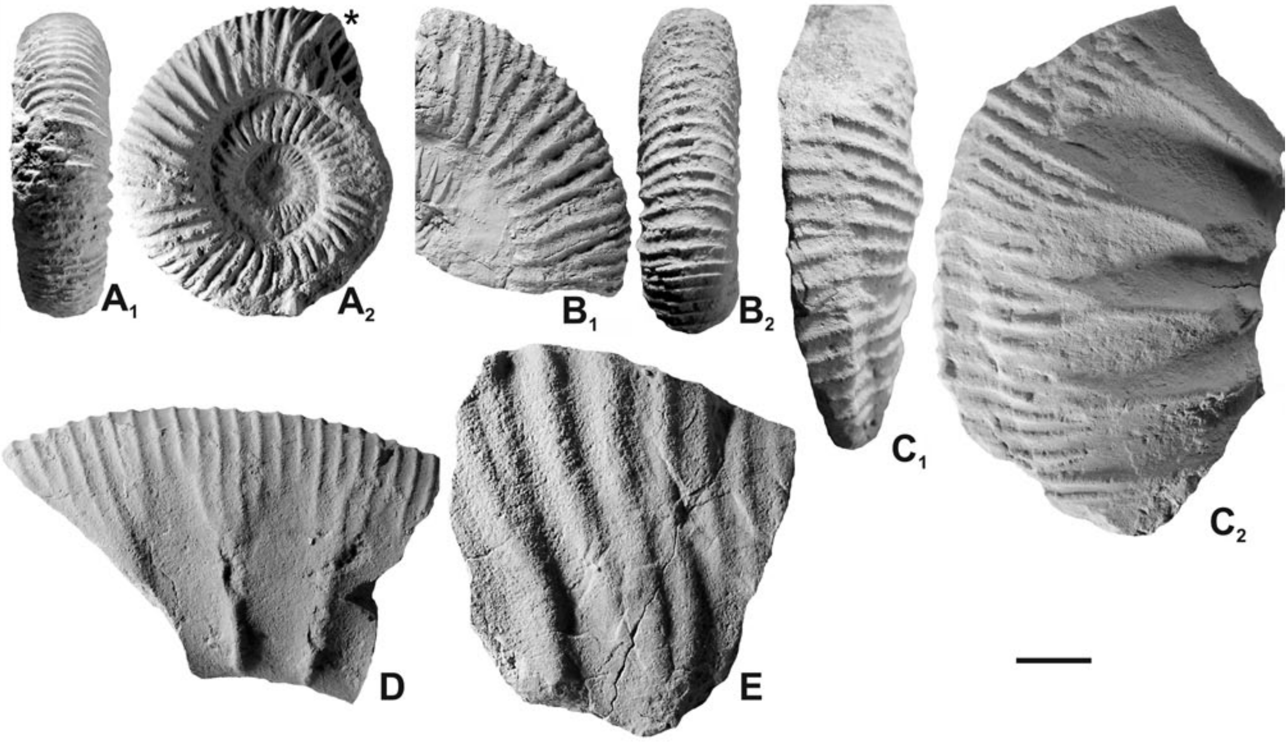


Fig. 31 : *Catutosphinctes* cf./aff. *guenenakenensis* n. sp. **A** : Complete phragmocone with remains of the beginning of the body chamber (MOZPI 7801) ; Picún Leufú, bed PL-7e, Picunleufuense Zone. **B** : Portion of an adult [M] phragmocone with beginning of the body chamber (MOZPI 7804/2) ; Picún Leufú, bed PL-7b, Picunleufuense Zone. **C** : Portion of an adult body chamber (MOZPI 7804/1) ; Picún Leufú, bed PL-7b, Picunleufuense Zone. **D** : Portion of a body chamber ; Picún Leufú, bed PL-7e. **E** : Portion of a body chamber (MOZPI 7804/4) ; Picún Leufú, bed PL-7b.

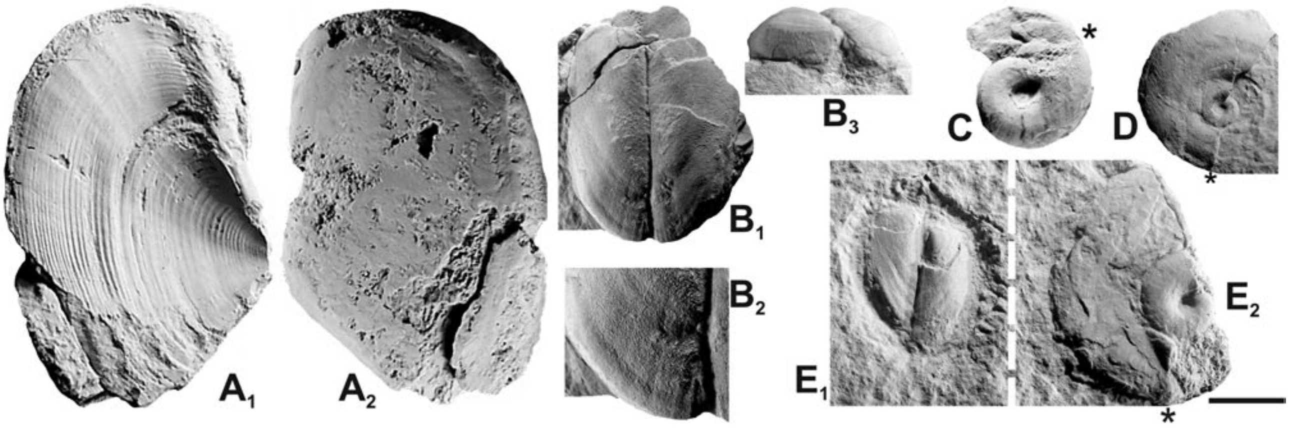


Fig. 32 : **A** : Aspidoceratidae indet. A [Laevaptychus] (MOZPI 7343/1), upper (**A$_1$**) and lower (**A$_2$**) faces of the same valve ; Picún Leufú, bed PL-5, *picunleufuense* α horizon. **B** : Aspidoceratidae indet. B [Laevaptychus] (MOZPI 7778/3), lower face (**B$_1$**), partial view enlarged (x2) showing ornamentation (**B$_2$**), and frontal view (**B$_3$**) ; Picún Leufú, bed PL-9, *perlaevis* horizon. **C** : *Physodoceras* sp. A, juvenile [M] with beginning of the body chamber (MOZPI sn). Picún Leufú, bed PL-9, *perlaevis* horizon. **D, E$_2$** : *Sutneria* sp. A, adult microconchs with almost complete body chamber (MOZPI 7773, 7776). Picún Leufú, bed PL-9, *perlaevis* horizon. **E$_1$** : Pair of haploceratoid mandibles [lamellaptychus] in the same piece of rock (MOZPI 7776).

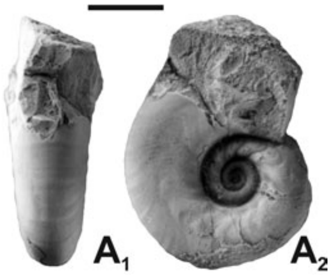


Fig. 33: *Sutneria parabolistriatum* (KRANTZ, 1926). Holotype by monotypy (IPB), adult [m] with incomplete body chamber figured by KRANTZ (1926, transl. 1928: pl. 3: 5); Arroyo Loncoche, unknown horizon within the Tithonian.

a mid-lateral sulcus and weak, wide falcoid ribs on the upper half of the flank. Peristome not preserved. Body chamber about half a whorl long.

Remarks and comparison: Determination in open nomenclature is denoting that, because of the absence of peristome in the described specimens, it remains open the possibility that they could be haploceratoids. However, the close resemblance of the phragmocone with the inner whorls of *Physodoceras* sp. A (Fig. 32C), associated in the same beds, suggests these specimens could likely be microconch aspidoceratids, probably conforming a sexual dimorphic pair with the mentioned juvenile macroconch, which is described below. Our crushed specimens preclude close comparison with described morphospecies of *Sutneria*. They show very similar body chamber with that of *Sutneria asema* (OPPEL, 1865) but this morphospecies has periumbilical lamellar tubercles in the inner whorls (BARTHEL, 1962: pls. 8-11, 17) indicating dimorphic correspondence with a macroconchiate *Physodoceras*; on the other hand the characteristic ventral sculpture composed by chevron-like ribs in *S. asema* can not be observed in the present specimens. *Sutneria parabolistriatum* (KRANTZ) is more evolute and shows periumbilical tubercles in the last whorl of phragmocone not seen in *Sutneria* sp. A.

Very similar specimens have been collected in similar horizons at Cerro Lotena and La Amarga-Cerro Granito. These specimens, complete with lappets and finely preserved, occur associated with *P. zitteli* and *Pasottia andina*. In La Amarga-Cerro Granito, from higher horizons, identical microconchs co-occurr with *Physodoceras* cf. *neoburgense*, and other more inflated microconchiate aspidoceratids with *Sutneria*-like morphology.

Occurrence: Lower part of the Zitteli Zone, *perlaevis* horizon.

Subfamily Aspidoceratinae ZITTEL, 1895

Genus *Physodoceras* HYATT, 1900

Type species: *Ammonites circumspinosus* OPPEL, 1863 (= *Ammonites circumspinosus* QUENSTEDT, 1849); by OD.

Remarks: The genus is relatively abundant in the Tithonian of the NB. There are early records of *Physodoceras neoburgense* (OPPEL, 1863) by STEUER (1897, transl. 1921: pl. 6: 5, under *Aspidoceras cyclotum* OPPEL, 1863) and KRANTZ (1928: pl. 1: 1, as *Aspidoceras* aff. *cyclotum*). Nevertheless, it was later only rarely recorded, e.g. *Physodoceras longaevum* (LEANZA, 1945). The main reason seems to have been misidentification of these featureless ammonites with the superficially similar *Pseudolissoceras* when incomplete specimens are at hand. Another example is the specimen figured by AGUIRRE-URRETA & VENNARI (2009: fig. 5f) under *P. zitteli*. That specimen is an evolute and inflated ammonite with wide, rounded periumbilical swelling-like lamellae as typical in some species of *Physodoceras*.

Physodoceras sp. A
Fig. 32C

Material: A single specimen (MOZPI) from bed PL-9.

Description: The specimen preserves the beginning of the body chamber but it seems to be a juvenile macroconch for uncoiling is not evident. The phragmocone is moderately compressed, involute subglobose with suboval whorl section, inflate flanks and narrow and deep umbilicus. The outer whorl is smooth from $D = 10$ mm. The body chamber which begins at $D = 17$ mm is smooth.

Remarks: Inner whorls of the present specimen are identical to those of *Sutneria* sp. A described above, but the outer whorl and remains of the body chamber are more inflated and do not show the lateral sulcus observed in *Sutneria* sp. A, indicating it is a juvenile macroconch. Comparable specimens of varying sizes have been recently collected in the middle and upper parts of the Zitteli Zone of La Amarga-Cerro Granito and Cerro Lotena (PARENT *et al.*, 2008: 25).

Occurrence: Lower Zitteli Zone, *perlaevis* horizon.

Superfamily Haploceratoidea ZITTEL, 1884
Family Haploceratidae ZITTEL, 1884

Genus *Pseudolissoceras* SPATH, 1925

Type species: *Neumayria zitteli* BURCKHARDT, 1903; SD by ROMAN, 1938.

Pseudolissoceras zitteli (BURCKHARDT, 1903)
Fig. 34A-C

non 1900. *Oppelia* aff. *perlaevis* STEUER.- BURCKHARDT, p. 46, pl. 26: 5-6.

* 1903. *Neumayria zitteli* n. sp.- BURCKHARDT, p. 55, pl. 10: 1-7.

1980. *Pseudolissoceras zitteli* (BURCKHARDT).- LEANZA, p. 17, pl. 1 : 1. [with additional synonymy].

non 1980. *Pseudolissoceras zitteli* (BURCKHARDT).- LEANZA, p. 17, pl. 1 : 2.

2001. *Pseudolissoceras zitteli* (BURCKHARDT).- PARENT, p. 23, fig. 7A-F. [with additional synonymy].

2009. *Pseudolissoceras zitteli* (BURCKHARDT).- AGUIRRE-URRETA & VENNARI, p. 35, fig. 5a-e, g [with complementary synonymy].

non 2009. *Pseudolissoceras zitteli* (BURCKHARDT).- AGUIRRE-URRETA & VENNARI, p. 35, fig. 5f.

non 2009. *Pseudolissoceras zitteli* (BURCKHARDT).- AGUIRRE-URRETA & VENNARI, p. 35, fig. 5h.

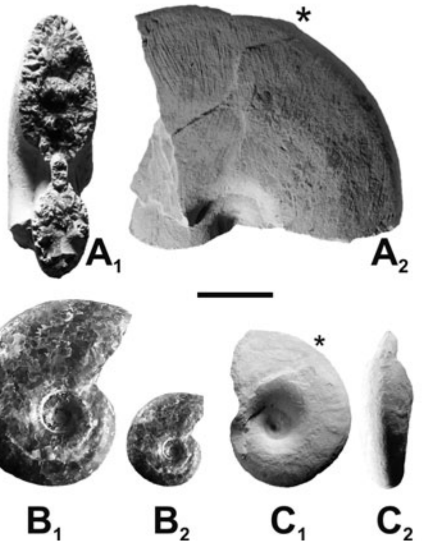


Fig. 34: *Pseudolissoceras zitteli* (BURCKHARDT, 1903). **A**: Adult [M] with beginning of the body chamber (MOZPI 7779). **B**: inner whorls (**B$_1$** enlarged x2) of a larger specimen (MOZPI 7780) showing the abrupt change of whorl section at D = 10 mm becoming much higher than wide. **C**: adult [m] with incomplete body chamber (MOZPI 7781). All specimens from Picún Leufú, bed PL-9, *perlaevis* horizon.

Material: Ten phragmocones, one macroconch with beginning of the body chamber and one adult microconch with incomplete body chamber from beds PL-8 – PL-9.

Description: The specimens available are typical for the species. At sizes smaller than 5 mm in diameter the whorls are smooth and subglobose with rounded flanks and venter. At $5 < D < 10$ mm the shell is smooth, evolute ($U/D = 0.23$, $H_2/H_1 = 0.90$), the whorl section rounded subrectangular, slightly higher than wide ($W/H_1 = 0.87$); the septal suture line shows the characteristic structure, mainly a broad, shallow lateral lobe and with no tertiary crenulation in all their elements (Fig. 34B). From about D = 10 mm the shell is more involute ($U/D = 0.18$, $H_2/H_1 = 0.74$), and the whorl section changes substantially becoming suboval, higher than wide (mean W/H_1 = 0.63); the remaining phragmocone retains this shape up to about the beginning of the body chamber at about D = 55 mm in the available material. The microconch differentiates from the macroconch only by its body chamber which begins at about 18 mm in diameter with a very weak ornamentation consisting of falcoid growth lines but retaining nearly the same whorl section.

Remarks: The genus was recently revised (PARENT, 2001), and so the present species which was found to be clearly sexually dimorphic. In Picún Leufú, as in almost every locality of the NB with middle Tithonian record, the species is abundant and has become one of the most characteristic fossils for the Andean Tithonian since early times of research. Nevertheless, some other ammonites have been misidentified as *P. zitteli* (see PARENT *et al.,* 2008, 2010), all of them more or less featureless forms as *P. zitteli* itself. The stratigraphic range of *P. zitteli* seems to be broader than currently considered, what has implications in biostratigraphy. Indeed, the Zitteli (non-standard) Zone is a derivation of the *Zitteli* (total range-) biozone, which on the other hand is defined by the stratigraphic range of the species (LEANZA, 1981).

The macroconch shown in Fig. 34A is morphologically identical with the lectotype (see PARENT, 2001: fig. 3A-B). The microconch in Fig. 34C is very similar but slightly more narrowly umbilicate than the other one known from the Zitteli Zone of Cañadón de los Alazanes (PARENT, 2001: fig. 7C-D). The inner whorls figured in Fig. 34B show the rather abrupt change in whorl section produced at about D = 10 mm, becoming higher than wide but with a slight decrease of the rate of diameter growth (H_2/D). In this specimen the septal suture line is visible on the flank. This feature is definitely unique and diagnostic for the genus (BARTHEL, 1962), especially for separation from other ammonites in which the macroconchs are homoeomorphic, e.g. *Pasottia andina* PARENT *et al.*, 2007. Separation of *Pseudolissoceras* from compressed aspidoceratids is also possible on the basis of the suture lines.

The specimens figured by BURCKHARDT (1900: pl. 26: 5-6) as *Oppelia* aff. *perlaevis* STEUER are very hardly included in *Pseudolissoceras* for they are very inflated and show a well developed sculpture on flanks – they could likely belong to *Cieneguiticeras*. The specimen figured by LEANZA (1980: pl. 1: 2) as *P. zitteli* is a macroconch phragmocone of *Cieneguiticeras perlaevis* (STEUER, 1897) as shown by the faint lateral ribbing in the upper flank and the narrow umbilicus (see PARENT *et al.*, 2010). The specimen figured by AGUIRRE-URRETA & VENNARI (2009: fig. 5f) was discussed above and assigned to *Physodoceras*. Another specimen figured by these authors (AGUIRRE-URRETA & VENNARI, 2009: 5h) consists of an inflated haploceratid with flattish flanks, wide rounded venter and high umbilical wall, very different from *P. zitteli* but close to *Neolissoceras grasianum* (D'ORBIGNY, 1841) which is currently recorded from the late Tithonian upwards in several regions but for the first time in the NB.

Occurence and distribution: See PARENT (2001).

Family Oppeliidae H. DOUVILLÉ, 1890
Subfamily Taramelliceratinae SPATH, 1928

Genus *Cieneguiticeras* PARENT, MYCZINSKY, SCHERZINGER & SCHWEIGERT, 2010

Type species: *Haploceras falculatum* STEUER, 1897; by OD.

Cieneguiticeras perlaevis (STEUER, 1897) [M&m]
Figs. 35A-G, 36A-D

Material: Three macroconchs (MOZPI 7317, 7762, LPB 819), 6 microconchs and five small portions of phragmocones (MOZPI 7269/6, 7296/0-5, 7319/5, 7482, 7480, 7482) from bed PL-5. A macroconch from bed PL-8 (LPB 859). A macroconch and two microconchs from bed PL-9 (LPB 860).

Description and remarks: The adult macroconch from bed PL-5 (Fig. 35F) preserves the body chamber apparently complete, it is less than a half whorl long, smooth, high oval in whorl section, with plain peristome. The last whorl of phragmocone is very similar with the lectotype (see PARENT *et al.*, 2010: fig. 2A), differing by being more coarsely ribbed on the upper half of flanks but showing the same kind of typical lunuloid primary ribs. The present macroconch, which preserves the aptychi in

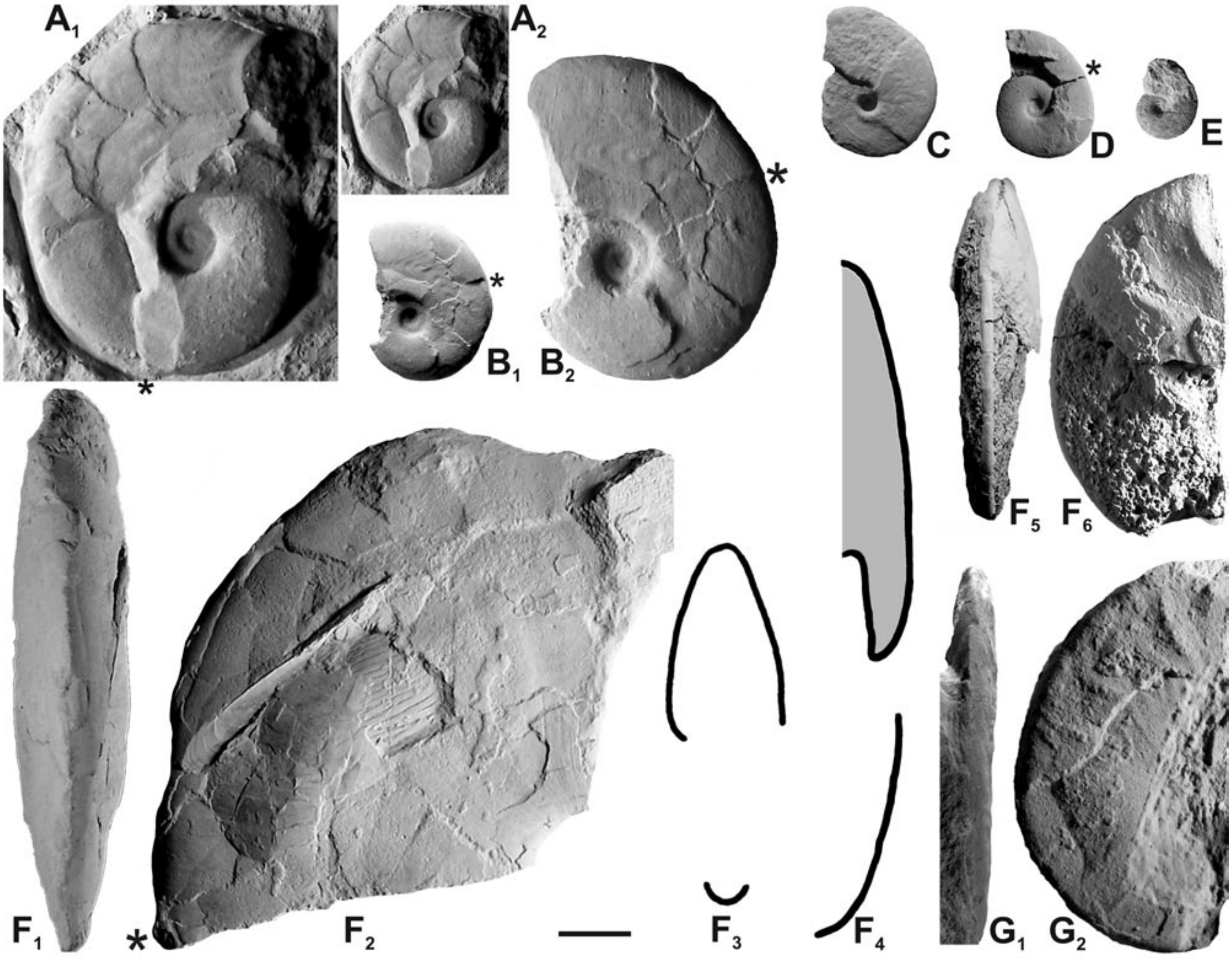


Fig. 35: *Cineguiticeras perlaevis* (STEUER, 1897). **A**: Complete adult [m] with lappets (MOZPI 7480); **A$_1$** enlarged (x2). **B-C**: Adult microconchs with incomplete body chamber (MOZPI 7269/6, 7482); **B$_2$** enlarged (x2). **D**: juvenile [M]? with incomplete body chamber (MOZPI 7296/0). **E**: Inner whorls showing the smooth flanks (MOZPI 7319/5). **F**: Adult [M] (MOZPI 7317) with complete body chamber (**F$_1$**-**F$_2$**) detached from the phragmocone (**F$_5$**-**F$_6$**); **F$_3$**-**F$_4$**: whorl section at different diameters (body chamber shaded); the short body chamber contains the upper and lower mandibles (**F$_2$**). **G**: Crushed last whorl of an adult [M] phragmocone (MOZPI 7762); the ventral view (**G$_1$**) shows the crushed venter given the false appearance of a keel. All from Picún Leufú, bed PL-5, *picunleufuense* α horizon.

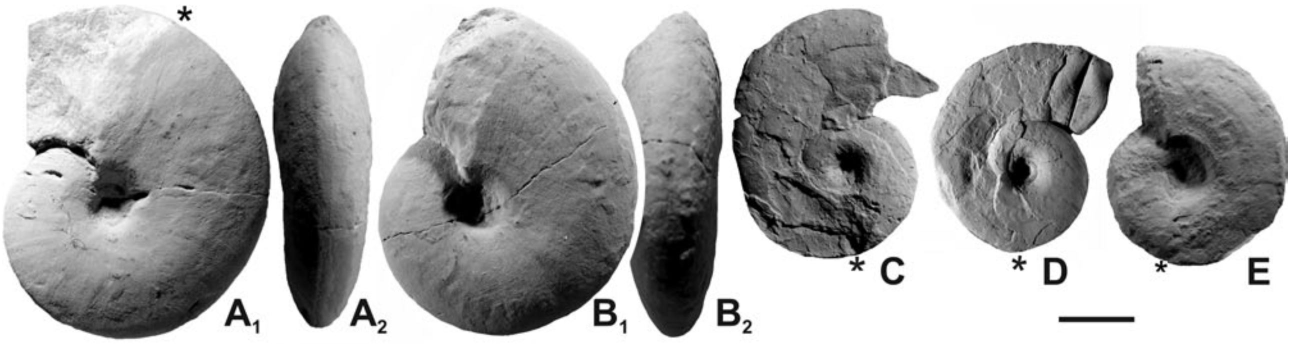


Fig. 36: **A-D**: *Cieneguiticeras perlaevis* (STEUER, 1897). **A-B**: Adult [M] phragmocones with beginning of the body chamber (LPB 859, 860). **C-D**: Complete adult [m] with lappets (**C**, MOZPI 7464) and with the pair of Lamellaptychus mandibles (**D**, MOZPI 7455). **E**: *Pasottia andina* PARENT *et al.*, 2008, adult [m] with almost complete body chamber (LPB 858). All from Picún Leufú, bed PL-9, *perlaevis* horizon, except **B** which comes from bed PL-8.

the form of a Lamellaptychus, is practically identical in size and shape with the paralectotype (see PARENT *et al.*, 2010: fig. 2B) which also preserves the body chamber but crushed. Two microconchs are finely preserved, being identical to the material from A. Cieneguita associated with the lectotype. It can be added that the peristome has narrow lappets projected from the row of lingulate structures, which extend though all the body chamber. The inner whorls are smooth from, at least, $D = 5$ mm.

The macroconchs from beds PL-8 and PL-9 are only phragmocones (Fig. 36A-B). They are somewhat more inflated and narrowly umbilicate, showing the same sculpture and morphology but the ribbing is weaker. The microconchs are almost indistinguishable from those of lower levels, including the lappets of the same shape and in the same position. The only difference is the more widely rounded umbilical shoulder of the specimens from beds PL-8 and PL-9. The microconch shown in Fig. 36D has its pair of aptychi finely preserved close to the peristome, they are of the Lamellaptychus type.

The phragmocone of macroconchs with very weak sculpture, like that of bed PL-8 (Fig. 36B), may be hardly distinguishable from the more inflate variants of *P. zitteli* which frequently occurr associated, nevertheless, this latter is more widely umbilicate and the suture line is very different, much simpler and less frilled, with a shallower and wider lateral lobe.

Occurence and distribution: See PARENT *et al.* (2010).

Genus *Pasottia* PARENT, SCHWEIGERT, SCHERZINGER & ENAY, 2008

Type species: *Pasottia andina* PARENT, SCHWEIGERT, SCHERZINGER & ENAY, 2008; by OD.

Remarks: comparison of *Pasottia* and *Cieneguiticeras* has been discussed in PARENT *et al.* (2010).

Pasottia andina PARENT, SCHWEIGERT, SCHERZINGER & ENAY, 2008
Fig. 36E

Material: Two microconchs (MOZPI 7271/2, LPB 858) form bed PL-9.

Remarks: The available microconchs are adults, identical to the paratype from the lower Zitteli Zone of La Amarga (PARENT *et al.*, 2008: fig. 3F), showing the characteristic sharpening of the umbilical shoulder in the adult body chamber which is strongly uncoiled with a row of mid-lateral linguiform structures.

Occurrence and distribution: This species is widely distributed through the NB in a narrow stratigraphic interval of the Zitteli Zone: La Amarga (TL), Cerro Lotena, Picún Leufú, Pampa Tril and Arroyo Cieneguita.

IV. BIOSTRATIGRAPHY AND TIME-CORRELATION

The chronostratigraphic scale of the Andean Tithonian

Biostratigraphic correlations based on the current chronostratigraphic scale of the Andean Tithonian (reviewed by LEANZA, 1981) is rather straight when few or isolated ammonites are at hand. Under the current usage the occurrence of *P. zitteli* or *Windhauseniceras internispinosum* is considered as indicating the Zitteli or Internispinosum zones respectively; the occurrence of perisphinctid ammonites below beds with *P. zitteli* is considered as indicative of the Mendozanus Zone; and the Proximus Zone is assumed as represented by beds overlying the occurrence of *P. zitteli* and/or underlying the occurrence of *W. internispinosum*. Each zone could be recognized by the occurrence of the guide or the index species as proposed by LEANZA (1981). In summary, the biostratigraphical chronostratigraphy of the Andean lower and middle Tithonian is based on the total range biozones of the apparently distinctive species *P. zitteli* and *W. internispinosum*.

Nevertheless, when samples in succession are considered the basic scheme may usually remain valid but the boundaries between the zones can not be recognized objectively. Indeed, the overlapping of the vertical ranges of the index-guide species avoids the application of the mentioned criteria of total range biozones. This is because each ammonite morphospecies has, by definition, a potentially different stratigraphic range in every locality, producing gaps and overlaps in the non-standard zonal chronostratigraphy based on total range biozones.

The stratigraphic position of the type material of *Choicensisphinctes mendozanus* is crucial for the biostratigraphic classification of the Andean Tithonian because it is the index species of the Mendozanus Zone, and the nominal species which conform the M17-assemblage have been used as the guide assemblage for recognition of the zone (LEANZA, 1980). Much new material has been collected in last years from several localities of the NB: Cerro Lotena, La Amarga, Portada Covunco, Mallín Quemado, Cañadón de los Alazanes, Pampa Tril, Vega de la Veranada, Arroyo Cieneguita and Casa Pincheira among others. Description of the large amount of material now available has been partially done (PARENT, 2001, 2003; PARENT *et al.*, 2006, 2008, 2010) and will take some time to be finished. However, some pertinent consistent observations are worth to discuss herein. The first is that ammonites comparable, even identical, to those of the M17-assemblage have been found to occur associated with *Pseudolissoceras zitteli* (BURCKHARDT) in most of the sampled localities mentioned. Their stratigraphic position is always above the early Tithonian Fauna A of PARENT *et al.* (2006), and ranging from the Fauna B up to the uppermost occurrences of *P. zitteli* in the level-3 of the uppermost part of the Zitteli Zone in La Amarga (PARENT *et al.*, 2008). This level of La Amarga and Cerro Lotena is approximately equivalent, in biostratigraphic terms, with the beds PL-11 to PL-12 (Figs. 3, 37) which have yielded representatives of *C. erinoides* and *C. australis* closely matching the type specimens (descriptions above) and overlying the beds PL-8 – PL-9 where a local acme of *P. zitteli* is recorded – above beds yielding ammonites of the Fauna B. The occurrence of *P. zitteli* with ammonites of the M-17 assemblage in south-central Neuquén was already described by WEAVER (1931: 47).

The current scheme is deeply entrenched in the literature and despite of these drawbacks it has been used practically throughout all the NB (e.g. LEANZA & HUGO, 1977). However, considering the problems cited above many of the published correlations might be revised.

Biostratigraphy of the studied section

The biostratigraphy and the derived chronostratigraphy of the succession at Picún Leufú based on the present study is interpreted as follows (Fig. 37):

- Beds PL-1 – PL-4 have not yielded ammonites.
- Beds PL-5 – PL-7e yielded assemblages of ammonites belonging to the Fauna A of PARENT *et al.* (2006), also recognized in other localities. These beds lay just below the occurrence of a fragmentary specimen of *Choicensisphinctes windhauseni* in bed PL-7f, below the first local occurrence of *P. zitteli*. *Ch. windhauseni* is a conspicuous ammonite abundant with both sexual dimorphs in the assemblage of the Fauna B in La Amarga where the assemblage already includes the first *P. zitteli* indicating the Zitteli Zone sensu LEANZA (1981), which is based on a total range *Zitteli* biozone. The Fauna A was originally attributed to the Mendozanus Zone (sensu LEANZA 1981) by laying below the first occurrence of *P. zitteli*. Nevertheless, the type material of the index *C. mendozanus* is associated in the type locality with other species of *Choicensisphinctes* (BURCKHARDT, 1900) forming the M17-assemblage, which can be considered the guide assemblage of the Mendozanus Zone. In Picún Leufú *C. australis* and *C. erinoides* (which are also part of the M17-assemblage) occur above the first occurences of *P. zitteli* showing that the Mendozanus and Zitteli (non-standard) zones overlap enough as to appear inverted, depending on the sampling and the locality. Therefore, the Fauna A can be separated from the Mendozanus Zone as an underlying assemblage.
- Beds PL-8 - PL-9 can be attributed to the Zitteli Zone by the occurrence of the index-guide species.
- Beds PL-10 - PL-12 contain almost exclusively species of *Choicensisphinctes* which characterize the M17-assemblage of BURCKHARDT (1900) so that nominally it should be Mendozanus Zone. However, as discussed above this inversion needs more investigation. Beds 10-12 are therefore included in the Zitteli Zone. As noted above in La Amarga, Cerro Lotena, Pampa Tril and Arroyo Cieneguita ammonites of the M17-assemblage (including specimens identical with the LT of *C. mendozanus*) co-occur with undoubted *P. zitteli*.
- Beds PL-13 - PL-14 are assigned nominally to the Proximus Zone for they lay above beds with *P. zitteli* (Zitteli Zone) and have yielded scarce crushed specimens of *Catutosphinctes*, but there is no direct evidence.
- Beds PL-15 - PL-60 have not yielded ammonites. However, LEANZA & HUGO (1997) have cited from a similar stratigraphic position the occurrence of *Catutosphinctes proximus* and Laevaptychus which suggest the Proximus to Internispinosum zones. The overlying beds have not been yet studied. They belong to the Picún Leufú Fm. from which LEANZA

(1973) and LEANZA & HUGO (1997) have cited the occurrence of *Corongoceras lotenoense* SPATH, 1925, *Catutosphinctes araucanense*, "*Berriasella*" sp. and *Substeueroceras* sp. suggesting the Internispinosum up to the Koeneni zones of the middle and upper Tithonian.

In the studied section the beds yielding ammonites of Fauna A span almost 8 m thickness, but in other close sections the thickness is singnificantly smaller (PARENT *et al.*, 2006). The Fauna A was proposed for seven levels with ammonites in the studied section (beds PL-5 – PL-7e of Fig. 3), and after the present description of these ammonites it can be subdivided in at least three bio-horizons (Fig. 37), from below:

1. *picunleufuense* α horizon, the older , represented by bed PL-5, characterized by "*L.* " *picunleufuense* n. sp. transient α, *C. platyconus* n.sp., *C. guenenakenensis* n. sp. and *L. perlaevis*. The value for time-correlation of this horizon is very high as was indicated formerly for it can be easily recognized in several localities from the southern (Cerro Lotena, La Amarga) to the northern (Pampa Tril, Vega Veranada, Arroyo Cieneguita) sectors of the NB (Fig. 38). The *picunleufuense* α hz. lies somewhere in the interval late Beckeri-Hybonotum

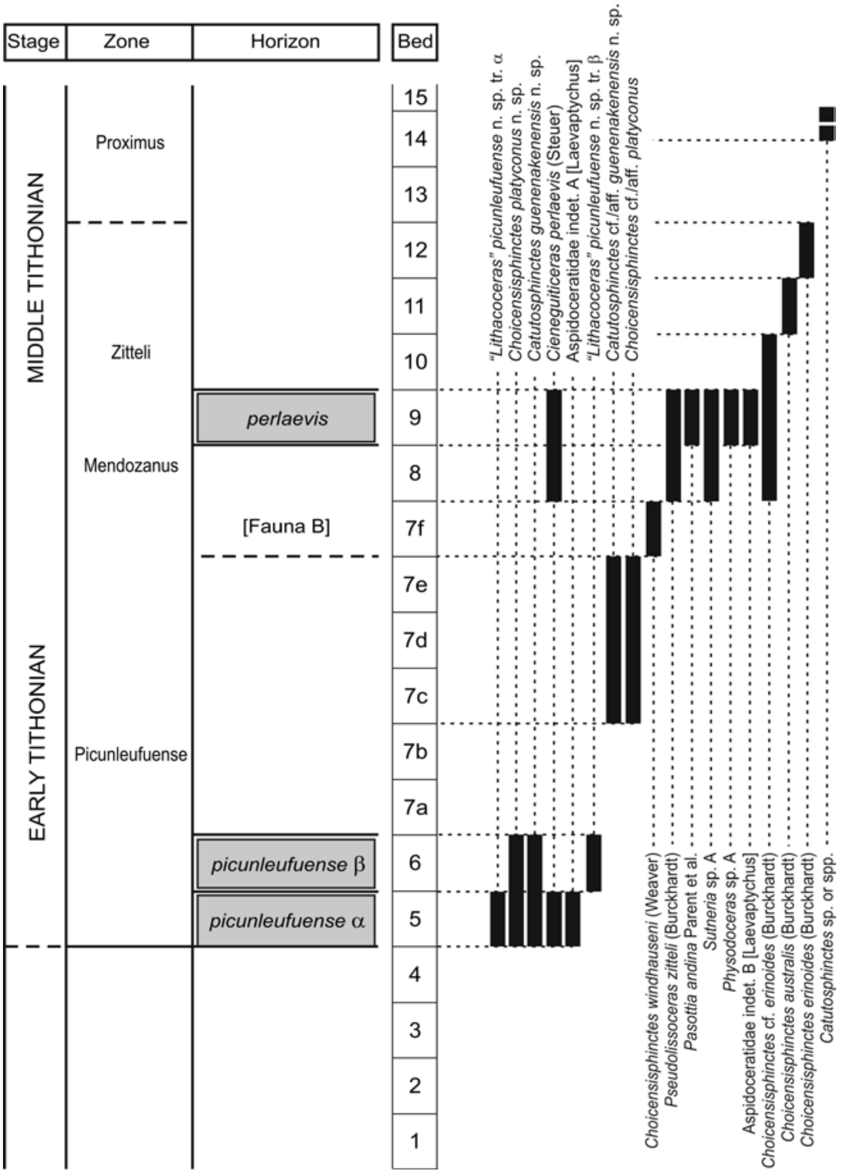


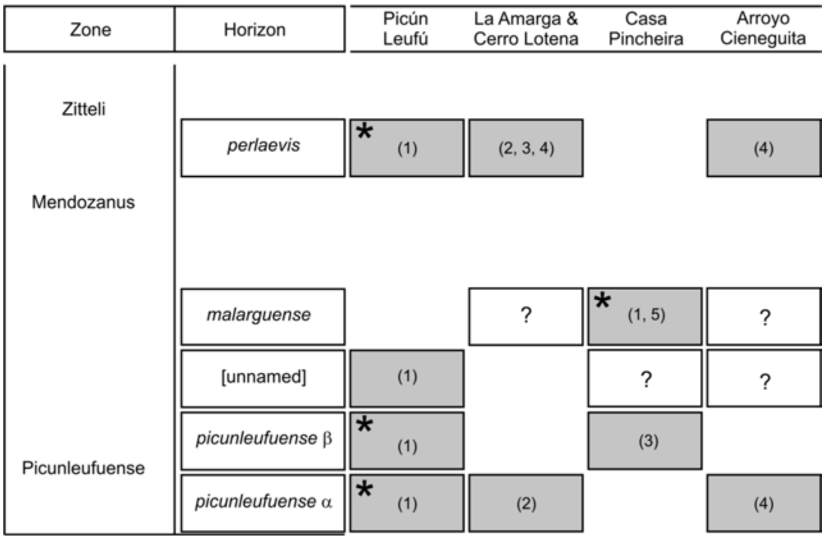
Fig. 37: Biostratigraphy and chronostratigraphic zonation of the section of Picún Leufú. Broken lines indicate a tentative correlation or non-standardized boundaries. Chronostratigraphy is based on LEANZA (1981) and PARENT *et al.* (2007). The Picunleufuense (standard chronostratigraphic) Zone and the *picunleufuense* α, *picunleufuense* β and *perlaevis* horizons are units introduced in this report as explained in text. Fauna B is an ammonite assemblage defined in PARENT *et al.* (2006). Height of the subdivisions is drawn on a scale of equispaced beds with neither implications on time duration nor bed thickness.

zones of the European chronostratigraphic scale as indicated by "*L.*" *picunleufuense* n. sp. (discussion above).

2. the *picunleufuense* β horizon, represented in the present section by the bed PL-6 and characterized by "*L.*" *picunleufuense* n. sp. transient β, *C. platyconus* n. sp. and *C. guenenakenensis* n. sp. The representatives of *C. platyconus* n. sp. and *C. guenenakenensis* n. sp. of this upper horizon show slight but consistent morphological differences respect to those of the older horizon (see descriptions above). Material under study indicates that this horizon could be represented in Pampa Tril, Arroyo Cieneguita and Casa Pincheira (Fig. 38).
3. The beds PL-7c – PL-7e yield a fauna of *Choicensisphinctes* cf./aff. *platyconus* n. sp. and *Catutosphinctes* cf./aff. *guenenakenensis* n. sp., moderately distinctive but poorly represented in our samples for characterization of an additional ammonite horizon. Much better material of these ammonites occur at Portada Covunco, Arroyo Cieneguita and Casa Pincheira.

We introduce herein the Picunleufuense (standard chronostratigraphic) Zone defined by its base at the *picunleufuense* α hz. Type locality and section: Picún Leufú, beds PL-5 – PL-7e (Fig. 37). Characteristic ammonite assemblage: "*L.*" *picunleufuense* n. sp., *C. platyconus* n. sp., *C.* cf./aff. *platyconus* n. sp., *C. guenenakenensis* n. sp., *C.* cf./aff. *guenenakenensis* n. sp. and *C. perlaevis* (STEUER, 1897); accessory elements are indeterminate aspidoceratids (Laevaptychus), the gastropods *Exelissa*? *arcuatoconcava* GRÜNDEL & PARENT, 2001 and *Dicroloma*? sp. in GRÜNDEL & PARENT (2001) and bivalves not yet studied but identificable with species described by WEAVER (1931). The ammonites of the informal Fauna A are nearly the characteristic assemblage of the Picunleufuense standard Zone. The upper part of the Picunleufuense Zone could be partially correlated with the horizon of "*Virgatosphinctes pseudolictor*" of GROEBER [1946; note that in this paper GROEBER cited *Virgatosphinctes pseudolictor* (CHOFFAT) as *Virgatosphinctes pseudolictor* BURCKHARDT]. This "horizon" was later considered as a zone by LEANZA (1973) but after this paper the Pseudolictor Zone was never used again in published papers. GROEBER (1929: 34, 1933: 21) pointed out that the basal beds of the Andean Tithonian are characterized by the occurrence of "*Perisphinctes pseudolictor*" (= *Subplanites malarguensis* SPATH, 1931), which is followed upwards by similar ammonites (GROEBER, 1952: 353). Nevertheless, as discussed above, "*L.*" *malarguense* belongs to a younger assemblage and GROEBER had never the opportunity to illustrate his material. The relative position of the Picunleufuense Zone, as defined in Picún Leufú and consistently in several other localities as discussed above, is definitely below the beds with *P. zitteli* and the M17-assemblage which characterizes the Mendozanus Zone in the classic subdivision.

The beds of the Casa Pincheira section (BURCKHARDT, 1900; PARENT, 2003) yielding the ammonites of the M6-assemblage discussed above are considered as a horizon, herein named *malarguense* horizon, situated above the



Zone	Horizon	Picún Leufú	La Amarga & Cerro Lotena	Casa Pincheira	Arroyo Cieneguita
Zitteli					
	perlaevis	▨ * (1)	▨ (2, 3, 4)		▨ (4)
Mendozanus					
	malarguense		?	▨ * (1, 5)	?
	[unnamed]	▨ (1)		?	?
	picunleufuense β	▨ * (1)		▨ (3)	
Picunleufuense	*picunleufuense* α	▨ * (1)	▨ (2)		▨ (4)

Fig. 38: The ammonite-horizons (bio-horizons) recognized in sections of selected localities with record of the lower Vaca Muerta Fm. in the Neuquén Basin. The horizons are labelled at left and where recognized they are shaded. The asterisk indicates the locality where the horizon is defined. Based on information as indicated by the numbers between brackets as discussed in text: (1) present paper, (2) PARENT *et al.* (2008), (3) PARENT (2003a), (4) PARENT *et al.* (2009), (5) BURCKHARDT (1900, 1903), GROEBER (1946). The *picunleufuense* α hz. is the base of the Picunleufuense Standard Chronostratigraphic Zone of the Andean Tithonian. The *perlaevis* hz. lies in some part of the Zitteli (non-standard) Zone.

picunleufuense β horizon and the yet unnamed horizon of beds PL-7a – PL-7e (see Fig. 38). Out of its type locality, the horizon could be represented in Arroyo Cieneguita, according with our sampling in this locality.

The Fauna B is only tentatively recognized in Picun Leufu by the occurrence of *Ch. windhauseni*, the first *P. zitteli* and *Cieneguiticeras perlaevis* (STEUER, 1897) in beds PL-7f - PL-8.

The assemblage of bed PL-9 is distinctive enough as to justifiy the introduction of the *perlaevis* horizon, named after *Cieneguiticeras perlaevis*. The characteristic assemblage includes, out of the name-bearing species: *P. zitteli* (abundant), *Pasottia andina*, *C.* cf. *erinoides*, *Physodoceras* sp. A and *Sutneria* sp. A; also occurs a macroconchiate aspidoceratid only known by its mandibles (Laevaptychus). *P. andina* is a distinctive ammonite recorded in other localities confined to a single horizon and associated with the same ammonites (see PARENT *et al.*, 2008). This biohorizon can be recognized by its ammonite assemblage in other localites (Fig. 38): La Amarga, Cerro Lotena, Pampa Tril and Arroyo Cieneguita.

GROEBER (1952: 388-389) provided a short description of the section of Picún Leufú and of the ammonite occurrences. He described a basal conglomerate (Quebrada del Sapo Fm.) underlying the following succession of beds, from below: (1) about one meter of sandy shales with crushed “*Virgatosphinctes*”, (2) few meters of bluish shales with *Perisphinctes* cf. *erinus*, (3) few meters of sandy shales with fish scales, (3) 50-60 m of shaly marls, (4) 65 m of shales, (5) a bank of one meter of sandstone, and (6) more than 100 m of limestones with bivalves and gastropods in the upper part. This succession is in accord with our observations although the thickness of the beds seems to differ. The lowermost bed (1) with crushed “*Virgatosphinctes*” should be equivalent with bed PL-5; the overlying beds (2) should be equivalent with beds PL-6 – PL-12 which bear, among other ammonites, *C. erinoides*; the sandy shales with fish scales (3) and (4) should be equivalente with beds PL-13 – PL-38, and the calcareous upper part of the section.

WEAVER (1931: 46-47) recognized within the Tithonian three “faunal zones” represented in his section of Picún Leufú and, in general, all throughout the NB: (1) the Lower Tithonian “Zone of *Virgatosphinctes mendozanus* BURCKHARDT”, (2) the middle Tithonian “Zone of *Haploceras (Pseudolissoceras) zitteli* BURCKHARDT”, and (3) the Upper Tithonian “Zone of *Perisphinctes internispinosum* KRANTZ”. These faunal zones consist of biozones of assemblages of the local horizons recorded at every of the localities he studied in Neuquén and souther Mendoza. WEAVER (1931: 47) indicated that the lowermost ammonite horizon consists of about 0.03 m of sandstone and shales with abundant specimens of “*Virgatosphinctes*”. Although he did not give any indication of the species to which they should belong to, it is evident that they correspond to the base of the Picunleufuense Zone herein described from bed PL-5.

LEANZA (1973) has provided a list of ammonites occurring at Picún Leufú, later expanded in LEANZA & HUGO (1977, 1997). The most complete of those lists is in LEANZA & HUGO (1977: 253) which includes eight levels with ammonites. Since there are no illustrations of the ammonites in those papers, it is impossible to make significant comparisons. In nominal terms the listing fits the usual succession and it seems that there is a close correspondence with the succession described in the present report. The cited “*Pavlovia* sp. indet. vel *Subdichotomoceras* sp. indet.” (LEANZA, 1973) most likely belong to *Catutosphinctes*.

V. CONCLUSION

The Tithonian rocks of the studied section of Picún Leufú belong to the Vaca Muerta Fm. (spanning about 362 m) and the base of the Picún Leufú Fm. There were recognized seven different lithofacies which represent at least five different episodes of sedimentation. The studied fauna indicates that the local stratigraphic age of the Vaca Muerta Fm. spans from the earliest Tithonian Picunleufuense Zone up to the middle Tithonian Internispinosum Zone.

The Tithonian perisphinctid fauna of Picún Leufú is composed by genera of the Ataxioceratidae: “*Lithacoceras*” and *Choicensisphinctes* of the subfamily Lithacoceratinae and *Catutosphinctes* of the Torquatisphinctinae. The ammonites assigned to these genera are the bulk of the perisphinctid fauna of the NB, and most of them have been described until recently as isolated species of several different genera, e.g. *Virgatosphinctes*, *Aulacosphinctoides*, *Pseudinvoluticeras*, *Aulacosphinctes*, *Subdichotomoceras, Parapallasiceras, Torquatisphinctes, Pachysphinctes* or *Katroliceras*. *Choicensisphinctes* and *Catutosphinctes* are two genera well represented throughout the NB which suggests biogeographic relationships with the Indo-Madagascan Province and with the Tethys.

The genus *Catutosphinctes* has a long record all throughout the Tithonian of the NB from the Picunleufuense Zone with *C. guenenakenensis* n. sp. up to latest Tithonian in Sierra Azul (Arroyo del Yeso - Mallín Redondo), Pampa Tril, and Arroyo Cieneguita. It seems to be an endemic lineage likely derived from latest Kimmeridgian *Katroliceras* of the Indo-Madagascan area and Eastern Africa. Intermediate forms are probably represented in the southern part of South America and in Antarctica.

The genus *Choicensisphinctes* has been recorded from the Picunleufuense Zone with *C. platyconus* n. sp. up to the upper Proximus or lower Internispinosum Zone in Cerro Lotena. It seems to be an endemic lineage derived from Tethyan lithacoceratids very close to “*Lithacoceras*” *picunleufuense* n. sp.

The Picunleufuense Standard Zone is introduced for the lowermost Tithonian (or uppermost Kimmeridgian), defined by its base at the *picunleufuense* α horizon which on other hand defines the standard base of the Andean Tithonian. The *picunleufuense* β and *malarguense* horizons (lower Tithonian) and the *perlaevis* hz. (Zitteli Zone) are also introduced herein.

It is envisaged the development of a fine ammonite horizon-based standard chronostratigraphy based on the successive associations dominated by the representatives of the evolving lineages *Choicensisphinctes* and *Catutosphinctes*, and the accessory elements of the Oppeliidae and Aspidoceratidae all throughout the NB. The results of the first step in this direction are illustrated in Fig. 38.

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Appendix 1: Dimensions of selected and type specimens. Abbreviations: ad (adult), juv (juvenil) or with no mark indicating portion of an incomplete shell. Other symbols and abbreviations as explained in text. The column Bc/Ph indicates the portion of the shell to which corresponds the measurement: Bc (bodychamber), Ph (phragmocone) or Ph-Bc (last septum). Where the length of the bodychamber is indicated, the corresponding *D* was measured at peristome (^{e}).

	Dimorph	**Ph/Bc**	***D*** [mm]	***U/D***	***W/D***	H_1/D	H_2/D	***P***	***V***	L_{BC} [°]
***«Lithacoceras» picunleufuense* n. sp. transient α**										
LPB 1098 [HT]	[M] ad	Bc	137.00	0.44		0.35		13	78	360(^{e})
		Ph-Bc	112.00	0.43		0.31		16	74	
		Ph	66.00	0.43				22		
		Ph	40.00	0.45				18		
		Ph	10.00	0.40				12		
		Ph	7.00	0.40				10		
MOZPI 7281	[M] ad	Bc	156.00	0.44		0.31	0.22	13		
		Ph-Bc	122.00	0.42				19		
		Ph	95.00	0.40				24		
		Ph	45.00	0.38				21		
S/N	[M] ad	Bc	128.00	0.45				17	69	
MOZPI 7799	[M] ad	Bc	132.00					16		
LPB 622	[M] ad	Ph	44.00	0.36		0.36		21		
		Ph	35.00	0.31				21		
		Ph	23.00	0.35				22		
MOZPI 6459	[M] ad	Bc	99.00	0.45				14		
		Bc	80.00	0.41				23		
		Ph	62.00	0.37				29		

	Dimorph	**Ph/Bc**	D [mm]	U/D	W/D	H_1/D	H_2/D	P	V	L_{BC} [°]
		Ph	45.00	0.40				22		
		Ph	30.00	0.40				19		
MOZPI 7305	[m] ad	Bc	52.00	0.40		0.38	0.30	23	47	180
		Bc	43.00	0.38	0.24	0.39		22		
		Ph-Bc	31.00							
MOZPI 7319/4	[m] ad	Bc	44.00	0.39		0.36		22		270
		Bc	35.00	0.37				20		
		Ph-Bc	28.00							
MOZPI 7473	[m] ad	Bc	68.00	0.46		0.29		20	49	240
		Bc	52.00	0.42		0.31		19		
		Ph	38.00	0.39				17		
S/N	[m] ad	Bc	46.00	0.41				20		270
	[m] ad	Ph-Bc	35.00	0.40				19		
MOZPI 7269/9	[m] ad	Bc	40.00					19		
		Bc	30.00					20		
MOZPI 7479	[m] ad	Bc	53.00	0.45		0.32	0.28	18	42	180
		Bc	47.00	0.37		0.37		18		
		Ph-Bc	37.00							
MOZPI 7772	[m] ad	Bc	54.00	0.51				21	41	240
		Ph	30.00	0.37				19		
		Ph	9.00	0.44				15		
		Ph	7.00	0.43				14		
***«Lithacoceras» picunleufuense* n. sp. transient β**										
MOZPI 7760	[M] ad	Bc	125.00	0.46	0.29			14	59	
		Ph	95.00	0.47				18	65	
MOZPI 7817	[M] ad	Bc	99.00	0.45				19	61	
LPB 836	[M] ad	Bc	144.00	0.47	0.22	0.29		20	68	
		Ph-Bc	132.00	0.46	0.19	0.29		22	65	
MOZPI 7464	[M] ad	Bc	158.00	0.45		0.32		20		
***Choicensisphinctes platyconus* n. sp.**										
MOZPI 6431 [HT]	[M] ad	Bc	125.00	0.35		0.38	0.27	9		
		Ph-Bc	93.00	0.31	0.31	0.33				
		Ph	70.00	0.26				20		
		Ph	20.00	0.50				25		
		Ph	13.00	0.48				13		
		Ph	7.00					9		
LPB 1099	[M]	Bc	82.00	0.36		0.38	0.26	19	62	
		Ph	64.00	0.34				23		
		Ph	50.00	0.44				30		
		Ph	30.00	0.33				27		
		Ph	14.00	0.36				22		
		Ph	8.00	0.32				16		
LPB 1100	[M]	Ph	56.00	0.34		0.41		33		
MOZPI 7797	[m] ad	Bc	110.00	0.35		0.30		12	48	210
		Ph	78.00	0.32				19	62	
MOZPI 6395	[M]	Ph	53.00	0.26		0.40		31	73	
MOZPI 7507	[M] ad	Bc	105.00	0.36		0.38		18	64	
		Ph-Bc	80.00	0.38				28	68	
MOZPI 7318/3	[M]	Ph-Bc	84.00	0.36	0.27	0.36	0.19	19		
		Ph	62.00	0.35	0.29	0.37		26		
		Ph	33.00					28		

	Dimorph	**Ph/Bc**	***D*** **[mm]**	***U/D***	***W/D***	**H_1/D**	**H_2/D**	***P***	***V***	**L_{BC} [°]**
MOZPI 7474	[m] ad	Bc	75.00	0.33				23	77	220
LPB 1095	[M] ad	Ph-Bc	64.00	0.30	0.41	0.38		25	110	
MOZPI 7354	[M] ad	Ph-Bc	45.00	0.30				36		
		Ph	34.00	0.30				28		
		Ph	12.00	0.33				18		
		Ph	6.00	0.35				16		
LPB 1097	[M] ad	Bc	125.00					12	83	
LPB 1094	[M] ad	Bc	86.00	0.40	0.23			20	110	
		Ph-Bc	61.00	0.34				39		
		Ph	9.00					22		
MOZPI 7762	[M] ad	Bc	122.00	0.36				16		
		Ph-Bc	80.00							
		Ph	70.00	0.30	0.39			37		
MOZPI 7532	[M] juv	Ph	35.00	0.23	0.30	0.46	0.30	29	72	
		Ph	16.00					19		
		Ph	5.40					12		
LPB 1101	[M] juv	Ph	48.00	0.31		0.38		31		
		Ph	19.00	0.34				28		
MOZPI 6397	[M] ad	Bc	100.00	0.39	0.30	0.36	0.22	14	44	
		Ph-Bc	80.00	0.36						
		Ph	38.00	0.37				25		
MOZPI 7469	[M] ad	Bc	97.00	0.42	0.29	0.31		22	50	280
		Ph-Bc	65.00							
		Ph	15.00					16		
	[m] ad	Bc	81.00	0.43	0.25	0.31		19	51	
		Ph-Bc	57.00							
		Ph	45.00	0.33				21		
		Ph	20.00	0.30				25		
Choicensisphinctes densistriatus **(Steuer, 1897)**										
MGAU 499-50 [HT]		Ph	73.00	0.40	0.41	0.36	0.25	26		
Choicensisphinctes mendozanus **(Burckhardt, 1911)**										
Lectotype	ad	Bc	84.00	0.42		0.33	0.29	13	45	
		Ph	65.00	0.37		0.32		21	53	
Paralectotype	ad	Bc	79.00	0.43		0.30	0.28	17	50	
Choicensisphinctes windhauseni **(Weaver, 1931)**										
BMS 346 [LT]	[M] ad	Ph	83.00	0.23	0.22	0.43	0.28			
BMS 345	[M] ad	Bc ?	66.00	0.21		0.47				
Choicensisphinctes lotenoensis **(Weaver, 1931)**										
BMS 343 [HT]		Ph	67.00	0.25		0.48	0.27	17	91	
Choicensisphinctes erinoides **(Burckhardt, 1903)**										
MOZPI 7806	[M] ad	Ph	188.00	0.26		0.43		7	90(^{e})	
Choicensisphinctes **cf.** ***mendozanus*** **(Burckhardt, 1911)**										
MOZPI 7440	[M] ad	Bc	112.00	0.45	0.34	0.33	0.25	20	60	180
Catutosphinctes guenenakenensis **n. sp.**										
MOZPI 7768 [HT]	[M] ad	Bc	158.00	0.47		0.32	0.29			

	Dimorph	**Ph/Bc**	***D*** [mm]	***U/D***	***W/D***	H_1/D	H_2/D	***P***	***V***	L_{BC} [°]
		Ph-Bc	115.00	0.50		0.27		11	48	
		Ph	92.00	0.46				19		
S/N	[M] juv	Ph	68.00	0.43		0.34	0.29	19	40	
		Ph	35.00					18		
		Ph	22.00					14		
MOZPI 7471	[m] ad	Bc	43.50	0.43		0.30	0.25	18		100
		Ph	22.00					17		
		Ph	14.00	0.43				14		
		Ph	5.00					9		
S/N	[M] ad	Ph	56.00	0.45		0.29		16	36	
		Ph	28.00					14		
		Ph	13.00					13		
S/N	[M] ad	Ph-Bc	70.00	0.41		0.31		20		
MOZPI 7487	[m] ad	Bc	65.00	0.42	0.25	0.31		17	39	
LPB 1103	[m] ad	Bc	66.00	0.41		0.29		17	44	
LPB 1104	[m] ad	Bc	41.00	0.44		0.34		19	38	
MOZPI 7764	[M] ad	Bc	92.00	0.42		0.35		15	45	
		Ph-Bc	75.00							
		Ph	65.00	0.42		0.34		19		
		Ph	19.00	0.46				13		
		Ph	10.00	0.45				12		
		Ph	6.00					10		
Catutosphinctes windhauseni **(Weaver, 1931)**										
BMS 323 [HT]		Ph	54.00	0.50	0.30	0.32	0.28	12	23	
Catutosphinctes proximus **(Steuer, 1897)**										
MGAU 499-31		Ph	35.00	0.40	0.26	0.26	0.23	12	22	
Reineckeia fraudans **(Steuer, 1897)**										
MGAU 499-33 [HT]	[M]? ad?	Bc	118.00	0.42	0.27	0.33	0.30	26	48	
Pseudolissoceras zitteli **(Burckhardt, 1903)**										
MOZPI 7779	[M] ad	Ph	36.20	0.15	0.30	0.52	0.40			
		Ph	21.80	0.20	0.34	0.52	0.39			
		Ph	13.50	0.18	0.31	0.52	0.37			
		Ph	7.50	0.23	0.45	0.52	0.47			
MOZPI 7780	[M]	Ph	12.20	0.20	0.38	0.51	0.39			
MOZPI 7781	[m] ad	Ph	20.40	0.19	0.32	0.48	0.35			
		Ph	12.90	0.19	0.38	0.47				