The Tithonian ammonite fauna of the transect Cerro Lotena-Cerro Granito, Vaca Muerta Formation, Argentina. I. Family Himalayitidae

Horacio Parent & Alberto C. Garrido

Abstract. The stratigraphy and palaeontology of the outcrops of the Vaca Muerta Formation along the transect between the hills Cerro Lotena and Cerro Granito were surveyed in detail by the authors during several years. The first part of the results of this study is presented in this paper, consisting of the description of the ammonites of the family Himalayitidae Spath. The family is well represented in the study area in the interval upper Proximus-lower Alternans ammonite zones by the genera *Windhauseniceras* Leanza (monotypic), *Corongoceras* Spath and *Steueria* Parent, Scherzinger & Schweigert. *Windhauseniceras internispinosum* (Krantz) is recorded as five transients, showing gradual phyletic changes and shiftings of the spectrum of variation, from stout serpenticonic to compressed suboxyconic morphotypes. Hybridization between early *W. internispinosum* and *Catutosphinctes proximus* (Steuer), from which the former originates, is proposed as explanation for the occurrence of persistent intermediate morphotypes and rare specimens of difficult interpretation. The type species of *Corongoceras* (*C. lotenoense* Spath) is for first time described from adult topotypes. The new species *Corongoceras huarpense* is introduced for the representatives of the genus of the lower Internispinosum Zone. The genus would have originated from *C. proximus* through *C.* aff. *huarpense* of the uppermost Proximus Zone. The genus *Steueria* is poorly represented by *S.* cf. *alternans* (Gerth) in the studied sections, but significant enough for dating the lower levels of the Alternans Zone as it occurs just above the latest occurrences of *W. internispinosum*. The complete successions of the abundant ammonites recorded in the studied sections are given in an appendix.
Key words: Upper Jurassic; Neuquén Basin; Ammonoidea; *Windhauseniceras*; *Corongoceras*; *Steueria*; Hybridization.

Resumen. *La fauna de amonites tithonianos de la transecta Cerro Lotena-Cerro Granito, Formación Vaca Muerta, Argentina. – I. Familia Himalayitidae.* A partir de un amplio estudio de los afloramientos de la Formación Vaca Muerta a lo largo de la transecta entre Cerro Lotena y Cerro Granito, se ha obtenido una gran cantidad de información sobre la estratigrafía y paleontología regionales. En este artículo presentamos la primera parte de los resultados obtenidos, consistente en la descripción de los amonites de la Familia Himalayitidae Spath. La familia está bien representada en un intervalo cronoestratigráfico que comprende la parte mas alta de la Zona Proximus hasta la base de la Zona Alternans, con los géneros *Windhauseniceras* Leanza (monotípico), *Corongoceras* Spath y *Steueria* Parent, Scherzinger & Schweigert. El registro de *Windhauseniceras internispinosum* (Krantz) comprende cinco transients que muestran cambios graduales en el espectro de variación intraspecífica, desde serpentíconos robustos hasta suboxíconos comprimidos. Hibridación entre representantes tempranos de *W. internispinosum* y su ancestro *Catutosphinctes proximus* (Steuer) es el fenómeno propuesto para explicar la ocurrencia de morfotipos intermedios persistentes y raros ejemplares de difícil determinación. La especie tipo de *Corongoceras* (*C. lotenoense* Spath) es por primera descripta a partir de topotipos adultos. La nueva especie *Corongoeras huarpense* es introducida para clasificar los representantes del género de la parte inferior de la Zona Internispinosum. El género se habría originado de *C. proximus* a través de *C.* aff. *huarpense* de la parte mas alta de la Zona Proximus. El género *Steueria* está representado en las secciones estudiadas por escasos ejemplares de *S.* cf. *alternans* (Gerth), los cuales permiten datar los niveles bajos de la Zona Alternans dado que se presentan por sobre de la ocurrencia terminal de *W. internispinosum*. La sucesión completa y detallada de todos los amonites colectados en las secciones estudiadas se presenta como un apéndice.
Palabras clave: Jurásico Superior; Cuenca Neuquina; Ammonoidea; *Windhauseniceras*; *Corongoceras*; *Steueria*; Hibridación.

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INTRODUCTION

The Tithonian Stage is extensively recorded along the Pacific border of America, from southern Chile and Argentina up to Alaska. In South America it is mainly distributed in two main Andean basins: the Neuquén Basin (Fig. 1), west-central Argentina and central-northern Chile, and the Tarapacá Basin, northern Chile, southwestern Bolivia and southwestern Perú (see details in Westermann 1992). The ammonite fauna is best recorded in the Neuquén Basin, where several local lineages, as well as Caribbean, Tethyan, and possibly Indo-malagasian forms are known. This fauna is composed of species of the families Lytoceratidae, Haploceratidae, Lissoceratidae, Oppeliidae (Taramelliceratinae), Aspidoceratidae (Aspidoceratinae), Ataxioceratidae (Zapaliinae, Torquatisphinctinae, ?Paraboliceratinae), Neocomitidae (Berriasellinae), Simoceratidae, and Himalayitidae.

In the Picún Leufú Subbasin (Hogg 1993; south of the Huincul High in Fig. 1), the Tithonian transect of outcrops between the hills Cerro Lotena and Cerro Granito (Fig. 2) bears

the richest successions of well preserved and densely distributed ammonites. The section of Cerro Lotena was published for first time by Windhausen (1914a, b). Ammonites from these localities have been studied by Haupt (1907), Krantz (1926, 1928), Weaver (1931), Leanza (1980), and Parent et al. (2008b).

During the last twenty years the present authors have been surveying the Picún Leufú Subbasin, collecting information and samples along the study area, the transect Cerro Lotena-Cerro Granito (Fig. 2). The present paper presents the first part of the results of this regional survey, consisting of the study of the Tithonian ammonites of the family Himalayitidae Spath, 1925 from the outcrops of the Vaca Muerta Formation between Cerro Lotena and Cerro Granito. The ammonite collection is composed of many hundreds of ammonites. The description of the whole fauna will be published in successive papers, because of the large amount of results and material to be figured. In this paper, first of the series, the ammonites are described after a brief description of the stratigraphic framework. The biostratigraphic distribution of the ammonites collected in the study area is reported in the Appendix 1, providing the local biostratigraphy as the base for the chronostratigraphic classification of the studied sections (Fig. 3).

The quality of the material has allowed detailed ontogenetic descriptions of macro- and microconch adults. Based on these descriptions and the occurrence of the different species in many levels showing morphological transitions, we have improved or elaborated evolutionary models for the genera *Windhauseniceras* Leanza and *Corongoceras* Spath, respectively.

The regional survey conducted in the study area is part of a research program on the Andean Tithonian-Berriasian ammonite fauna and stratigraphy of the whole Neuquén Basin. This program is based on the description of the fauna and stratigraphy of many key localities, with revision of old collections, under strict bed by bed samping through sections studied and described in detail. Early results (Parent & Capello 1999, Schweigert et al. 2002, Parent 2001, 2003b, Parent et al. 2006) form the base of our current reseach program which includes many localities through the basin. The studies already published cover the following localities (Fig. 1): Picún Leufú (Parent et al 2011a, 2019b), Estancia María Juana and Carrín Curá (Parent et al. 2013b, Parent et al. 2019a, b), Barda Negra (Parent et al. 2007), Cañadón de los Alazanes (Parent 2001), Portada Covunco-Cerrito Caracoles (Parent & Cocca 2007, Parent et al. 2013a), Mallín Quemado (Garrido & Parent 2017, Garrido et al. 2018), Pampa Tril (Parent et al. 2015, Parent et al. 2017b), Casa Pincheria (Parent & Capello 1999, Parent 2003a), and Arroyo Cieneguita (Parent et al 2011b).

These studies have provided a vast amount of new information on the stratigraphy of the Neuquén Basin and the systematics and biostratigraphy of the fauna. Some of the advances produced by the results of the mentioned studies have been: (1) the refinement of the chronostratigraphic classification at the highest resolution level possible, i.e. down to the level of the ammonite horizon (biohorizon), (2) the demonstration that the ammonite fauna is much more homogeneous than previously assumed, (3) the classification of most of the ammonites in well delimited Andean evolutionary lineages, leading to (4) the correction of most of the misidentifications of Andean forms with exotic genera (e.g. *Aulacosphinctes*, *Virgatosphinctes*, *Pseudinvoluticeras*, among others).

STRATIGRAPHIC FRAMEWORK

The Neuquén Basin (Fig. 1) is well known by its vast Jurassic and Cretaceous ammonite-bearing successions (Groeber 1952, Digregorio 1978, Digregorio & Uliana 1980, Howell et al. 2005). The basin can be subdivided in three parts with different geological characteristics, from south: (1) the Picún Leufú Subbasin (De Ferraris 1947, Ramos et al. 2011), limited by the Huincul High in the North and including the study area, (2) the central basin with a pronounced eastern expansion, and (3) the Aconcagua Platform (or Malargüe Shelf) extended through the Mendoza and San Juan provinces and Central Chile.

The most complete and detailed record of Tithonian ammonites in the Picún Leufú Subbasin is in the study area, in the localities named after the Cerro Lotena and the Cerro Granito (Fig. 2). The regional geology and stratigraphy were preliminary described by Windhausen (1914a, b), later in detail by Suero (1951) and updated by Leanza (1980).
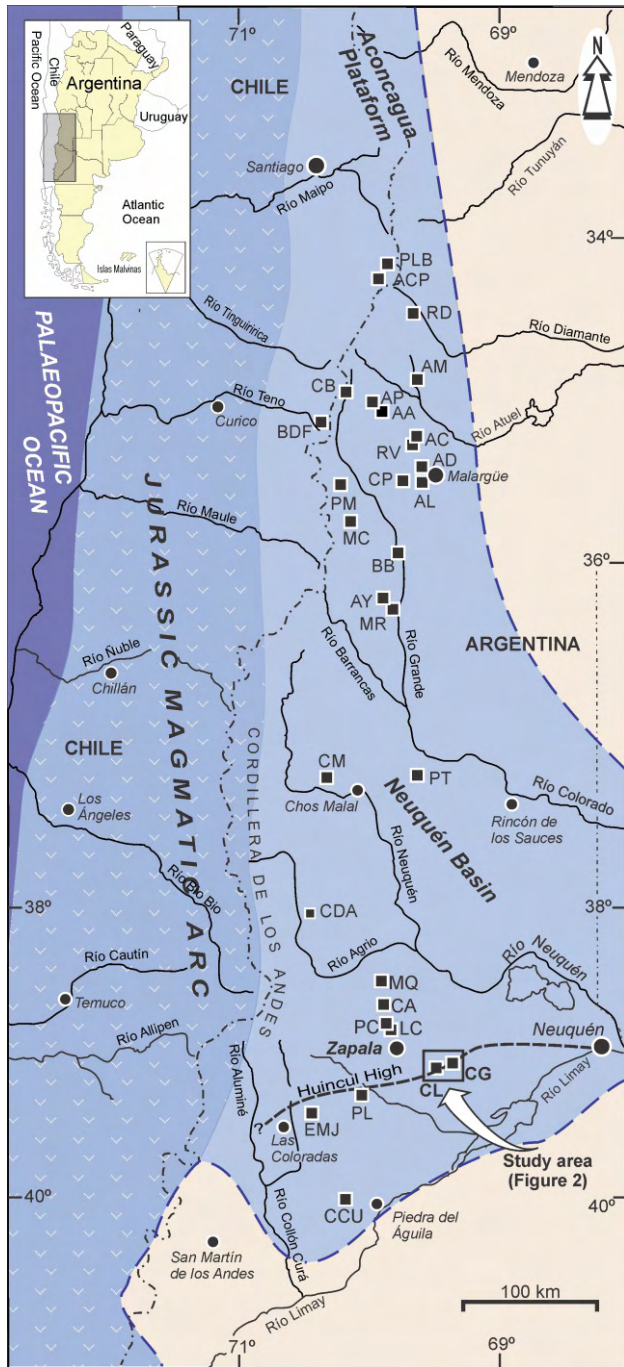
In the study area we have sampled ammonites and complementary fauna, bed by bed through a long transect (about 12 km) of outcrops of Tithonian rocks of the Vaca Muerta Formation. The four sections which correspond to the main outcrops were logged (Fig. 3), named as CL, CG-III, CG-II, and CG-I, of which the sections CG-II and CG-III had never been studied before.

A simplified version of our log-section of Cerro Lotena (Fig. 3: CL) was presented by Gouiric-Cavalli (2017: fig. 1). The suspension-feeder pachycormid studied in this latter paper was collected from level CL-23, Zitteli/Mendozanus Zone, well above the first occurrences of *Pseudolissoceras zitteli* (Burkckhardt, 1903); the corresponding ammonite fauna is given in App. 1.

Biostratigraphic chronostratigraphy. Tithonian ammonites from CL and CG-I have been studied by Haupt (1907), Krantz (1926, 1928), Weaver (1931), Leanza (1980), and Parent et al. (2008b). The most comprehensive of these studies (Leanza 1980) has been taken as the main reference for the Lower and Middle Tithonian (= Lower Tithonian of the international bipartite subdivision) in many studies. Neverhtless, the ammonites described there were collected with few or no stratigraphic control by A. Windhausen in 1912 (Leanza 1980: 6). This situation has created misidentifications and misinterpretations which were first noted by Parent et al. (2011a), later recalled by Vennari (2016), and have begun to be solved slowly. The most notorious biostratigraphic problem is the overlaping, even inversion according to the results of sampling effort and locality, of the local *Mendozanus* and *Zitteli* biozones. The root of this problem is that *Pseudolissoceras zitteli* (Burckhardt, 1903) occurs from a lower stratigraphic position than the guide assemblage of the "Mendozanus" Zone described by Burckhardt (1903) and recently revised by Parent et al. 2011a, b, 2015). According to this inconsistency we refer the corresponding interval to a single unit: Zitteli/Mendozanus Zone, pending a solution. Recently, Vennari (2016) introduced new zones and subzones, but unfortunately overlooking previous contributions. However, her units are defined on the basis of misindentifications and create inconsistencies (see discussion in Garrido et al. 2018).

The chronostratigraphic classification of the studied sections (Fig. 3) is derived from the biostratigraphy of the ammonite succession (App. 1) under the adopted chronostratigraphic framework (Fig. 4).

General features of the fauna. The study area, a not very deep marginal northeastern dependency of the Picún Leufú Subbasin, may be considered as a template for all the eastern sector of the subbasin. The Tithonian environments must have been very favourable for the necto-benthic (demersal) fauna, rich in nutrients and well-oxygenated. This is inferred from the abundant and diversified fauna composed by juvenile and adult ammonites, nautiloids, bivalves (including many oysters), gastropods, and marine reptiles and fishes, in many of the levels in which we have subdivided the sections. Ammonites outnumber largely the other mollusks, occurring in more than the 40% of the levels of the studied sections. Nautiloids occur as scarce accessory elements; a single belemnite was found.

Figure 2. Outcrops of the Vaca Muerta Formation (brown; black: Mutrucó Formation) through the transect (about 14 km long) between the Cerro Lotena and the Cerro Granito. The four sections logged (Fig. 3) are named after Cerro Lotena (CL) and Cerro Granito (CG-I, CG-II, CG-III).

There is strong evidence pointing to a rather quiet sea bottom in which the freshly dead animals must have been buried in situ and/or very close to their habitat, with very little or no transport or postmorten drift:

- the integrity of the shells of the mollusks,
- the almost absence of shell debris (except rare coquina levels),
- the occurrence of complete macro- and microconch ammonites delicately preserved, including the peristomes and the thin lappets in the microconchs,
- great abundance of aptychi and ammonites with their aptychus in the bodychamber,
- the good preservation of mostly complete reptiles in concretions, and
- the occurrence of well preserved fishes.

SYSTEMATIC PALAEONTOLOGY

Conventions and notation. The material described is housed at the Museo Provincial de Ciencias Naturales "Prof. Dr. Juan A. Olsacher", Zapala (MOZ-PI). Bodychamber is abbreviated with Bc and phragmocone with Ph; macroconch (female shell): [M], microconch (male shell): [m]. Measurements: diameter (D), diameter at the last adult septum (D_{ls}) and diameter at adult 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]; length of bodychamber (L_{BC}) in degrees [°]. Number of primary (P) and ventral (V) ribs, and lateral (T_L) and ventro-lateral (T_{VL}) tubercles per half whorl. The index $i = V/P$ is a measurement of the degree of furcation and occurrence of intercalary ribs. These measurements per-half-whorl are more sensitive to the ontogenetic changes in density than per-whorl, and are less exigent with quality of material. Report of biometric features is given in the form of dimensionless numbers or "indexes", mainly relative to the corresponding value of D, allowing plain comparisons of shell shape in a range of sizes. C_V: percentual coefficient of variation (100 times the ratio of the standard deviation to the mean), a measure of the variation scaled by the mean value, allowing plain comparisons unaffected by size. Abbreviations in synonymy lists: p (pars), n (non), ? (doubtful assignation), * (type specimen figured).

Study area

Transect Cerro Lotena (CL) - Cerro Granito (CG).

Other localities

CCU: Carrín Curá, EMJ: Estancia María Juana, PL: Picún Leufú, PC: Portada Covunco, LC: Los Catutos, CA: Cañadón de los Alazanes, MQ: Mallín Quemado, CDA: Cajón de Almanza, CM: Chacay Melehué, PT: Pampa Tril, MR: Mallín Redondo, AY: Arroyo del Yeso, BB: Bardas Blancas, MC: Molinos Colgados, PM: Paso del Montañés, CP: Casa Pincheira-Arroyo Los Troncos, AL: Arroyo Loncopué, AD: Arroyo Durazno, RV: Rodeo Viejo, AC: Arroyo Cieneguita, BF: Baños del Flaco, AA: Arroyo Alberjillo, AP: Arroyo Paraguay, CB: Cajón del Burro-Río Choicas, AM: Arroyo de la Manga, RD: Río Diamante, ACP: Arroyo Cruz de Piedra, PLB: Paso Los Bayos.

Figure 1. The Neuquén Basin (eastern border indicated by broken lines) with indication of the localities cited in text and others showing Tithonian outcrops. The study area is in the Picún Leufú Subbasin, south of the Huincul High. Modified from Garrido et al. (2018).
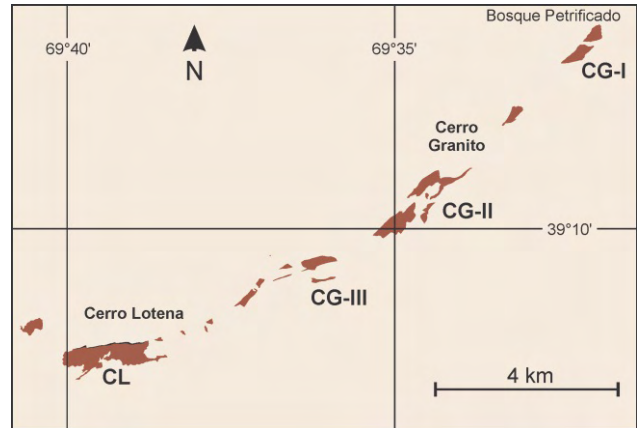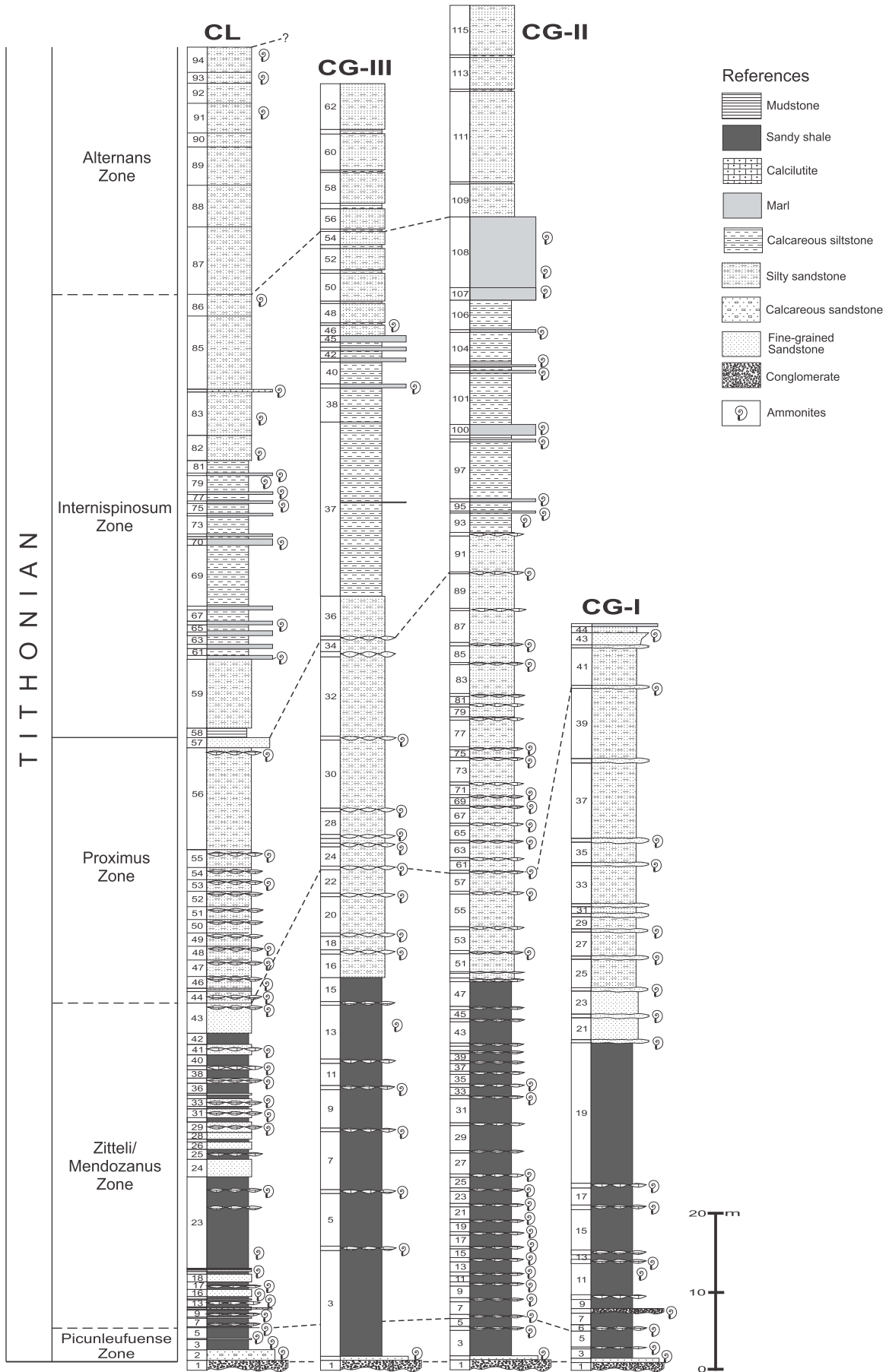
Figure 3. Studied sections of the Vaca Muerta Fm: Cerro Lotena (CL), Cerro Granito I (CG-I), Cerro Granito II (CG-II), and Cerro Granito III (CG-III). The sections are time-correlated from the chronostratigraphic zones (Fig. 4) based on the ammonite biostratigraphy (App. 1) as explained in the text.
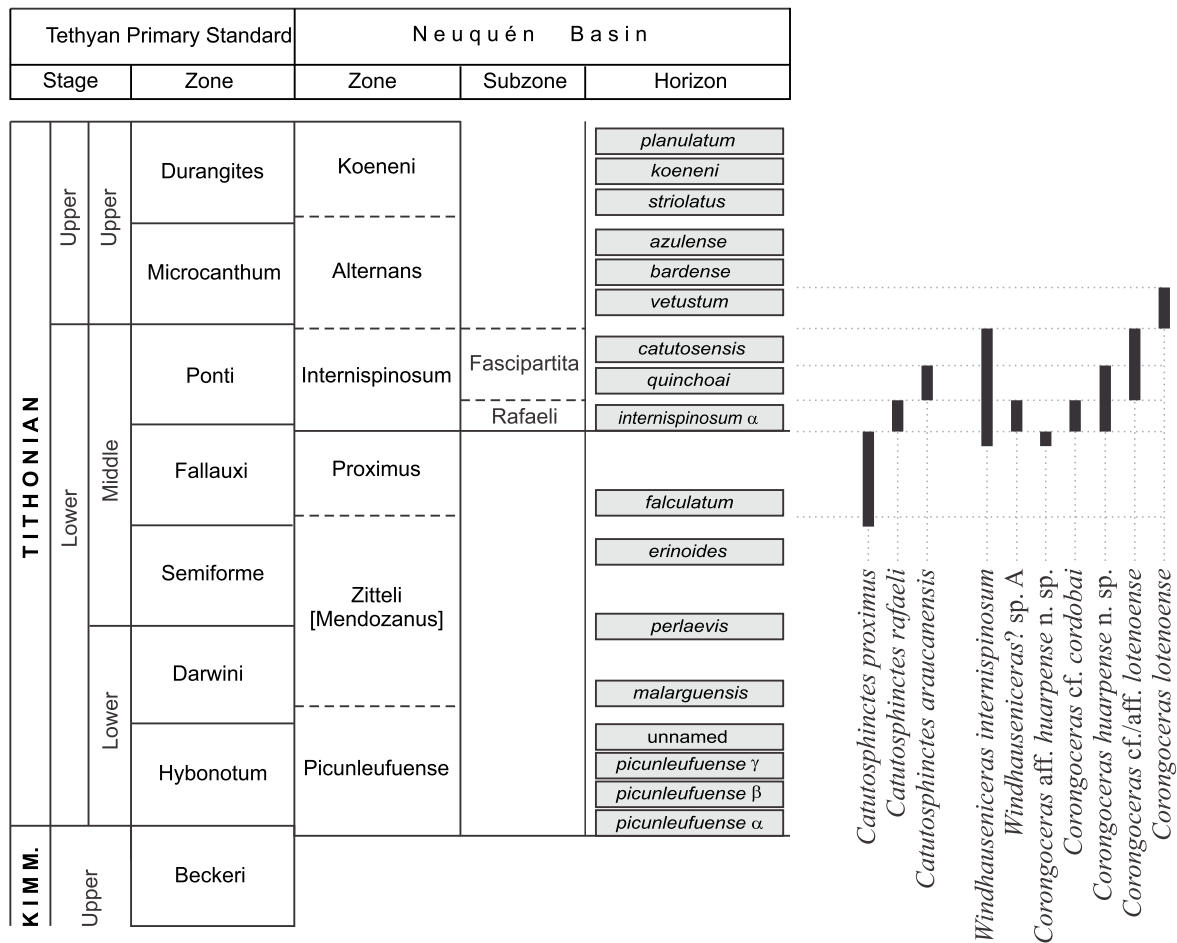
Figure 4. Chronostratigraphic framework and distribution of the studied species of the family Himalayitidae and others of the genus *Catutosphinctes* (explanation in the text). Details of the ammonite successions in App. 1 and indicated in the text for each species, level by level of the four sections. Broken lines for non-standard zones. Andean zonation and ammonite-horizons correlated with the Tethyan Primary Standard, with bi- and tripartite subdivision (updated from Parent et al. 2015, 2019b and Garrido et al. 2018). The Rafaeli and Fascipartita subzones of the Internispinosum Zone (Leanza & Zeiss 1992) defined in Los Catutos (Portada Covunco) seem applicable in the study area according to the ammonite succession (see App. 1). Not only the index species occur, but also others of the guide assemblages in the same succession as in the type locality. The distribution of the ammonite-horizons within these subzones is provisional. The many subzones of Zeiss & Leanza (2010) are not considered herein for they were introduced in nominal form only.

The occurrence of the specimens is denoted by a level-number with the prefix of the corresponding section in Fig. 3: CL (Cerro Lotena), CG-I (Cerro Granito I), CG-II (Cerro Granito II) or CG-III (Cerro Granito III).

Sexual dimorphism and intraspecific variation. Sexual dimorphism is interpreted according to Klug et al. (2015, 2021) and Parent & Zatón (2016), assuming that macroconch ammonites were the females and the microconchs the males. It remains, however, useful to add the former terms, mainly because of some complex cases reported which seem to involve some form of hermaphroditism or sex change (Parent et al. 2008a) which could be also the case of the "intersexes" of Brochwicz-Lewiński & Różak (1976), and possibly some of the cases studied by Frau & Boursicot (2021).

A critical factor in ammonite systematics is that most ammonite species are widely variable intraspecifically in shell shape and adult size (e.g. Sturani 1971, Howarth 1973, Callomon 1985, Bonnot 1993, Parent 1998, Zatoń 2008, Landman et al. 2010, Scherzinger et al. 2015, 2018; recent review in De Baets et al. 2015). However, the sequence of sculptural stages, the sculpture ontogeny, is rather constant. This variation in shell shape and rib density (but not style) between coeval individuals, arises mainly because of size/age variation in the onset and duration of the ontogenetic stages, in sequences which are otherwise very constant (cf. Hantzpergue 1989: 80, Tajika et al. 2018). These variations in developmental timing are developmental heterochronies which modulate the phenotypic variation through a range of more or less paedo- or peramorphic intraspecific variants (McKinney & McNamara 1991; examples in Meister 1989, Hammer & Bucher 2006, Parent et al. 2011b, 2015, Scherzinger et al. 2015), mainly as response to different environmental conditions during development as well as genetic variability (Mitta 1990, Matyja & Wierzbowski 2000, Wilmsen & Mosavinia 2011). These changes in the timing of expression of the successive morpho-ornamental stages originate the gradual variation that the fossil record usually shows as a more or less continuous spectrum of variation through different morphotypes.

Resting on these statements, we consider that the comparative study of the sexually dimorphic morpho-ornamental ontogeny under control of adult size and
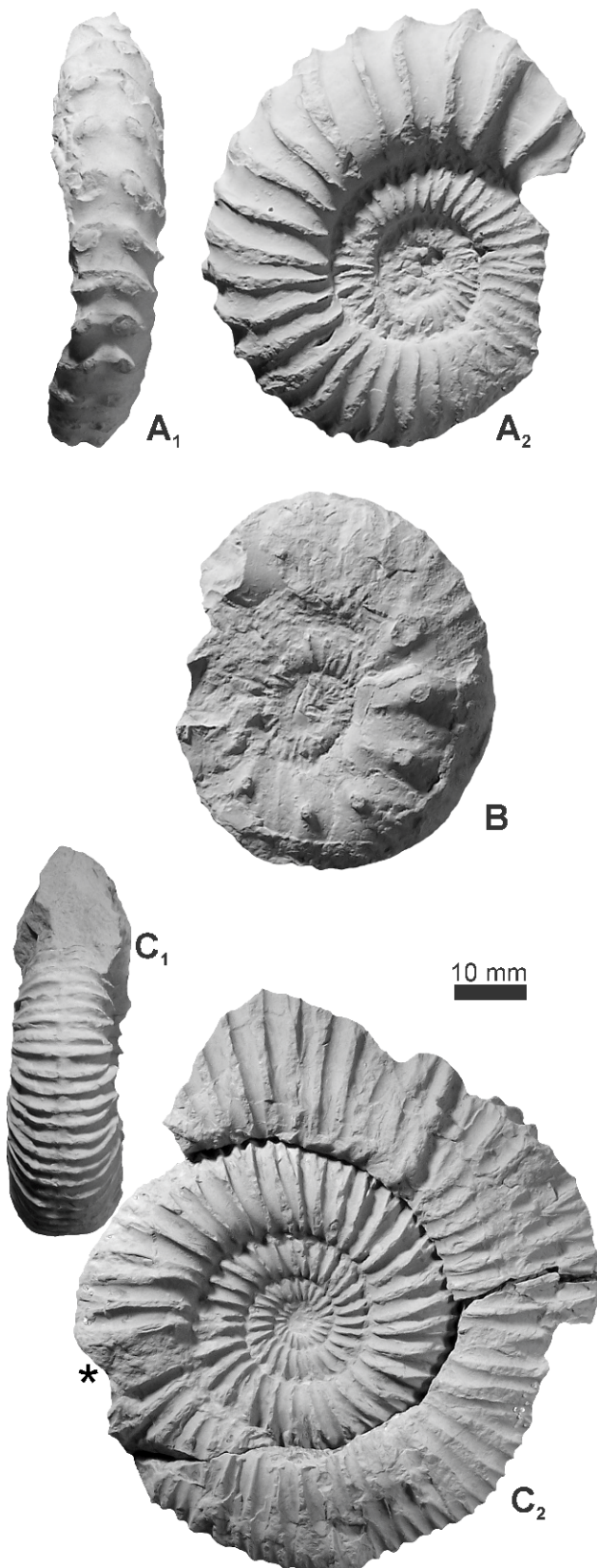
morphologic variation is the best way for obtaining natural and robust classifications.

For the cases of different morphotypic composition of stratigraphically differentiated samples of a species, we use the common term transient. This term refers to the phenotypic steps of evolutionary changes observed (mainly in the ranges and/or patterns of variation) within a lineage (see details and further discussion in Callomon 1985, Dietze et al. 2005).

Order Ammonitida Fischer, 1882
Suborder Ammonitina Fischer, 1882
Superfamily Perisphinctoidea Steinmann, 1890
Family Himalayitidae Spath, 1925

Remarks. In the most recent and complete revision Énay & Howarth (2019) present the family subdivided in two subfamilies, both of them including Andean genera: Himalayitinae Spath, 1925 and Suaritinae Cantú-Chapa, 1998. This latter is differentiated from the former by having primary ribs looped to ventro-lateral tubercles or secondary ribs at some stage of growth. However, this classification is conflictive since most of the Andean genera included in the Suaritinae do not have looped ribs (cf. Zeiss & Leanza 2008), except probably *Wichmanniceras* Leanza, 1945. Most of the Andean and many Caribbean himalayitids form a separate lineage, or lineages, from the Tethyan ones which should certainly be separated at the subfamily level. In the Indo-Malagasian domain both groups of himalayitids are present. The few records of *Himalayites* and *Micracanthoceras* in the Neuquén Basin must correspond to ephemeral inmigrants which do not settled in the basin, as they occur only saltuary (see below). These forms do not pose problems for the separation of Andean and Tethyan forms.

Under these circumstances we provisionally consider the family undivided and represented in the Neuquén Basin by the following genera:

- *Windhauseniceras*, *Corongoceras*, and *Steueria* (discussed below).

- *Hemispiticeras* Spath, 1925. The type species, *Reineckeia steinmanni* Steuer, 1897, was described from specimens from two different localities (La Manga and Rodeo Viejo), with no designation of a type specimen. The only specimen figured by Steuer (1897: pl. 8: 1-3, refigured 1921: pl. 8: 1-3), a phragmocone from an unknown horizon of Arroyo La Manga, is herein designated as lectotype. Énay & Howarth (2019: 108) referred erroneously this specimen as holotype. Spath (1925: footnote in 144) referred only this specimen to the genus *Hemispiticeras*. The inner whorls of the lectotype are subrectangular, covered by fine and dense, flexuous primary ribs which bifurcate from a mild bulla, and ending in a ventral/ventro-lateral tubercle besides a wide ventral furrow (Steuer 1897: 155, pl. 8: 3); the outer whorls have suboval to subrectangular whorl section with strong primary ribs, bi- and trifurcating from a rounded and prominent upper flank tubercle; the ventral ribbing is densely spaced and slightly curved adapically. In *Windhauseniceras* there is only a single row of ventro-lateral, lamelliform tubercles in the inner whorls, the ribbing is rectiradiate and stronger, and the whorl section is suboval depressed passing, in the macroconchs, to higher than wide suboval in the adult bodychamber.

The only guide to estimate the age of *H. steinmanni* is the stratigraphic position of the paralectotypes. These were collected in the locality Rodeo Viejo, from levels IV or V of Steuer (1897). The assemblage of ammonites from these levels studied by Steuer (1897; revised by Parent et al. 2011b) include species known to occur mainly in the Alternans Zone, some of them with extension into the Koeneni Zone. Thus, a late Alternans Zone age is the most likely for the

Figure 5. **A**: *Lotenia* aff. *neuquenensis* Zeiss & Leanza, 2008; adult? phragmocone (MOZ-PI-6561), upper Alternans-lower Koeneni Zone, Cajón de Almanza (see Fig. 1). **B**: *Himalayites* cf. *treubi* Boehm, 1904; macroconch phragmocone (MOZ-PI-7206); upper Alternans-lower Koeneni Zone, Cajón de Almanza. **C**: *Catutosphinctes proximus* (Steuer, 1897) [M]; level CL-56, upper Proximus Zone; almost complete adult macroconch (MOZ-PI-8340) of a late (probably latest) transient. - All natural size (x1). The asterisk indicates the last septum.
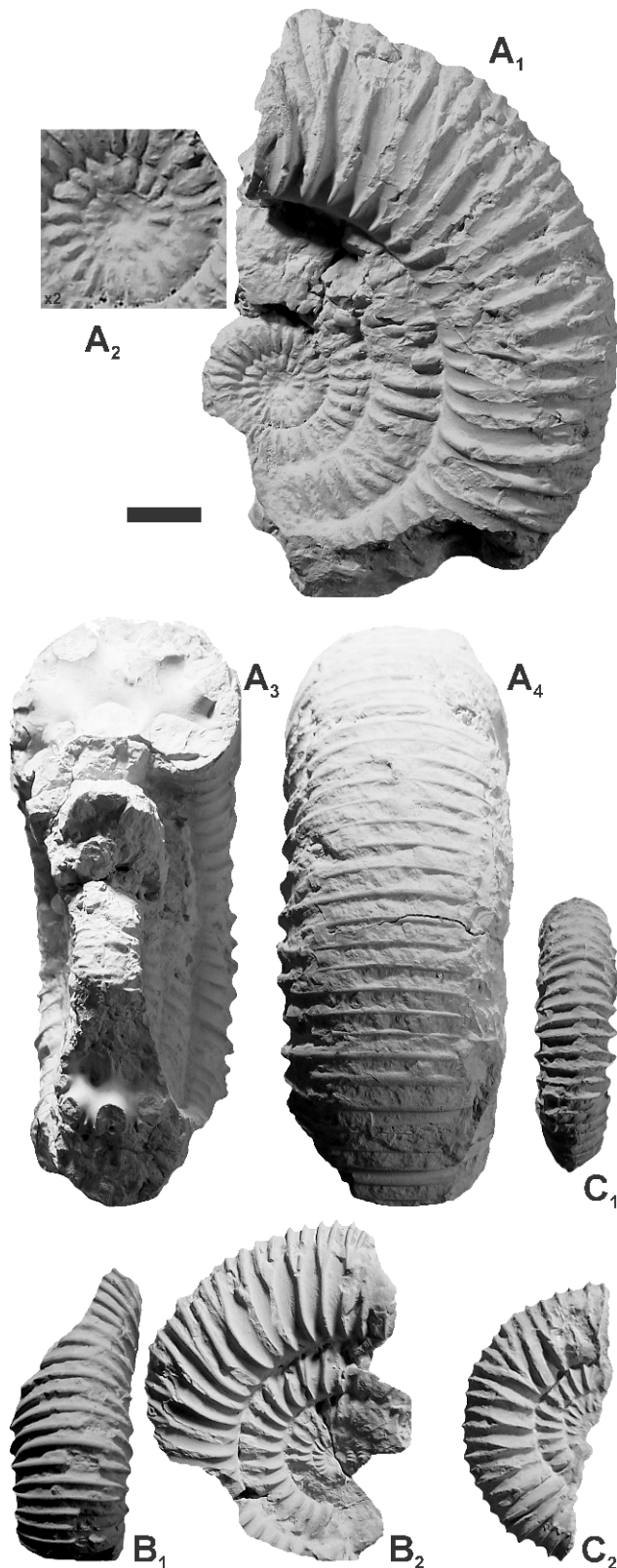
Figure 6. *Windhauseniceras internispinosum* (Krantz, 1926), upper Proximus Zone. Earliest representatives of the species (transitional from *Catutosphinctes proximus*) assigned by the incipient ventro-lateral tuberculation in the inner whorls and the depressed outermost whorl. **A**: adult macroconch phragmocone (MOZ-PI-7447/1), level CL-56; lateral (A_1) and ventral (A_4) views, inner whorls (A_2, x2), and whorl section (A_3). **B**: juvenile macroconch? phragmocone (MOZ-PI-7447/2), level CL-56. **C**: microconch? phragmocone (MOZ-PI-8399/3), level CG-II-84. – The bar is 10 mm for all except A_2 (5 mm).

paralectotypes, and so possibly for the lectotype of *H. steinmanni*.

- *Wichmanniceras* Leanza, 1945 is known in the Neuquén Basin only by the holotype of its type species, *Wichmanniceras mirum* Leanza, 1945.

- *Acevedites* Cantú-Chapa, 1967 (type species: *Acevedites acevedense* Cantú-Chapa, 1967). It seems to be a single citation for the Neuquén Basin, that of Leanza et al. (2003: 252) in the Upper Tithonian of the area Nonial-Huncal, but unfortunately not figured. According to the material figured by Cantú-Chapa (1967), the holotype of the type species (pl. 7: 7) is indistinguishable from the inner whorls of the holotype of "*Wichmanniceras*" *hernandense* Cantú-Chapa (1967: pl. 7: 5) which only differs by the last whorl (adult bodychamber?). The remaining material of these two nominal species shows the same close resemblance, even identity, and occur intimately associated (pls. 4: 2, 4, 7: 2), strongly suggesting that all these ammonites are macro- and microconchs of a single species: *Acevedites acevedense*.

- *Lotenia* Zeiss & Leanza, 2008, based only in the holotype of the type species *Simplisphinctes* (*Lotenia*) *neuquensis* Zeiss & Leanza, 2008, from an unknown stratigraphic horizon of the Tithonian of Cerro Lotena. The specimen from Cajón de Almanza in Fig. 5A would be the second record of the genus in the Neuquén Basin.

- *Micracanthoceras* Spath, 1925 (type species: *Ammonites microcanthus* Oppel in Zittel, 1868). Few specimens from a handful of localities of the basin have been described by Steuer (1897), Burckhardt (1900b), Leanza (1945), and Parent et al. (2011b).

- *Himalayites* Uhlig in Boehm, 1904 (type species: *Himalayites treubi* Uhlig in Boehm, 1904) has been described from few localities of the basin, in the form of "*Himalayites*" *andinus* Leanza, 1975 and *Himalayites* cf. *treubi* Boehm, 1904 (see Leanza & Hugo 1977, Parent et al. 2011b, 2015, Garrido et al. 2018). The holotype and only specimen known of *Himalayites peregrinus* Leanza (1967: pl. 3: 10) is an indeterminable fragment of ammonite. *H.* cf. *treubi* seems to be well represented in the basin. A new specimen from Cajón de Almanza is shown in Fig. 5B. "*Himalayites*" *andinus* is well known from the Koeneni Zone of Mallín Quemado (Leanza 1975, Garrido & Parent 2017, Garrido et al. 2018). The assignment of this latter to *Himalayites* is provisional since the well formed ventro-lateral bullae of the holotype is a feature not known in the holotype of the type species (observations from a cast of *H. treubi*, courtesy of Camille Frau, 30/03/21). The closest Andean species is the Upper Tithonian-Berriasian "*Spiticeras*" *tripartitus* (Hupé, 1854) as figured by Biró-Bagoczy (1980: pl. 3: 1-3) and Salazar (2012: figs. 4.45-4.48), which certainly belongs to an undescribed genus. "*Himalyites*" *seideli* var. *ampanihyensis* Collignon (1960: fig. 743) from the Upper Tithonian of Madagascar is also very similar in size (adult?) and ornamentation, suggesting this group of ammonites could have had a wide palaeobiogeographic distribution.

The genus *Djurjuriceras* Roman, 1936 (type species: *Djurjuriceras djurdjurense* Roman, 1936) has been cited from the locality Los Catutos by Leanza & Zeiss (1990). Nevertheless, these specimens have nothing to do with this genus, but they are clearly assignable to *Catutosphinctes* Leanza & Zeiss, 1992. *Djurjuriceras* includes ammonites with small and irregularly distributed ventro-lateral bullae at the end of some ribs in the phragmocone, with fine and dense, flexuous ribbing which turns to strong blade-like primaries in the adult

Figure 7. **A-B:** *Windhauseniceras internispinosum* (Krantz, 1926) [M], transient alpha; Cerro Lotena, level CL-60, Internispinosum Zone. A: Adult or subadult macroconch bodychamber (MOZ-PI-9367). B: adult? macroconch phragmocone (MOZ-PI-9350/1). **C**: *Windhauseniceras*? sp. A, portion of bodychamber with remains of phragmocone (MOZ-PI-7279/1), level CL-60. - All natural size (x1). Asterisk at last septum.

Figure 8. *Windhauseniceras internispinosum* (Krantz, 1926) [M], transient CG-II-98, Cerro Granito II, level CG-II-93, Internispinosum Zone. Slightly crushed adult macroconch phragmocone (MOZ-PI-8404). Extreme platyconic and finely ribbed morphotype. - Natural size (x1).

bodychamber. These features, observed from a new photograph of the holotype of the type species (courtesy of C. Frau, 30/03/21) and in the specimen from the Microcanthum Zone of Ghelpach, Italy figured as *Djurjuriceras* sp. by Sarti (2020: pl. 27: 6), hardly conform to the himalayitid bauplan in morphology and ornamentation. We suggest it could be an endemic Mediterranean ataxioceratid, assignable to the subfamily Lithacoceratinae Zeiss, 1968, or as an extension into the Tithonian from the subfamily Paraboliceratinae Spath, 1928. The classification into the Lithacoceratinae would be similar to that of Arkell (1957) who assigned *Djurjuriceras* to the

Virgatosphinctinae Spath, 1923 because of alleged close similarities with *Subplanites* Spath, 1925. This latter genus is currently placed in the Lithacoceratinae, but formerly in the Virgatosphinctinae (Arkell 1957).

It is interesting to note that after the many decades in that himalayitid ammonites have been described all over the world, sometimes from abundant material, neither a single himalayitid aptychus seems to have been reported. This was confirmed by G. Schweigert (personal communication 20/10/2020) and V. Mitta (pers. comm. 10/01/2021).
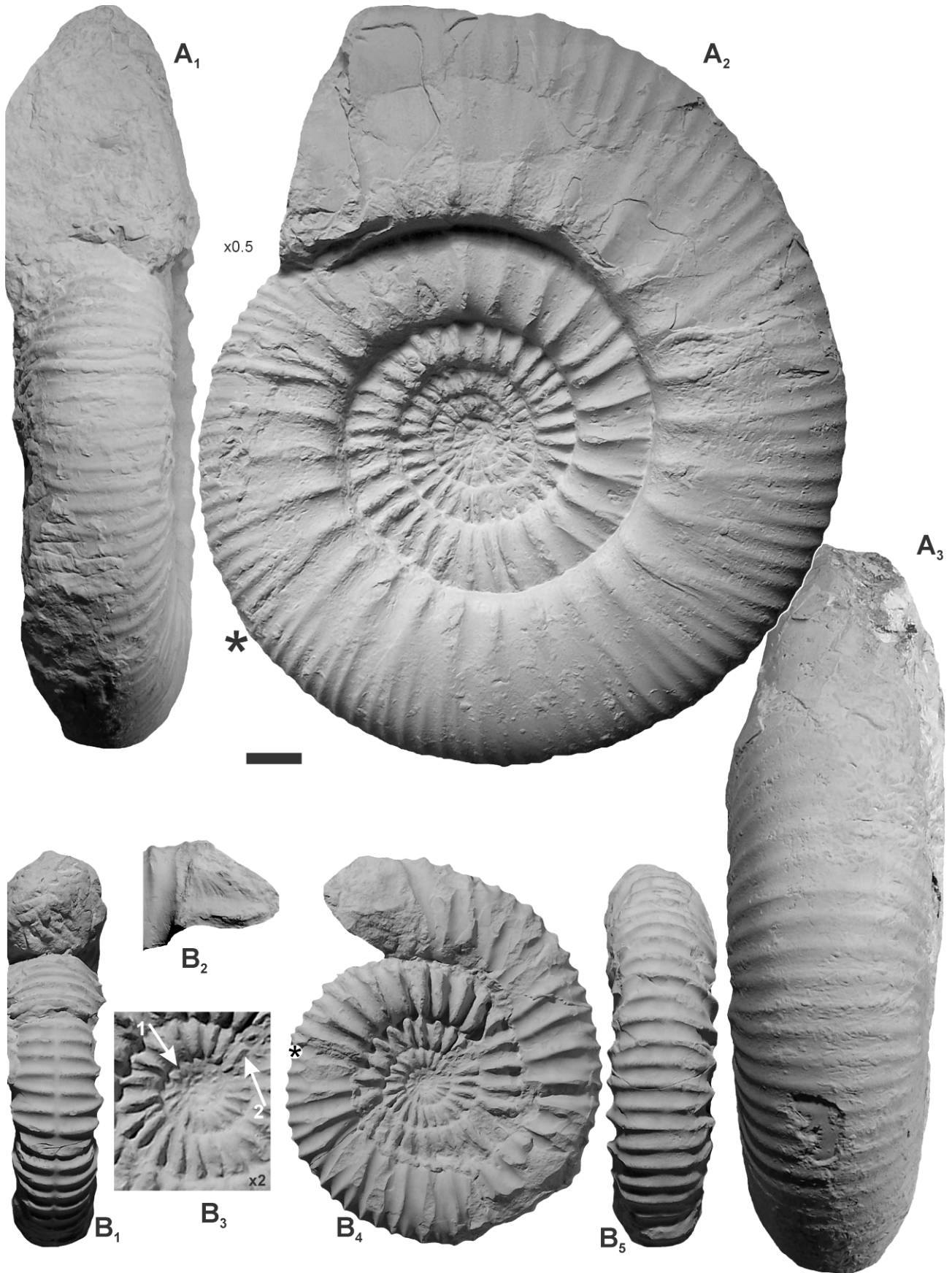
Figure 9. *Windhauseniceras internispinosum* (Krantz, 1926) [M&m], transient CG-II-98, Cerro Granito II, level CG-II-98, lower Internispinosum Zone. **A**: almost complete adult macroconch (MOZ-PI-5786), half-size (x0.5); shown in natural size in Fig. 10A. **B**: complete adult microconch (MOZ-PI-8405/4); B₂: detail of the lappet of the opposite side of B₄; B₃: inner whorls (x2) showing the sequence of three isolated tuberculate ribs (arrow 1) , followed by finer ribbing, and then followed by the onset of the ventro-lateral tuberculation (arrow 2) which persists up to the end of the phragmocone. - Asterisks indicating the last septum. The bar is 20 mm for A₁-A₃, 10 mm for B₁-B₂, B₄, and 5 mm for B₃.
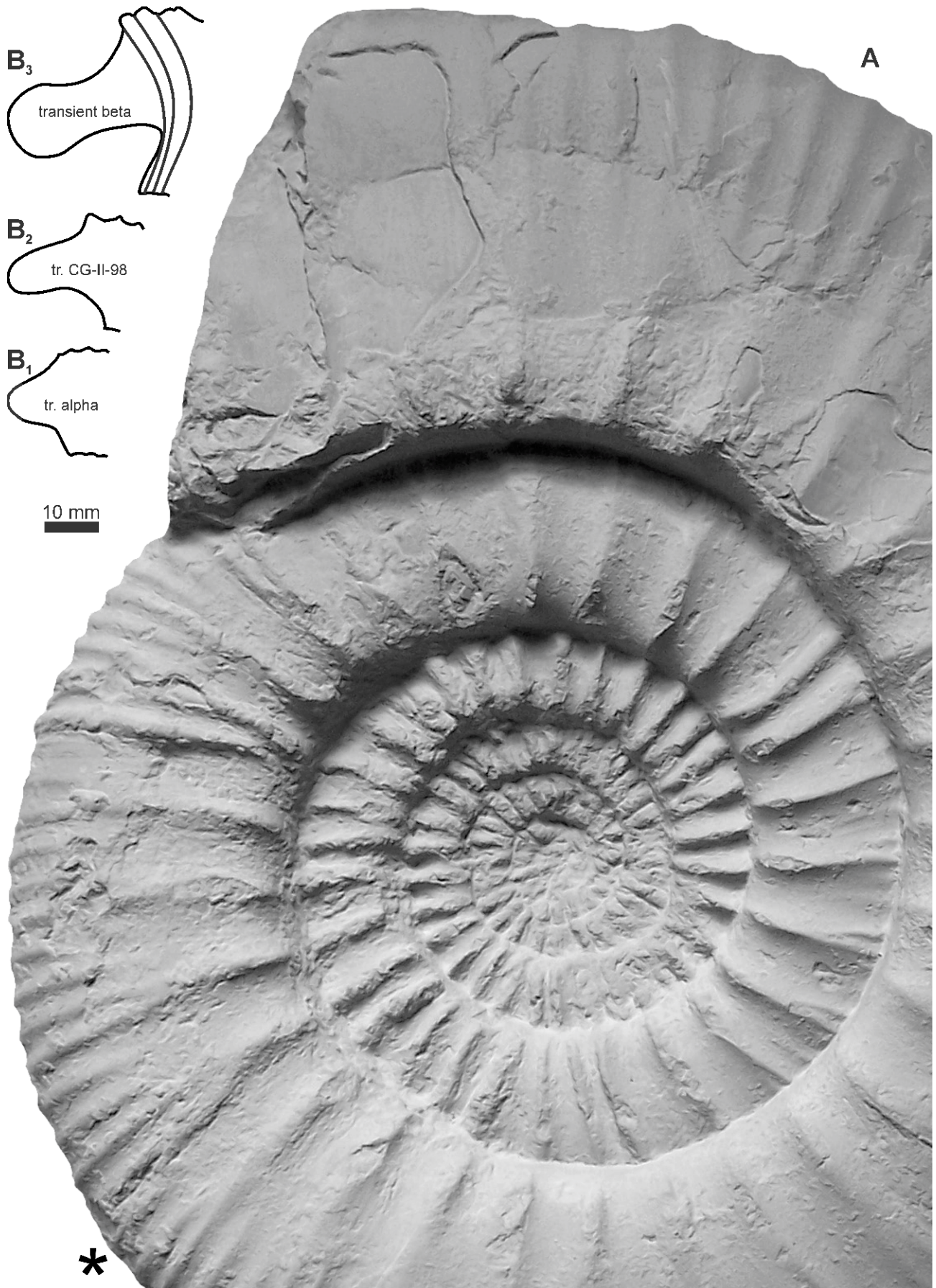
Figure 10. *Windhauseniceras internispinosum* (Krantz, 1926), Internispinosum Zone. **A:** almost complete adult macroconch of transient CG-II-98 (MOZ-PI-5786), level CG-II-98; shown half size in Fig. 9A. **B:** evolution of the lappets of the microconchs in the species (B_1: transient alpha, specimen in Parent et al. 2017b: fig. 9C; B_2: transient CG-II-98, specimen in Fig. 9B; B_3: transient beta, specimen in Fig. 15B). - All natural size (x1). Asterisk at last septum.
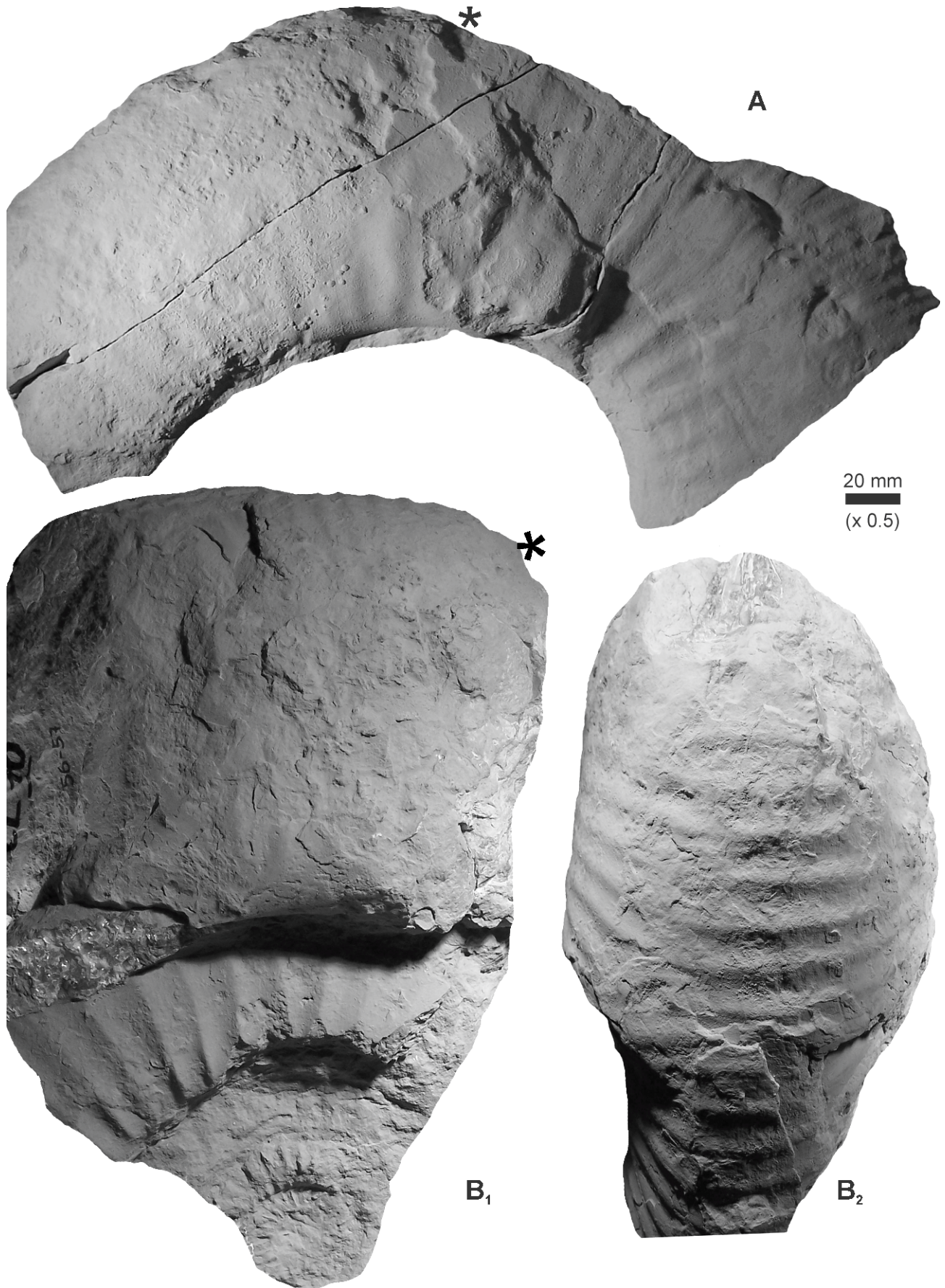
Figure 11. *Windhauseniceras internispinosum* (Krantz, 1926) [M], transient beta. Internispinosum Zone, Cerro Lotena. **A**: portion of terminal adult phragmocone and beginning of the bodychamber (MOZ-PI-7655), level CL-68. **B**: adult phragmocone with beginning of the bodychamber (MOZ-PI-7651), level CL-70. - All half-size (x0.5). Asterisk at last septum.
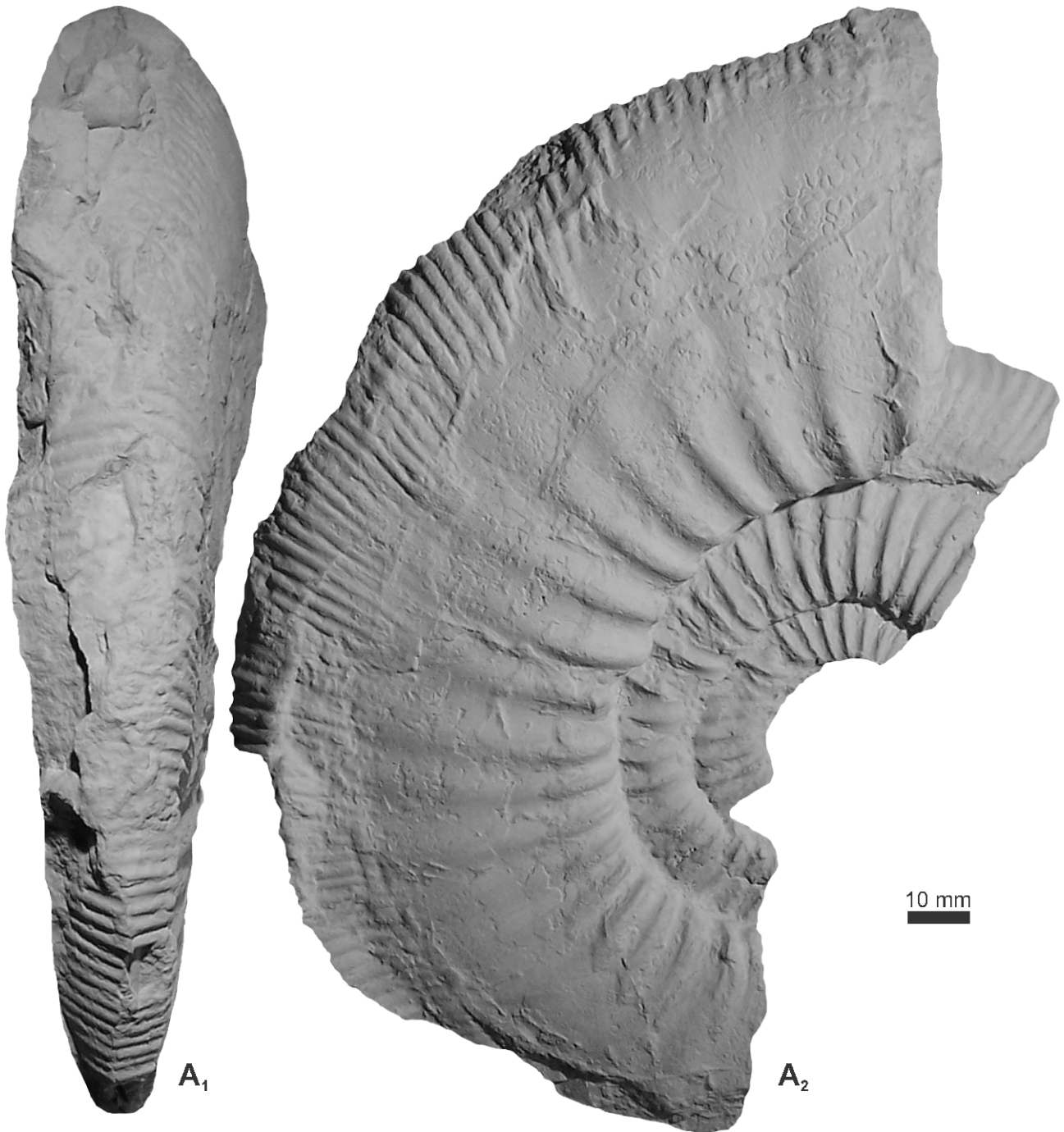
Figure 12. *Windhauseniceras internispinosum* (Krantz, 1926) [M], transient beta, Cerro Granito II, level CG-II-102, Internispinosum Zone. Slightly crushed adult macroconch phragmocone (MOZ-PI-5801) with remains of the umbilical seam of the bodychamber in the last whorl. Suboxyconic morphotype. - Natural size (x1).

Genus *Windhauseniceras* Leanza, 1945

Type species. *Perisphinctes internispinosus* Krantz, 1926 by monotypy.

Windhauseniceras internispinosum (Krantz, 1926)
Figs. 6-19

1897 *Reineckeia* cf. *stephanoides* Oppel sp. – Steuer: 157, pl. 14: 11-12

1921 *Reineckeia* cf. *stephanoides* Oppel sp. – Steuer: 58, pl. 14: 11-12

* 1926 *Perisphinctes internispinosus* Krantz – Krantz: 453, pl. 14: 1-2 (lectotype), pl. 15: 5-6

1928 *Perisphinctes internispinosus* Krantz – Krantz: 39, pl. 2: 3 (lectotype), 4

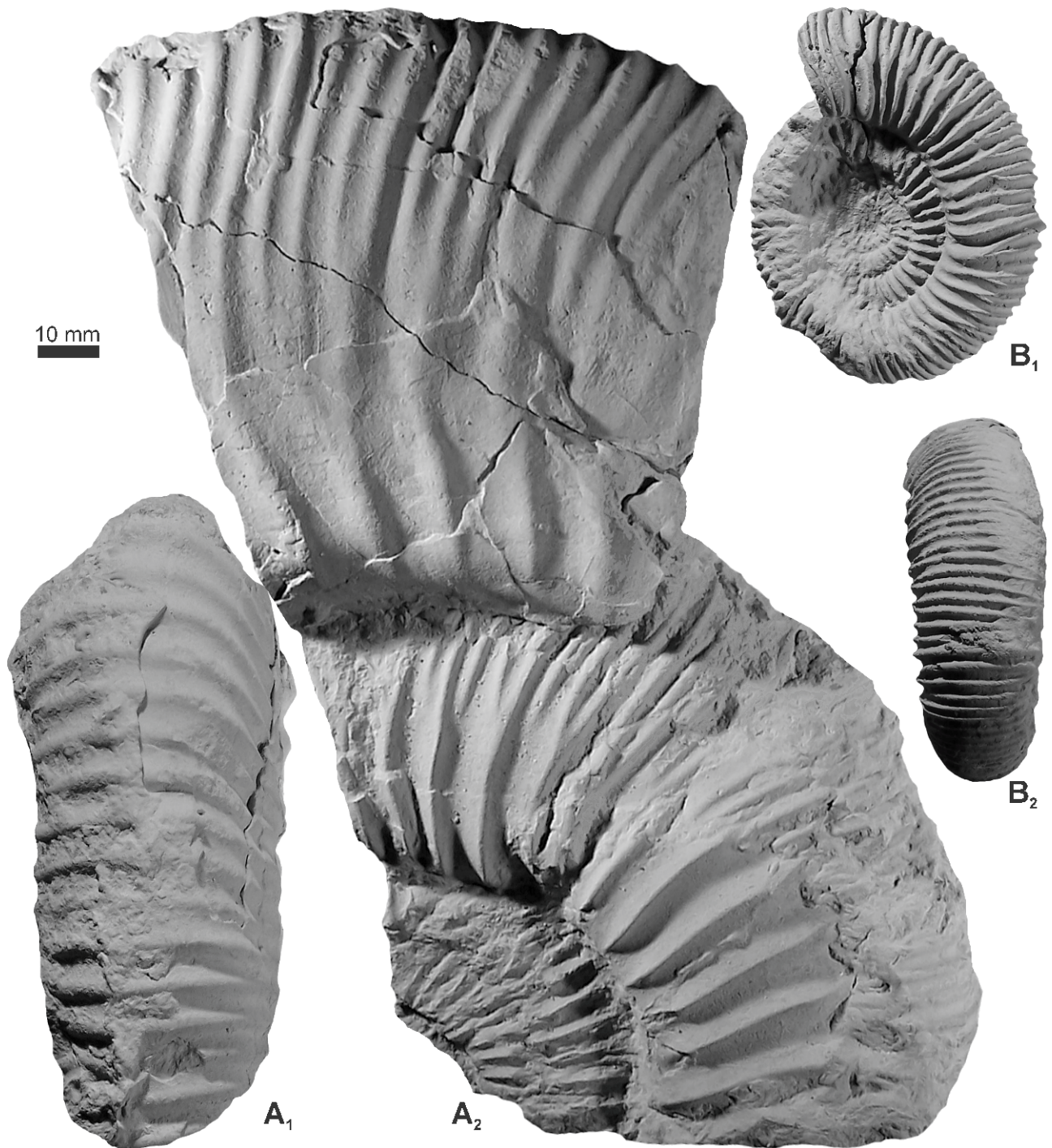1931 *Perisphinctes internispinosus* Krantz – Windhausen: pl. 28: 6

Figure 13. *Windhauseniceras internispinosum* (Krantz, 1926) transient beta, Cerro Granito II, level CG-II-105, Internispinosum Zone. **A**: adult macroconch with the terminal portion of bodychamber (MOZ-PI-8406/4). **B**: macroconch phragmocone (MOZ-PI-8406/2). - All natural size (x1).

1931 *Perisphinctes internispinosus* Krantz – Weaver: 419, pl. 47: 312

1945 *Windhauseniceras* cf. *internispinosum* (Krantz) – Leanza: 23, pl. 21: 6

? 1949 *Windhauseniceras humphreyi* n. sp. – Leanza: 240, figs. 1-2

* 1957 *Windhauseniceras internispinosum* (Krantz) – Arkell: L356, fig. 468(7)

* 1958 *Windhauseniceras internispinosum* (Krantz) – Corvalán & Pérez: pl. 10: 23

? 1959 *Windhauseniceras internispinosum* (Krantz) – Corvalán: 16, pl. 4: 16-17

? 1960 *Windhauseniceras* aff. *internispinosum* (Krantz) – Bürgl: 197, pl. 1: 5

? 1962 *Windhauseniceras* cf. *internospinosum* (Krantz) – Latorre: 107

1980 *Windhauseniceras internispinosum* (Krantz) – Leanza: 43, pl. 8: 2, 4, pl. 9: 1
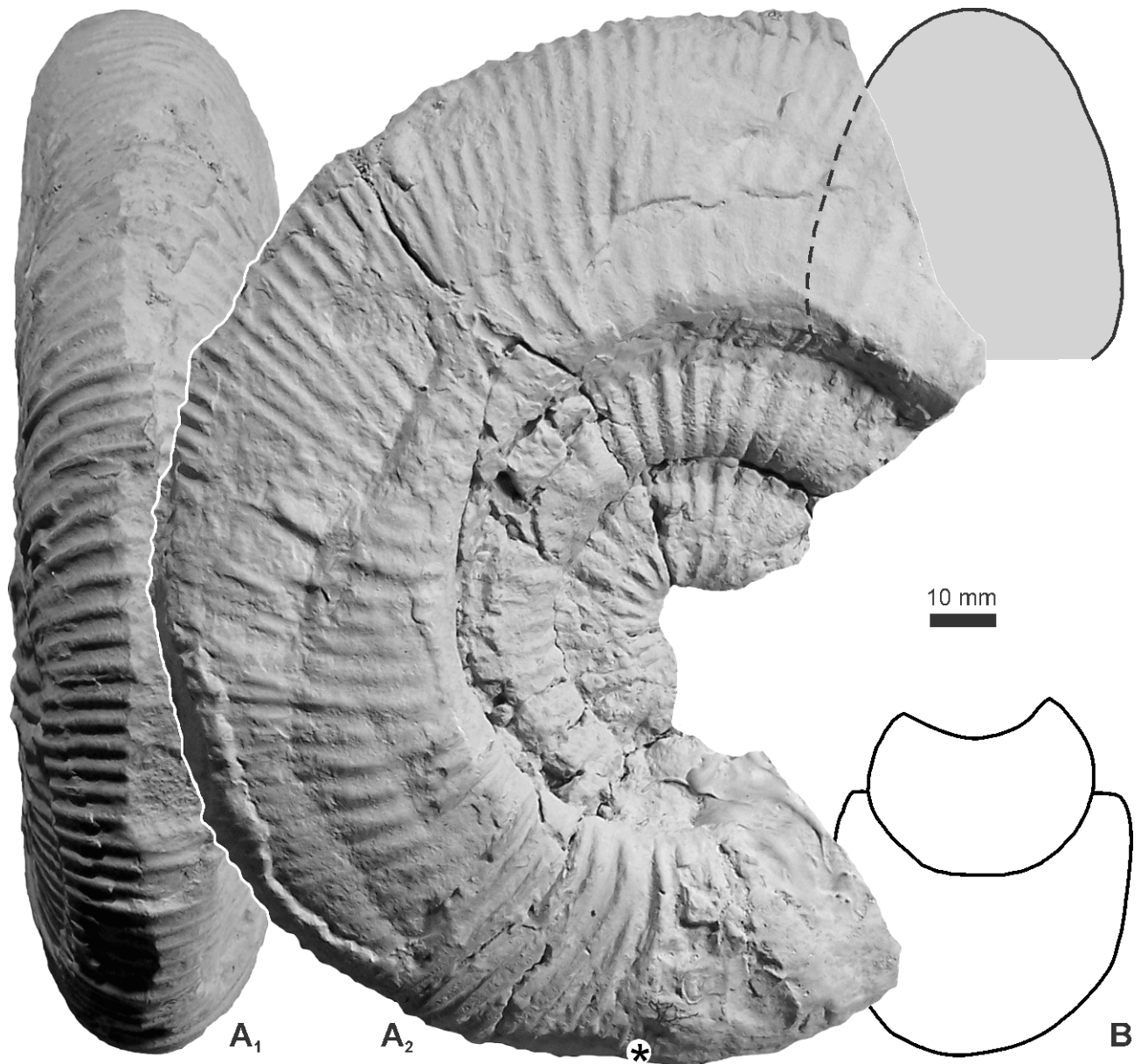
Figure 14. *Windhauseniceras internispinosum* (Krantz, 1926) [M] transient beta, Cerro Lotena, Internispinosum Zone. **A**: Almost complete adult macroconch (MOZ-PI-7431) from level CL-80. **B**: Whorl section (bodychamber gray) of the adult macroconch (MOZ-PI-7654) from level CL-84 shown in Fig. 15A. - Natural size (x1). Asterisk at last septum.

1980 *Hemispiticeras* aff. *steinmanni* (Steuer) – Leanza: 43, pl. 9: 2

1981 *Windhauseniceras internispinosum* (Krantz) – Leanza: pl. 2: 7-8

? 1990 *Windhauseniceras* cf. *internispinosum* (Krantz) – Dorado-Galindo: 14

? 1990 *Windhauseniceras* cf. *internispinosum* (Krantz) – Aguirre-Urreta & Charrier: 265, pl. 1: 9

1992 *Windhauseniceras internispinosum* (Krantz) – Leanza & Zeiss: 1844

1992 *Aulacosphinctes proximus* (Steuer) – Westermann: pl. 81: 2

* 2003 *Windhauseniceras internispinosum* (Krantz) – Parent: 354, fig. 2A-D (lectotype), E-F

2005 *Windhauseniceras internispinosum* (Krantz) – Klein: 3

2007 *Windhauseniceras internispinosum* (Krantz) – Parent et al.: 20, figs. 9-10

2008 *Windhauseniceras internispinosum* (Krantz) – Zeiss & Leanza: 233, figs. 5-6

2008 *Windhauseniceras internispinosum* (Krantz) – Riccardi: fig. 9.20-21

2008 *Aulacosphinctes proximus* (Steuer) – Riccardi: fig. 9.14-15 (refigured from Westerman 1992: pl. 81: 2)

p 2010 *Windhauseniceras internispinosum* (Krantz) – Zeiss & Leanza: 36, pl. 2: 1; non pl. 2: 2, 4-5

p 2010 *Windhauseniceras stipanicici* n. sp. – Zeiss & Leanza: 36, pl. 2: 6; non pl. 2: 3

2011 *Windhauseniceras internispinosum* (Krantz) – Parent et al.: 65, fig. 29F, G; app.-fig. H

2011 *Windhauseniceras* cf. *internispinosum* (Krantz) –

Figure 15. *Windhauseniceras internispinosum* (Krantz, 1926) transient beta, Cerro Lotena, level CL-84, Internispinosum Zone. **A**: adult macroconch with beginning of bodychamber (MOZ-PI-7654), The arrowhead indicates the equivalent size of the lectotype. **B**: complete adult microconch (MOZ-PI-7461/2), L_{BC} = 220°. **C**: ribbing profile through the typical ontogeny of the transient beta. - All natural size (x1). Asterisk at last septum.
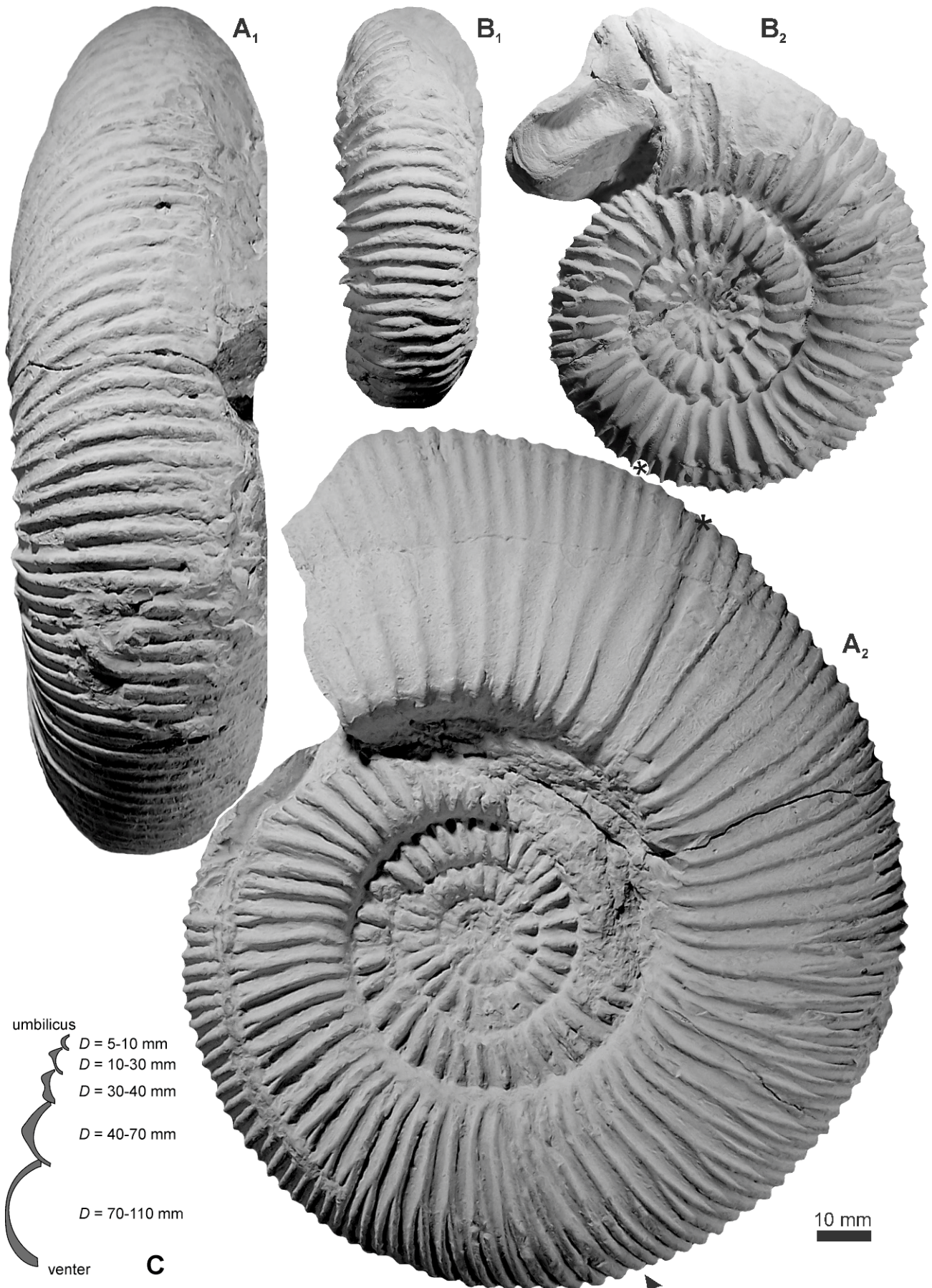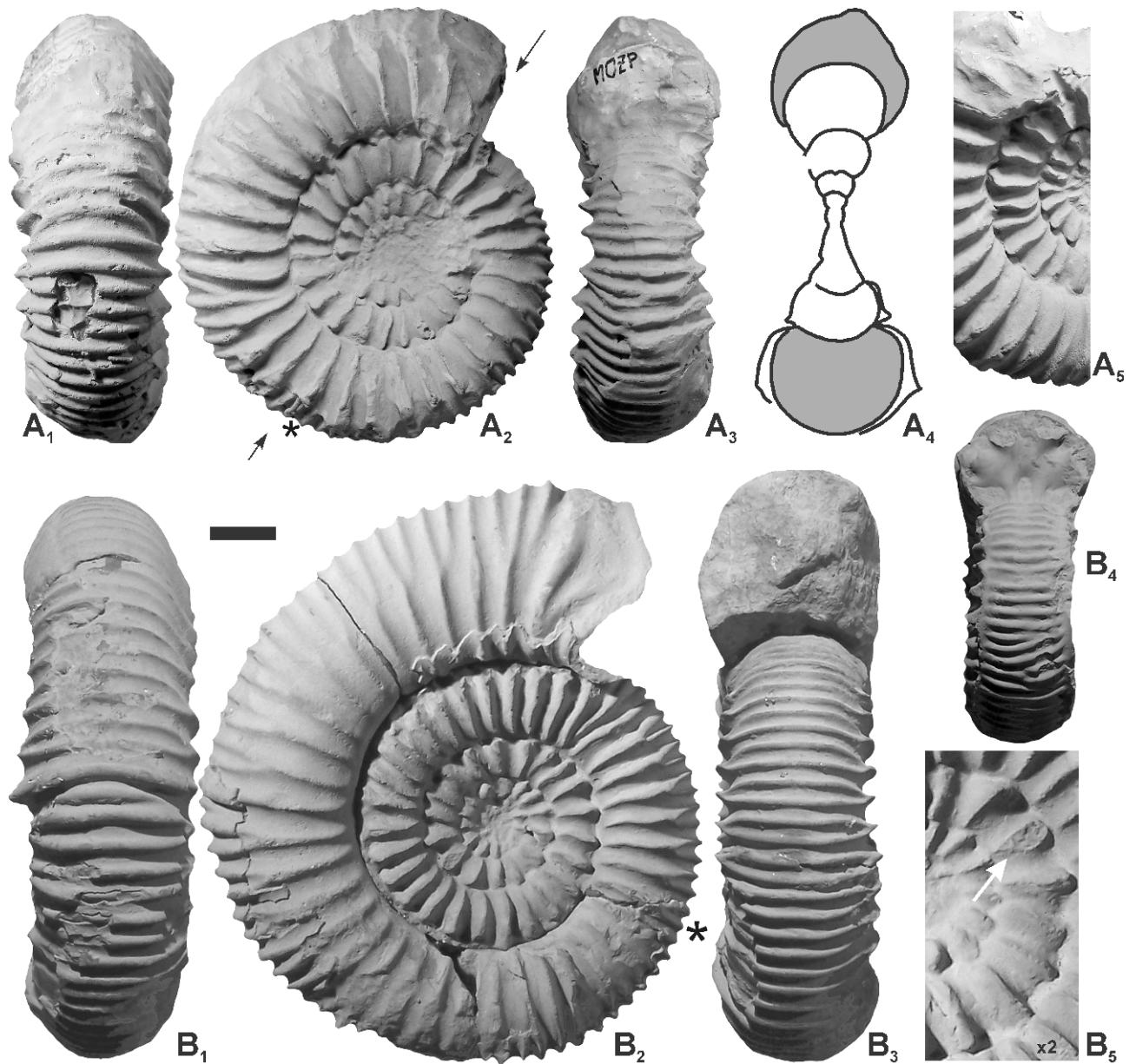
Figure 16. *Windhauseniceras internispinosum* (Krantz, 1926) [m] transient beta, Cerro Lotena, level CL-84, Internispinosum Zone. **A**: Adult microconch with incomplete bodychamber (MOZ-PI-7461/4); ventral (A_1), lateral (A_2), and apertural (A_3) views; A_4: whorl section (bodychamber gray) through the plane of the line indicated by arrows in A_2; A_5: detailed view of the ornamentation of the inner whorls. **B**: complete adult microconch (MOZ-PI-7461/1); ventral (B_1), lateral (B_2) and apertural (B_3) views; B_4: apertural view of the complete phragmocone (bodychamber removed). Note the depressed mid-venter passing to flatten (B_3) then rounded (B_1) in the bodychamber; B_5: detailed view (x2) of the inner whorls, the broken tubercle (arrow) shows a solid structure. - All natural size (x1) except B_5 (x2). Scale bar is 10 mm for all except for B_5 (5 mm). Asterisk at last septum.

Parent et al.: 65, App.-fig. G

? 2012 *Windhauseniceras internispinosum* (Krantz) – Salazar: 81, Fig. 4.10a-10t

2013 *Windhauseniceras internispinosum* (Krantz) – Parent et al.: 23

2015 *Windhauseniceras internispinosum* (Krantz) – Parent et al.: 72, figs. 73-75

? 2016 *Windhauseniceras internispinosum* (Krantz) – Salazar & Stinnesbeck: 15, fig. 12

2017 *Windhauseniceras internispinosum* (Krantz) – Parent et al.: 145, figs. 9B-C, 10-11

2018 *Windhauseniceras internispinosum* (Krantz) –

Garrido et al.: 13, fig. 13A

2018 *Windhauseniceras internispinosum* (Krantz) – Parent et al.: 30, fig. 4A

2019 *Windhauseniceras internispinosum* (Krantz) – Aguirre-Urreta et al.: fig. 8I (refigured from Zeiss & Leanza 2008: fig. 5)

* 2019 *Windhauseniceras internispinosum* (Krantz) – Énay & Howarth: 108, fig. 76(2a-b) lectotype; 76(2c-f)

? 2020 *Windhauseniceras* cf. *internispinosum* (Krantz) – Aldana et al.: 67, 127, 226, 232

? 2020 *Windhauseniceras* sp. – Aldana et al.: 66, 127, 226, 232

Lectotype. The specimen figured by Krantz (1926: pl. 14: 1-2; 1928: pl. 2: 3), designated and refigured by Parent (2003a: fig. 1A). This specimen, an incomplete adult macroconch, comes from Cerro Lotena, from a stratigraphic horizon indicated by Krantz (1928: 47) as "upper Tithonian", actually Internispinosum Zone. The specimen from Cerro Lotena in Fig. 15A is more complete, but at comparable diameter identical in all respects (shell shape and sculpture ontogeny) to the lectotype. This specimen from level CL-84 represents a morphotype of the transient beta of the species, typical in levels CL-80-84 (description below), clearly suggestng that the type horizon of the species must fall within this interval.

Material. Two phragmocones [M], level CL-56; one phragmocone [m?], level CG-II-84; two phragmocones with part of bodychamber [M] and a fragmentary bodychamber [M], level CL-60; one adult [M] phragmocone (MOZ-PI-8404), level CG-II-93; one complete adult [M] and one complete adult [m] (MOZ-PI-7655), level CG-II-98; one juvenil phragmocone, level CG-II-99; one adult bodychamber [M], level CL-68; one adult phragmocone [M], level CL-70; one fragmentary bodychamber [M] (MOZ-PI-7138) and one adult [M] phragmocone (MOZ-PI-5801), level CG-II-102; six phragmocones [M], level CG-II-105 (MOZ-PI-8406/1-6); two almost complete [M] (MOZ-PI-7431/1-2), level CL-80; three complete adult [m] (MOZ-PI-7461/1-3) and two incomplete [M] (MOZ-PI-7654/1-2), level CL-84; one almost complete, adult macroconch (MOZ-PI-7464) loose from levels CL-85-87.

Biometry. The Fig. 18 shows comparatively the shell shape and sculpture ontogenies of the different transients and morphotypes of the species.

General description. The ontogeny of the species has been described in detail, including the lectotype by Krantz (1926, 1928) and Parent (2003a); see also Leanza (1980) and Parent et al. (2007, 2015, 2017b). However, the present material shows a range of morphotypes which much enlarges the spectrum of variation of the species, especially by the occurrence of compressed platyconic and suboxyconic macroconchs – not rare in perisphinctoids. On the other hand there is significant variation between samples of different stratigraphic levels, described below as five transients.

- Macroconch: large to very large (D_p = 200 to 600 mm). Inner whorls evolute, more or less depressed with sharp primaries bi- or rarely trifurcating from a ventro-lateral, spiny tubercle which is lost from different sizes. These tuberculate whorls define a coronate stage. The ventral ribbing may be interrupted or weakened in different parts of the phragmocone, rarely with small spiny tubercles beside a ventral groove. From about D = 30 mm there are 2-4 narrow constrictions per whorl, irregularly distributed and flanked by flared or swollen ribs.

From the last whorl of the phragmocone the range of variation is usually broad, ranging from coarsely ribbed serpenticones to more finely ribbed platyconic to suboxyconic shells.

The adult bodychamber is more compressed, with primaries unevenly divided into two to five secondaries around the mid-flank, dependind on the morphotype – the more compressed the whorl, the lower the point of furcation.

- Microconch: one-sixth to one-half the size of the adult macroconch with the phragmocone indistinguishable from the inner whorls of the macroconch at comparable diameter.

Adult bodychamber isocostate to slightly variocostate. Peristome with short to long lappets which may be projected from swollen ribs.

Transients. A clear characterization of the transients of the

species is important for reconstructing the phylogeny of the species, and for stratigraphic purposes.

- Earliest transient (Fig. 6). In the levels CL-56 and CG-II-84 occurs a very early form of the species, transitional from its ancestor *Catutosphinctes proximus* (Steuer, 1897), but the material is still poor for complete characterization. The phragmocone of the macroconch (Fig. 6A-B) has depressed whorl section with sharp primariy ribs bifurcating in the upper third of the flank; the secondaries cross the broad venter evenly spaced. The innermost whorls are more coarsely ribbed by primaries which bear a spiny ventro-lateral tubercle in the point of furcation, almost covered by the subsequent whorl. Bodychamber not known. The possible microconch (Fig. 6C) is an incomplete, small adult which only differs from the macroconch at comparable diameter by being more strongly ribbed; indistinguishable from the somewhat later microconch in Fig. 9B.

- Transient alpha (Fig. 7), levels CL-58-62. The available specimens are incomplete adults or subadults matching to the specimens of this transient from Pampa Tril as originally described in Parent et al. (2015, 2017b). On the other hand there are more involute and finely ribbed specimens which enlarge the range of variation formerly described.

- Transient CG-II-98 (Figs. 8-9, 10A, B$_2$), levels CG-II-93-99. Macroconch: inner whorls (D < 30 mm) typical for the species, depressed with sharp ribbing and a row of tubercles in the uppermost part of the flank or in the ventro-lateral shoulder. Adult phragmocone and bodychamber broadly variable: from serpenticonic and coarsely ribbed to compressed platycone more involute and densely ribbed. Adult size medium to large: D_p = 200 to 350 mm; the beginning of the adult bodychamber is variable: D_{ls} = 120 to 200 mm. The adult bodychamber length of a specimen of the serpenticonic morphotype (Figs. 9A, 10A) is at least 270°.

Microconch: indistinguishable from the inner whorls of the macroconch at comparable diameter, isocostate, with moderately long lappets (Fig. 9B, 10B$_2$). D_{ls} = 46 mm, D_p = 72 mm, L_{BC} = 305°.

- Transient beta (Figs. 11-16), levels CL-68-86, CG-III-39-45 and CG-II-102-105. The transient beta includes the typical form which has characterized the species in the literature since its introduction. The mode of variation in this transient follows a pattern similar to that of the transient CG-II-98, but extended up to range into compressed and involute suboxyconic shells.

Macroconch: the adult size ranges D_p = 400 to about 600 mm (exceptional specimens). The serpenticonic morphotype is the typical of the species, as represented by the lectotype. Inner to middle whorls (juvenil phragmocone): coronate, whorl section suboval depressed, with sharp and strong ribs bi- or trifurcating from a lamelliform ventro-lateral (or upper flank) tubercle. The tubercles are solid, not hollow, formed from the base of the bearer-rib. The secondary ribs are somewhat finer than the primaries. The coronate stage is variable in extension, from D = 5 mm up to D = 20 to 70 mm, ending in a point of the ontogeny marked by a pair of bifurcated primaries joined in the umbilical shoulder. Adult phragmocone and bodychamber whorl section suboval, becoming higher than wide towards the peristome, especially in the suboxyconic morphotype. Primaries sharp, curved forward, bifurcating in the upper half of the flank in secondaries of the same strength; intercalatories more frequent close to the peristome; all ventral ribs cross the venter unchanged, evenly spaced. D_{ls} = 110 to about 450 mm. The length of the bodychamber, estimated from few incomplete specimens with peristome, ranges from 220° up to at least 280°. Peristome plain and sigmoidal.

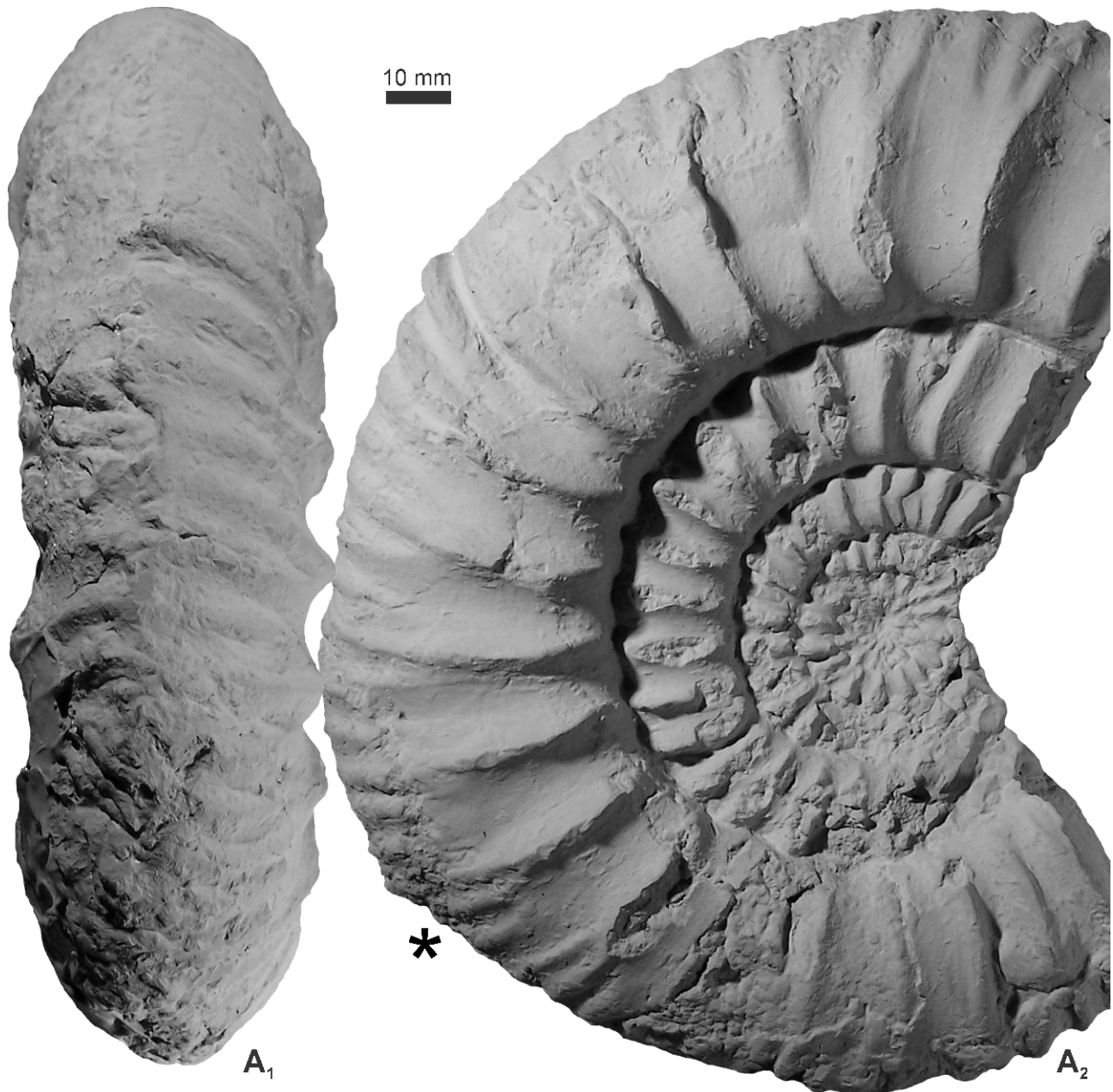The suboxyconic morphotype is, from the subadult

Figure 17. *Windhauseniceras internispinosum* (Krantz, 1926) [M], latest transient, Cerro Lotena, loose from levels CL-85-87, Internispinosum Zone. Adult macroconch with incomplete bodychamber (MOZ-PI-7464). - Natural size (x1). Asterisk at last septum.

phragmocone, more involute and compressed with a very densely ribbed venter.

Microconch: adult size one-fifth to one-third that of the macroconch at peristome. Phragmocone identical to the inner whorls of the macroconch at comparable diameter. The peristome bears long, spatulate lappets preceeded by one or two strong inflate ribs (Fig. 15B, 16B).

- Latest transient (Fig. 17). One macroconch from the interval of levels CL-85-87. It is moderately large with incomplete bodychamber; $D_{ls} = 140$ mm, maximum preserved $D = 172$ mm. Phragmocone with suboval whorl section and widely spaced

sharp, strong primaries; long tuberculate stage from the innermost whorls up to about $D = 100$ mm. The bodychamber, incompletely preserved, remains strongly ribbed in the flanks but with no tubercles, and coarse secondaries and intercalatiories which cross the venter unchanged.

Remarks and comparison. The characteristic juvenile coronate stage of the species consists of lamellar, solid tubercles formed from a suboval widening of the bearer-rib (Fig. $16B_5$). These tubercles are visible from the umbilical window, in contact with the umbilical seam of the subsequent whorl (Fig. $16A_5$). In the best preserved specimens it can be observed that

some primary ribs of the coronate stage show two prominences, one in the umbilical margin and the other forming the ventro-lateral tubercles (Figs. 9B$_3$-B$_4$, 16A$_4$-A$_5$, 15C). It is interesting to note that in the macroconchs of the transient beta studied herein, there are no signs of the short ontogenetic stage with ventral spines observed in the phragmocone of one macroconch from Pampa Tril (Parent et al. 2015: figs. 75A, 76).

Platyconic (Fig. 8) as well as suboxyconic (Fig. 12) specimens are rare, they have been observed mostly as impressions in sections CL, CG-III and CG-II. In these specimens the ribbing is dense to very dense as the whorl section becomes more compressed from middle whorls. The furcation point is situated in lower positions of the flanks in these more compressed morphotypes with respect to the more inflate and evolute ones. This pattern of covariation is commonly observed in perisphinctoids as intraspecific variation, where the most compressed and involute morphotypes show higher proportion of secondary to primary ribs. This pattern could be valuable for the study of the meaning and causes of the broad variation in the relative whorl width within most ammonite species (cf. Hammer & Bucher 2005, Checa & Westermann 1993).

Parent et al. (2015, 2017b) differentiated the transients alpha and beta from Internispinosum Zone assemblages of Pampa Tril (see Fig. 1), and showed that the species evolved from late representatives of *Catutosphinctes proximus*. The material studied herein shows the same morphologic pattern of phyletic evolution recorded in Pampa Tril, but the stratigraphic record is more complete in the study area, allowing to differentiate even earlier and later forms as well as an intermediate one (transient CG-II-98).

The specimens which could be considered as the earliest representatives of *W. internispinosum* (Fig. 6) are superficially similar to the late representatives of *C. proximus* (e.g. Fig. 5C), but can be differentiated by (1) the incipient ventro-lateral tuberculation in the inner whorls, (2) the narrowly splayed secondaries from a lower position in the flank, crossing the venter evenly spaced and unchanged, and (3) the suboval depressed whorl section of the phragmocone. These specimens, from the upper part of the Proximus Zone (level CL-56) and associated with a late transient of *C. proximus* (App. 1), differ from those of the *internsipinosum alpha* Hz. by the shorter coronate stage. These differences and the stratigraphic position are coherent in that these specimens are somewhat earlier than *W. internispinosum* tr. alpha which has been recorded somewhat higher, in the *internispinosum-alpha* Hz. The faunal assemblage which characterizes the *internispinosum-alpha* Hz. in Pampa Tril (Parent et al. 2015: 88) consists of *Parastreblites*? cf. *comahuensis* Leanza, 1980, *Choicensisphinctes* sp. A (in Parent et al. 2011b), *C. proximus*, *Cieneguiticeras* n. sp. A (in Parent et al. 2015), *W. internispinosum* tr. alpha, *Aspidoceras euomphalum* Steuer, 1897, *Pseudhimalayites subpretiosus* (Uhlig, 1878), and *Toulisphinctes* cf. *rafaeli* (Oppel, 1863). The assemblage from the level CL-56 (App. 1) is similar with almost the same species, but the morphotypes of *C. proximus*, *W. internispinosum*, and *P. subpretiosus* show morpho-ornamental differences which become significant when assembled, indicating a different biohorizon, therefore different in age.

The specimens from levels CG-II-93-99 (Figs. 8-10) are intermediate in shell morphology and ornamentation between the transients alpha and beta. Thus, according to its stratigraphic position these specimens are provisionally labelled as transient CG-II-98, in reference to the level of its main occurrence in the section Cerro Granito-2.

The microconch is very characteristic in each transient, especially distinguished by their lappeted peristomes (Fig. 10B), and the slight increase of adult size through the lineage, especially in the transient beta. These microconchs are clearly progenetic, maturing earlier than the macroconchs, halting shell growth at smaller size. This mode of development produces the identity of the microconch with the inner whorls of the macroconch at comparable diameter, differing only by terminal apertural modifications like the lappets, sometimes preceeded by swollen ribs. The size (and age) of male maturation may be more or less variable (Klug et al. 2015, Parent et al. 2019a), but in our sample of microconchs of the transient beta from level CL-84 (three complete, lappeted specimens: mean $D_p = 85$ mm), the variation is low: $C_v = 8\%$.

The specimen figured by Leanza (1980: pl. 9: 2) as *Hemispiticeras* aff. *steinmanni* (Steuer, 1897) is a perfect macroconch of *W. internispinosum*, with a ventro-lateral tuberculated (coronate) stage up to about not less than 80 mm in diameter, ending sightly earlier than in the specimen described above from a similar stratigraphic position, in the upper part of the Internispinosum Zone (Fig. 17). According to the succession given by Leanza (1980: 9), his specimen comes from the uppermost part of the Internispinosum Zone, approximately equivalent to our levels CL-84-87.

Windhauseniceras humphreyi Leanza, 1949 was introduced from an incomplete, possibly adult phragmocone, collected loose from the locality named Arroyo de Los Molles, in the Picún Leufú Subbasin, not far from our study area. The late Tithonian age assumed by Leanza (1949: 241) for this specimen was based on a specimen (presumibly associated) of *Anditrigonia eximia* (Philippi, 1899). This trigoniid is not useful for dating for it ranges most of the Tithonian and Berriasian (Leanza 1993) and the specimens were collected loose in the field. The two inner whorls preserved in the holotype are depressed and coarsely ribbed, as typical for *W. internispinosum*; the outer whorl is suboval-subtriangular higher than wide, bearing primaries that polyfurcate, some in polyschizotomic style, in finer secondaries from the middle third of the flank. This sculpture is identical, at comparable diameter, to that of the suboxyconic morphotypes of transient beta described above (Fig. 12). The "virgatotomic" ribs mentioned by Leanza (1949: 241) are not virgatotomic but polyschizotomic. Thus, *W. humphreyi* should be considered a junior synonym of *W. internispinosum*, matching the morphotypes with densely ribbed outer whorls.

The holotype of *Windhauseniceras stipanicici* Zeiss & Leanza (2010: pl. 2: 6) is indistinguishable from the compressed and finely ribbed, platyconic morphotype of *W. internispinosum* transient CG-II-98 (Fig. 8). This holotype, collected without stratigraphic information, could likely come from the Internispinosum Zone.

Age and distribution. *W. internsipinosum* was recorded in the following intervals: CL-56 to CL-86(87?), CG-III-35 to CG-III-55, and CG-II-90 to CG-II-108. Thus, in the study area the species ranges from the uppermost Proximus Zone up to the top of the Internispinosum Standard Zone, and perhaps the base of the Alternans Zone. Nearly complete specimens, as well as fragmentary macro- and microconchs and material loose in the field, are abundant through the Internispinosum Zone outcrops of Cerro Lotena and Cerro Granito-II and III. The species is not only abundant but the predominant element in the fauna of the Internsipinosum Zone, especially in its biozone. This fauna includes (see details in App. 1): *Indansites zapalensis* (Zeiss & Leanza, 2010), *Zapalia triplex* Zeiss & Leanza, 2010, *Zapalia* cf. *fascipartita* Leanza & Zeiss, 1990, *Choicensisphinctes* n. sp. A, *Cautosphinctes rafaeli* Leanza & Zeiss, 1992, *Catutosphinctes araucanensis* (Leanza, 1980) [M&m], *Catutosphinctes* n. sp. A, Simoceratidae? indet., *Aspidoceras euomphalum*, *Pseudhimalayites subpretiosus*, *Toulisphinctes* cf. *rafaeli*, *Corongoceras huarpense* n. sp. (described below), and *Corongoceras* cf./aff. *lotenoense*.

Within the Neuquén Basin the species is well represented, mostly restricted to the Internispinosum Standard Zone (see synonymy for a full list of published records). The specimen from Mina La Eloisa, Mendoza Province, figured without stratigraphic information as *Aulacosphinctes proximus* (Steuer)
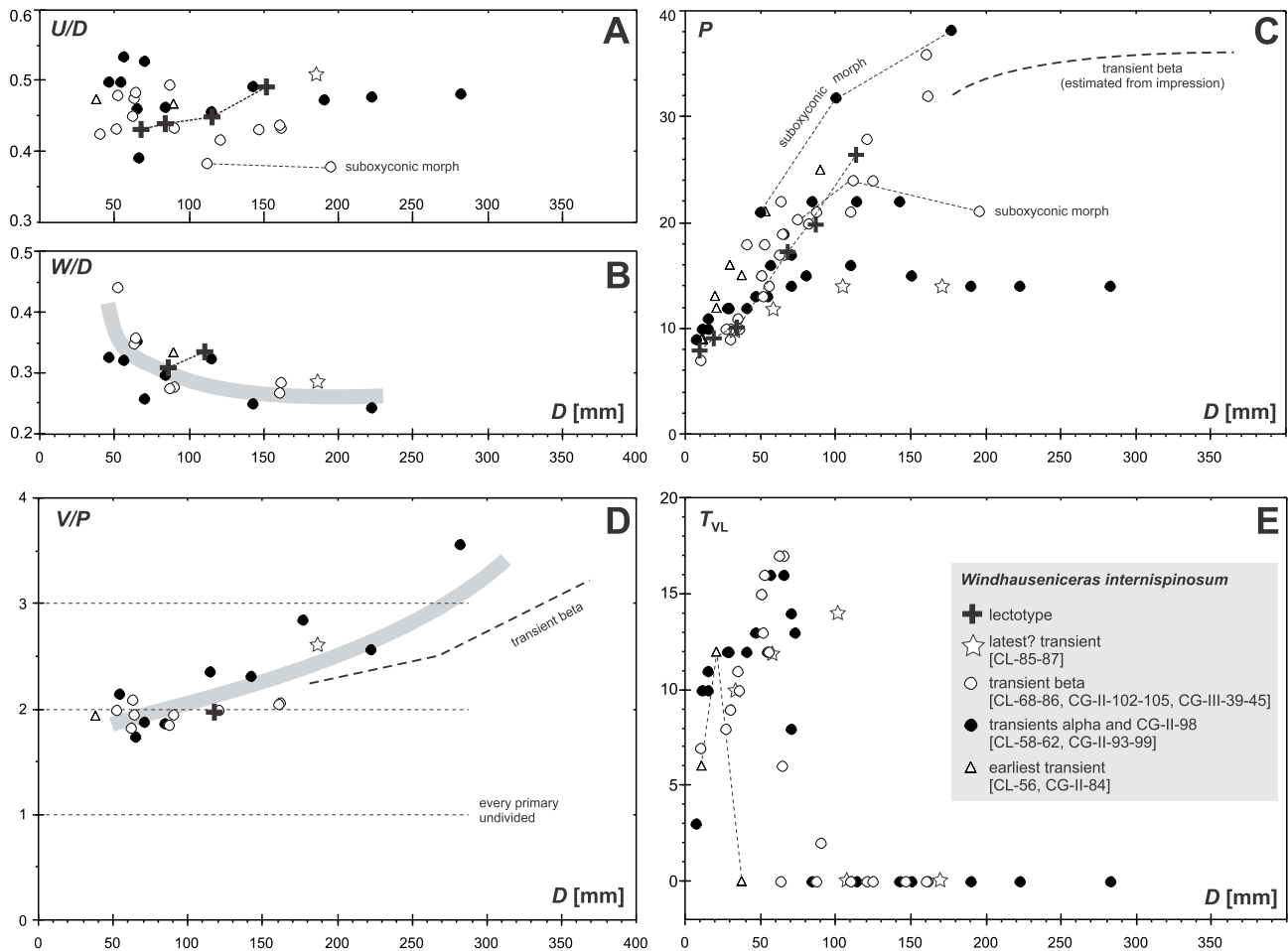
Figure 18. Biometric characterization of the ontogeny of shell-shape and ornamentation of the transients of *Windhauseniceras internispinosum* (Krantz, 1926). **A**: relative umbilical diameter versus diameter. **B**: relative whorl width versus diameter. **C**: number of primary ribs per half whorl versus diameter. **D**: ratio of ventral to primary ribs versus diameter. **E**: number of ventro-lateral tubercles per half whorl versus diameter, showing the duration of the coronate stage which ceases by fading of the tubercles (measured as zero in the T_{VL}-axis). The bold gray curves in B and D show the general trends of the species as a whole. The broken line in C and D represents observations made on molds of not preserved portions of the specimens.

in Westermann (1992: pl. 81: 2; redundantly refigured by Riccardi 2008), seems to be an evolutionary transitional form, likely already a *W. internispinosum* transient alpha (Parent et al. 2015: fig. 74A, C), with incipient ventro-lateral tubercles from the inner whorls, thus, most likely collected from the base of the Internispinosum Zone.

The specimens from the Tithonian of Baños del Flaco Fm (Chile) figured as *W. internispinosum* by Salazar & Stinnesbeck (2016: fig. 12) do not seem to belong to *Windhauseniceras*, because of the densely and finely ribbed phragmocone, lacking the diagnostic coronate stage. However, these Chilean specimens have some resemblance with the earliest transients of the species in Fig. 6. The occurrence of *W. internispinosum* in northwestern South America and the Caribbean area seems possible but the documentation is not conclusive. The fragment of ammonite from the Upper Tithonian of Boyacá (Central Colombia) figured as *W.* aff. *internispinosum* by Bürgl (1960: pl. 1: 5) is indeterminable. The citations from Perú (Aldana et al. 2020) have not been illustrated, and are not currently available (M.I. Aldana, pers. comm. 06/11/2021). In Mexico there are no records up today (A.B. Villaseñor, pers. comm. 29/08/2019). In Cuba the species has been only cited in unpublished reports

(compilation in Pszczółkowski & Myczyński 2003: table 4); unfortunately the specimens are not traceable (A. Pszczółkowski, pers. comm. 06/01/2021). The only we can conclude is that ammonites at least similar to *W. internispinosum* occur along northwestern and Central America, what rise interest for future studies.

Origin and evolution of the genus *Windhauseniceras*

Only one species is recognized in the genus: *W. internispinosum*. The new material described above allows to refine the interpretation of the origin of *Windhauseniceras* from *C. proximus* and its evolution, elaborated in Parent et al. (2015, 2017b) based mainly on the records from Pampa Tril. Intermediate froms between *C. proximus* and *W. internispinosum* occur through several levels in the study area, in a more expanded and fine record than north of the Huincul High, in Pampa Tril, Mallín Quemado, and Arroyo Cieneguita. The phyletic evolution of *W. internispinosum* shows a trend of slow changes in the ontogeny of the successive transients (Fig. 19):
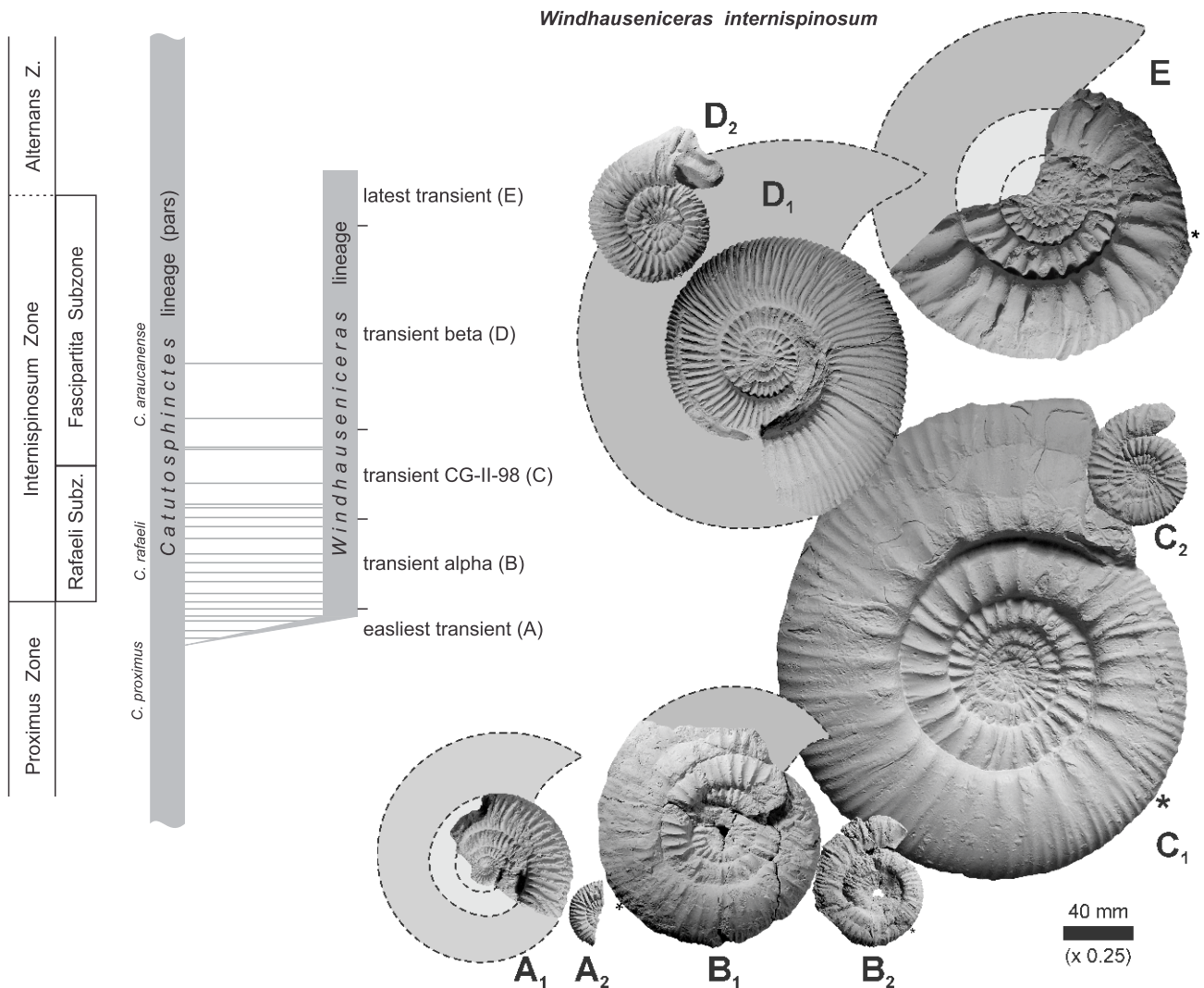
Figure 19. Model for the origin and evolution of *Windhauseniceras internispinosum* with hybridization (represented by the gray horizontal lines) with its ancestor *Catutosphinctes proximus* and later forms of the *Catutosphinctes* lineage. As the differentiation progresses the hybridization would decay rapidly. The chronostratigraphic age of the transients is an approximation based on the occurrences in Cerro Lotena-Cerro Granito, Portada Covunco, Mallín Quemado, Pampa Tril, and Arroyo Cieneguita as explained in the text. The lineage is represented by typical individuals: **A**: macro- and microconch of the earliest transient, from level CL-56 (in Fig. 6A, C herein). **B**: macro- and microconch of transient α (from Parent et al. 2017: figs. 9C and 10). **C**: macro- and microconch of transient CG-II-98 from level CG-II-98 (in Fig. 9A-B herein). **D**: macro- and microconch of transient β (in Fig 15A-B herein). **E**: macroconch of the latest transient, from level CL-85-87 (in Fig. 17 herein). - All x0.25. The asterisks indicate the last septum.

- The macroconchs show a general pattern of enlargement of the adult size and widen of the spectrum of variation, including compressed and involute platyconic to suboxyconic morphotypes; the coronate stage tends to be stronger and to reach larger diameters towards the late transients (Fig. 18E).

- The microconchs become sligthly larger, with larger lappets in the late transients (Fig. 10B).

Beside intermediate forms between *W. internispinosum* and *C. proximus* (Figs. 6, 9B; see also Parent et al. 2015, 2017b: fig. 9C) of the lower Internispinosum Zone, also occur rare specimens hard to classify (e.g. Fig. 7C), sharing features of these species. Some of these forms could belong to *Windhauseniceras* or could be closely related, somehow, to *C. proximus* and/or *C. rafaeli*. The occurrence of these intermediate forms in several stratigrahic levels and falling out of the ranges of variation, indicate they cannot be considered as merely intraspecific transitional forms.

Similar cases, of forms with intermediate or hybrid morphology between coexisting closely related species, have been described, e.g., in cardioceratids (Callomon 1985), reineckeids (Jain et al 1996), and early members of the Zapaliinae (Parent et al. 2011a). In these cases hybridization between members of different but closely related species has been suggested, as producing new and/or intermediate morphologies. Hybridization is a fairly common and widespread phenomenon (e.g. Gardner 1997, Abbott et al. 2013); in living cephalopods several cases are reported (e.g. Naef 1972: 602, Gabel-Deickert 1995, Roper et al. 1998: 421) and could likely be more frequent but hard to detect in natural habitats. Translation of this condition to ammonoids is natural, and so it is not unreasonable to assume that the intermediate and the rare forms could be hybrids between early *W. internispinosum* and the *Catutosphinctes* lineage, producing more or less persistent or just ephemeral "sublineages". The

early representatives could have hybridized with *C. proximus* and later with *Catutosphinctes rafaeli* (see associations in App. 1) for a time interval of many (perhaps hundreds) generations, seen as fossil "recorded instances" (Parent et al. 2017b: 149). The hybridization rate would have declined exponentially with the progress of the differentiation, as seen in living dioecious organisms (Mallet et al. 2015).

This hypothesis of early evolutionary stages of *W. internispinosum* hybridizing with the lineage of its ancestor is represented in Fig. 19, where the thin gray connecting lines represent the hypothesis of episodic and mostly ephemeral hybridization.

Hybridization leads to the model of reticulated evolution (e.g. Sylvester-Bradley 1977, Callomon 1985, Turner 2002, Arnold & Fogarty 2009). It is interesting to note that considering reticulated evolution in ammonoids could solve many taxonomic puzzles as a matter of non-sharp boundaries between closely related species – especially in the early stages of their evolution, and possibly even later (Mallet et al. 2007).

Genus *Corongoceras* Spath, 1925

Type species. *Corongoceras lotenoense* Spath, 1925; by original designation.

Remarks. As pointed out by Parent et al. (2011b) the concept of the genus *Corongoceras* was very limited because the holotype of the type species is an incomplete phragmocone, with no indications of the sex and growth stage of the specimen. After the first description of abundant horizoned material of the genus from Arroyo Cieneguita (Parent et al. 2011b) and Pampa Tril (Parent et al. 2015), and the separation (Bulot et al. 2014) of the Tethyan forms formerly included in the genus, it was possibly to elaborate a revised definition of the genus (Énay & Howarth 2019). The new material described herein, including the type species in its type locality and probably type horizon, fits well this revised definition indicating its suitability. Furthermore, the new material has given the basis for the elaboration of the evolutionary model proposed below.

Corongoceras cf. *cordobai* Verma & Westermann, 1973
Fig. 20

Material. One almost complete, adult ?microconch (MOZ-PI-9367/2) from Cerro Lotena, level CL-60, lower Internispinosum Zone (*internispinosum-alpha* Hz.).

Description. Small and slender serpenticone, very evolute from the inner whorls (U/D ranging 0.43 at D = 23 mm to 0.51 at maximum preserved D = 55 mm). The whorl section is suboval depressed in the inner whorls passing to subrectangular in the bodychamber (W/H_1 = 1.1). Ribbing strong and sharp. Primaries subradial, borning in the umbilical wall; most of them simple, undivided, only one each three-six bifurcating in the middle of the flank from a mild prominence that in the adult phragmocone is already an incipient tubercle. All ribs reach the venter evenly spaced, each one ending in a small, elongated tubercle besides a well marked ventral smooth band.

The bodychamber begins at D_{ls} = 42 mm; L_{BC} = 270° but a little incomplete; it is uncoiled and slightly compressed indicating unquestionably the specimen is adult. The isocostate sculpture suggests the specimen is an adult microconch.

Remarks and comparison. The present specimen is very similar to the holotype and the paratype of *C. cordobai* (Verma & Westermann 1973: pl. 53: 2-3), however differing by the presence of a ventral groove. *C.* cf. *cordobai* differs from *C. huarpense* n. sp. (described below) by the slender shell and the predominance of undivided, stiff primary ribs. Nevertheless, the
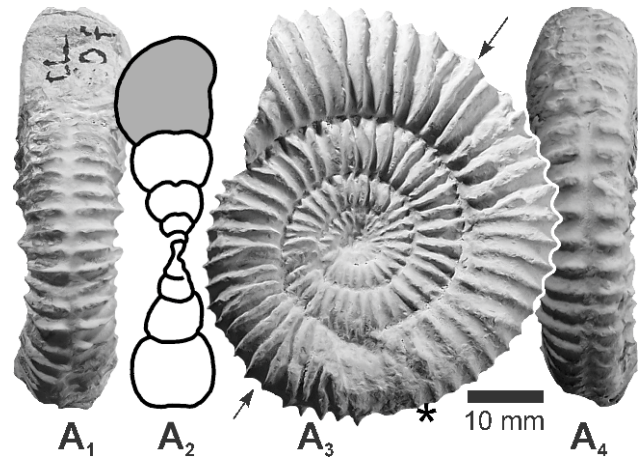

Figure 20. *Corongoceras* cf. *cordobai* Verma & Westermann, 1973. Adult ?microconch with incomplete bodychamber (MOZ-PI-9367/2), level CL-60, Internispinosum Zone. A$_2$: whorl section (bodychamber gray) through the plane of the line indicated by arrows in the lateral view A$_3$. - Natural size (x1). Asterisk at last septum.

relationships cannot be evaluated significantly from the single specimen known of *C.* cf. *cordobai*.

Wichmanniceras mirum Leanza, 1945 is also very similar in shell-shape and ribbing, but differs by the ribs looped into rounded ventral tubercles in the outermost whorl. On the other hand the stratigraphic positon of the holotype is in the lower Alternans Zone (possibly in the *vetustum* Hz.), well above the occurrence of *C.* cf. *cordobai* (lowermost Internispinosum Zone, *internispinosum alpha* Hz.).

Corongoceras huarpense n. sp.
Fig. 21

?	1907	*Hoplites koellikeri* Oppel – Haupt: 201, pl. 9: 7d-e
p	1973	*Corongoceras cordobai* n. sp. – Verma & Westermann: 248, pl. 53: 4-5, pl. 54: 1
?	1973	*Corongoceras cordobai* n. sp. – Verma & Wertermann: 248, pl. 54: 2
	1980	*Corongoceras lotenoense* (Spath) – Leanza: 45, pl. 6: 6
?	1995	*Corongoceras alternans* (Gerth) – Romero et al.: pl. 16: 5
	2009	*Corongoceras* sp. A – Shome & Bardhan: 3, pl. 1: e, pl. 2: a-b
?	2016	*Corongoceras evolutum* Corvalán – Salazar & Stinnesbeck: 174, fig. 21J-Q

Derivation of the name. After Huarpes (or Warpes), one of the groups of native American, Andean-Subandean inhabitants of Argentina, mainly in the provinces Mendoza and San Juan.

Type locality and horizon. Cerro Lotena (Fig. 1), Vaca Muerta Fm, lower part of the Internispinosum Zone, level CL-66 (Fig. 3).

Holotype. The adult macroconch with one quarter whorl of bodychamber (MOZ-PI-7434/2) from level CL-66, shown in Fig. 21F.

Other material. 7 well-preserved specimens from Cerro Lotena (MOZ-PI-7434/1, 3-7), levels CL-62-70. Fragmentary specimens from level CL-70.
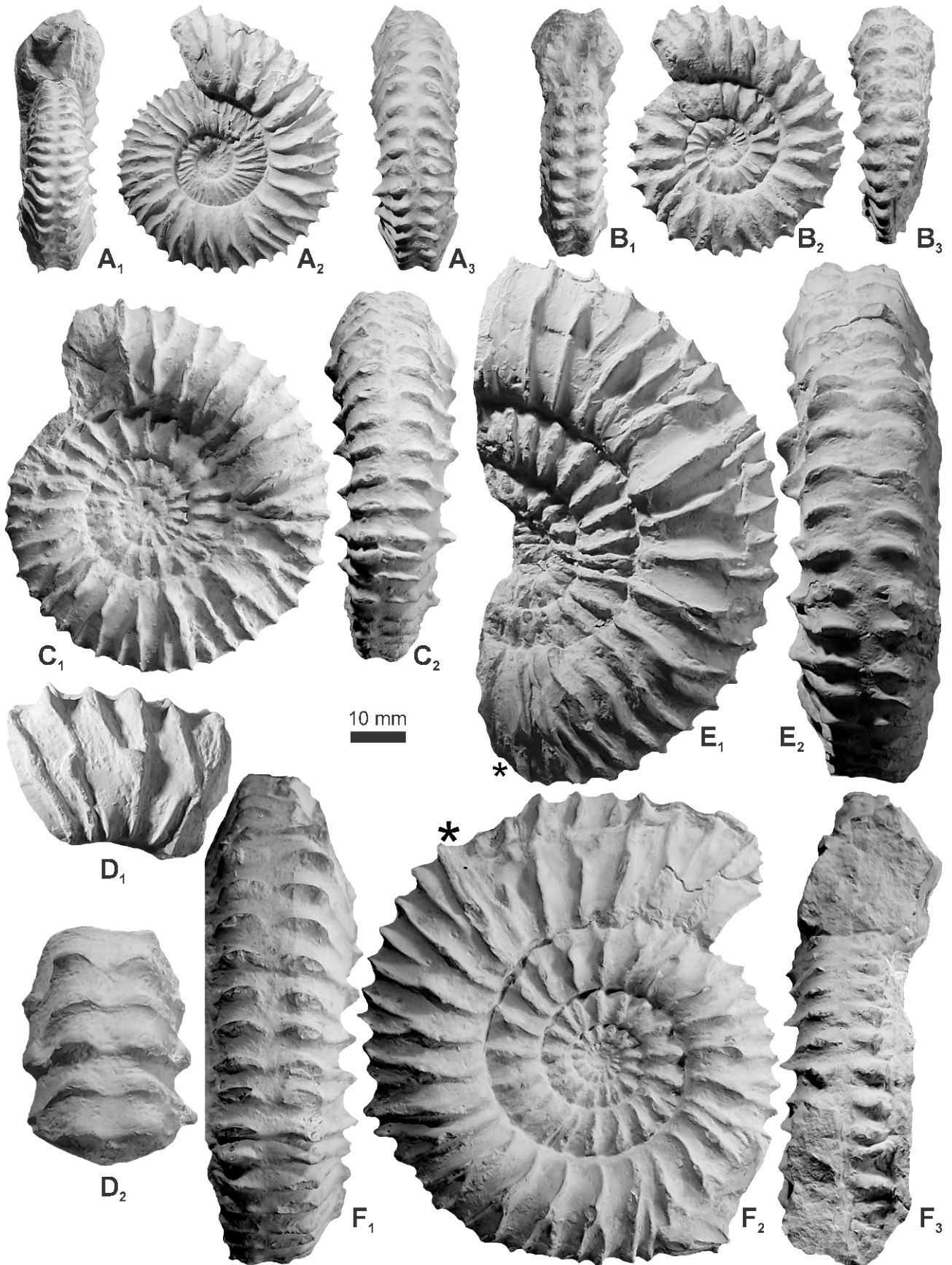
Figure 21. *Corongoceras huarpense* n. sp., Cerro Lotena, lower Internispinosum Zone. **A**: phragmocone (MOZ-PI-7434/4), levels CL-62-66. **B**: phragmocone (MOZ-PI-7434/1), level CL-66. **C**: macroconch phragmocone (MOZ-PI-7434/5), levels CL-62-66. **D**: fragment of adult bodychamber (MOZ-PI-7434/6) showing the strong development of the lateral and ventral lamellar tubercles, level CL-70. **E**: adult macroconch with incomplete bodychamber (MOZ-PI-7434/3), level CL-70. **F**: holotype, adult macroconch with incomplete bodychamber (MOZ-PI-7434/2), level CL-66; remains of shell indicate the bodychamber is at least half-whorl long. - All natural size (x1). Asterisk indicating the last septum.

Description. Macroconch. Shell-shape and ornamentation very constant throughout the ontogeny and among individuals, just varying in rib density in the inner whorls. Widely umbilicated (U/D = 0.36-0.54) and very evolute (H_2/H_1 = 0.70-0.80), with suboval to subrectangular whorl section (W/H_1 = 0.90-1.20). Ornamentation composed of sharp, slightly prosocline primary ribs born in the umbilical seam. Most primaries form, in mid-flank or slightly upper, a radially elongate, sharp swollen or tubercle from which originate the secondaries. Every secondary rib, as well as the undivided primaries, end in the ventro-lateral shoulder, with formation of an elongate lamellar spine, leaving a well defined and persistent smooth ventral band.

The adult bodychamber (best preserved in the specimen in Fig. 21E and the holotype) retains the style and density of ribbing, but rare simple primaries occur, some flared. It is uncoiled and occupies, at least, the last half-whorl from D_{ls} = 83 mm; peristome unknown.

Microconch. The slender specimen in Fig. 21B could be a microconch; it is completely septated, but incipiently uncoiled pointing to a small adult.

Remarks and comparison. The new species is included in *Corongoceras* because of the evolute mid-sized shell, with sharp ribbing and tubercles in the middle-upper flank and in the flattish venter, flanking a smooth ventral band or groove.

The only significant variation between the available specimens is observed in the rib-density of the inner whorls, but under an invariable ornamental style: some rare specimens show a short stage of finer and denser ribbing, of variable duration, through one-half to an almost a whole whorl. The little changing ontogeny of *C. huarpense* n. sp. produces an evolute ammonite with sharp ribbing bifurcating from a spiny tubercle, and ending over the ventro-lateral shoulder forming rows of evenly spaced tubercles besides a persistent smooth ventral band.

Considering the abundant fragmentary specimens of the new species loose in the scree, it is clear that in the lower part of the Internispinosum Zone in Cerro Lotena it must be abundant. However, fresh specimens are very difficult to obtain and prepare from the hard marls and the hard concretions in the calcareous siltstones.

C. huarpense n. sp. differs from *C. lotenoense* by its constant ontogeny including the whorl section, the consistent lateral tuberculation, and the well marked smooth ventral band flanked by tubercles formed at the end of each ventral rib.

The short stage of the early ontogeny in which the ribbing is denser (Fig. 21A-B) is also observed in *Corongoceras mendozanum* (Behrendsen, 1891), described in Parent et al. (2011b, 2015), and *C. lotenoense* (Fig. 23A), appearing as a characteristic of the genus. Notably, this stage of dense and fine ribbing is developed in the adult macroconch bodychamber of *C.* aff. *mendozanum* from the upper Internispinosum to lower Alternans zones of Mallín Quemado (Fig. 26; specimen figured as *C. mendozanum* in Garrido et al. 2018: fig. 13D), and Pampa Tril (Parent et al. 2015: fig. 77A). The close genetic relationships between *C. mendozanum* and *C. huarpense* n. sp. is evidenced by the specimen in Fig. 21A. This ammonite could pass as a perfect *C. mendozanum* if not making part of an assemblage of older age and with transitional forms between the coarsely and the densely variants of *C. huarpense* n. sp.

Macroconchs of *C. mendozanus* are differentiated from *C. huarpense* n. sp. by its different ontogeny, showing a change from stout innermost whorls to compressed platyconic juvenile and adult whorls, with relatively narrower umbilicus (cf. Parent et al. 2011b: figs. 33B and 34F, Garrido et al. 2018: fig. 13D). The Internispinosum Zone *C. huarpense* n. sp. could have been considered as an early transient of *C. mendozanum*, but the stratigraphic gap and the consistent differences between the ontogenies lead us to separate them as a different species.

Furthermore, although the most compressed specimens of *C. huarpense* n. sp. are similar to those densely ribbed *C. mendozanum*, in this latter the very evolute specimens with low flanks looking like the typical *C. huarpense* n. sp. are very rare (Parent et al. 2011b: fig. 34G).

The holotype of *Corongoceras evolutum* Corvalán, 1959 (a fragment of whorl), from about the Alternans Zone of central Chile, differs from *C. huarpense* n. sp. by the more densely ribbed venter by ribs with no tubercles, and the intercalation of simple primaries between the bifurcates. The specimens from central Chile figured by Salazar & Stinnesbeck (2016: fig. 21J-Q) as *C. evolutum* are actually closer to *C. huarpense* n. sp. because of the ventral tuberculation.

The Internispinosum Zone specimen figured as *C. lotenoense* by Leanza (1980: pl. 6: 6) clearly belongs to *C. huarpense* n. sp. This specimen is very interesting because of the irregular occurrence of bold, bituberculate ribs. This structure is also present in the phragmocone of late representatives of *W. internispinosum* (Fig. 15C, 16A; see description above) and in some specimens of *C. huarpense* n. sp. (Fig. 21E), but it is not known in any other species of the abundant ammonite fauna of the Internispinosum Zone. The occurrence of this character is here interpreted as additional evidence of close genetic relationships between these genera, rooted in *Catutosphinctes proximus* which bears the genus-diagnostic character of sharp, more or less risen points of rib furcation throughout the phragmocone.

The fragmentary *Corongoceras* specimen from Cerro Yana Allpa (southwestern Peru) figured by Romero et al. (1995: pl. 16: 5) seems comparable with *C. huarpense* n. sp. or *C.* cf./aff. *lotenoense* (described below). However, the Peruvian specimen is only a fragment and the stratigraphic position is barely informed as "upper Tithonian", preventing further discussion.

Corongoceras fibuliferum Enay, 2009 and *Corongoceras helmstaedti* Enay, 2009 from the Blanfordiceras-assemblage of the Tithonian of Thakkhola, Central Nepal (rather equivalent with the Alternans Zone; see Parent et al. 2015) are somewhat similar in shell-shape and ornamentation to *C. huarpense* n. sp. Nevertheless, both species are more involute, the spines are very small, the bifurcation is in a low angle, and secondaries are regularly looped on the ventro-lateral spines. These differences are significant enough for distinguishing these species from *C. huarpense* n. sp. as well as from *C. lotenoense* and *C. mendozanum*. *Corongoceras* sp. A (in Shome & Bardhan 2009: pl. 1: e, pl. 2: a-b) can be assigned to *C. huarpense* n. sp. according to its morphology and ornamentation.

Age and distribution. The stratigraphically controlled material of *C. huarpense* n. sp. comes from levels CL-62-70 of the Internispinosum Zone. In this stratigraphic interval we have recorded a very rich fauna characteristic of the lower part of the zone (see App. 1), including some diagnostic elements of the zone: *W. internispinosum* [M&m] transient alpha, *Catutosphinctes rafaeli* [M], *Catutosphinctes araucanensis* [M&m], and *A. euomphalum* [M] (see also Leanza 1981a, Leanza & Zeiss 1992, Zeiss & Leanza 2010, Parent et al. 2007, 2008, 2015).

Corongoceras cf./aff. *lotenoense* Spath, 1925
Fig. 22

Material. Several fragmentary specimens (MOZ-PI-7440, 7458) from the interval of levels CL-74-86, mostly ex-situ. Five incomplete specimens (MOZ-PI-8405/1-5) from level CG-II-99. Middle to upper part of the Internispinosum Zone.

Remarks and comparison. Abundant fragmentary specimens which seem to represent a species exhibiting a combination of sculptural characters (or character states) of *C. huarpense* n. sp. and *C. lotenoense*. The stratigraphic occurrence is consistently
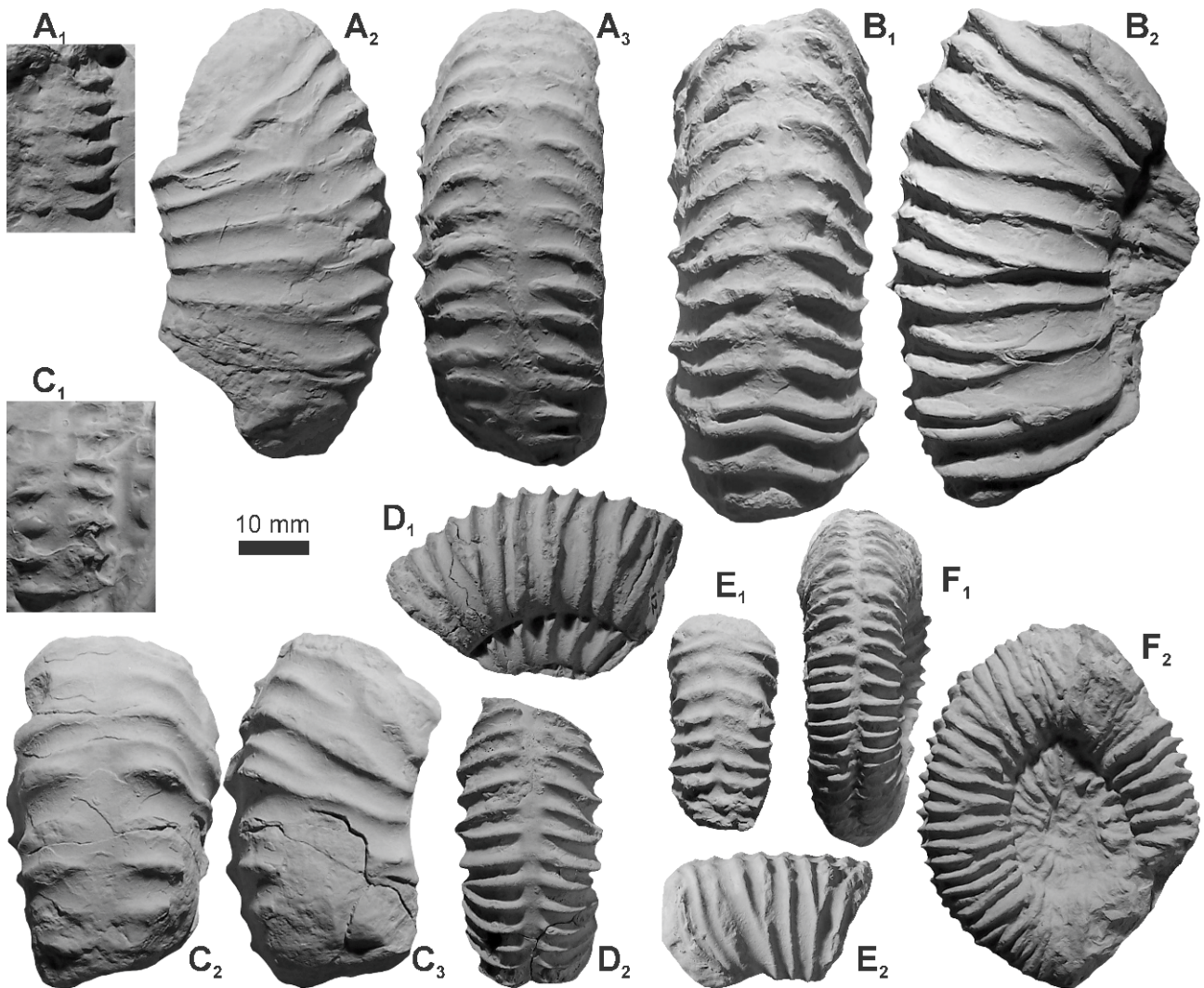
Figure 22. *Corongoceras* cf./aff. *lotenoense*, middle-upper Internispinosum Zone. **A**: portion of a macroconch adult bodychamber with remains of phragmocone (MOZ-PI-7440), Cerro Lotena, levels CL-74-80; A₁: plaster cast of the ventral area of the preceding whorl (phragmocone). Note the persistence of the smooth ventral band flanked by lamellar tubercles. **B**: portion of an adult macroconch bodychamber (MOZ-PI-7458), Cerro Lotena, levels CL-74-80, ventral ribbing weakened, with no ventro-lateral tubercles. **C**: portion of an adult macroconch bodychamber (MOZ-PI-7456), Cerro Lotena, levels CL-74-80; C₁: plaster cast, ventral area of preceding whorl (phragmocone). **D-F**: incomplete phragmocones with remains of bodychamber (MOZ-PI-8405/1-3), level CG-II-99. - All natural size (x1).

between the ranges of these latter species in the sections CL, CG-II and CG-III.

These specimens are characterized by a subrectangular, ventrally tabulate whorl section, with the last whorl of the phragmocone and the bodychamber tuberculated. The lateral ribbing is more or less dense, composed of sharp primaries, most of them bifurcating from a more or less marked swollen or radially elongate tubercule in the upper half of the flank. The ventral ribbing is evenly distributed; all the ribs end besides a more or less wide smooth band. One of the specimens has stronger and more distant lateral and ventral tubercles, and the mid-ventral band is broad.

The closest resemblance of the present species is with *C. lotenoense*, differing by the more compressed adult whorls and the invariably interrupted ventral ribbing. We have labelled this form as *C.* cf./aff. *lotenoense* (cf. because of the fragmentary condition of the available specimens, which seem to differ significantly from the aff. species). It can be assumed it must be

an phyletic intermediate form between *C. huarpense* n. sp. and *C. lotenoense*.

One of the specimens (Fig. 22E) could be the terminal part of the bodychamber of a microconch. Based on estimations of adult sizes, this specimen is smaller than the remaining ones. It is more compressed, and the ventral ribbing is slightly projected forwards. The last ribs are undivided and bending forward, as typical in perisphinctoids preceeding the lappets.

The specimen figured by Haupt (1907: pl. 9: 7d-e; refigured in Parent 2001: fig. 9C) could be assigned to *C.* cf./aff. *lotenoense*, but the ribs cross the venter uninterrupted, and its stratigraphic position is uncertain.

Corongoceras lotenoense Spath, 1925
Fig. 23A-E

*   1907 *Hoplites köllikeri* Oppel – Haupt: 201, pl. pl. 9: 7a-b
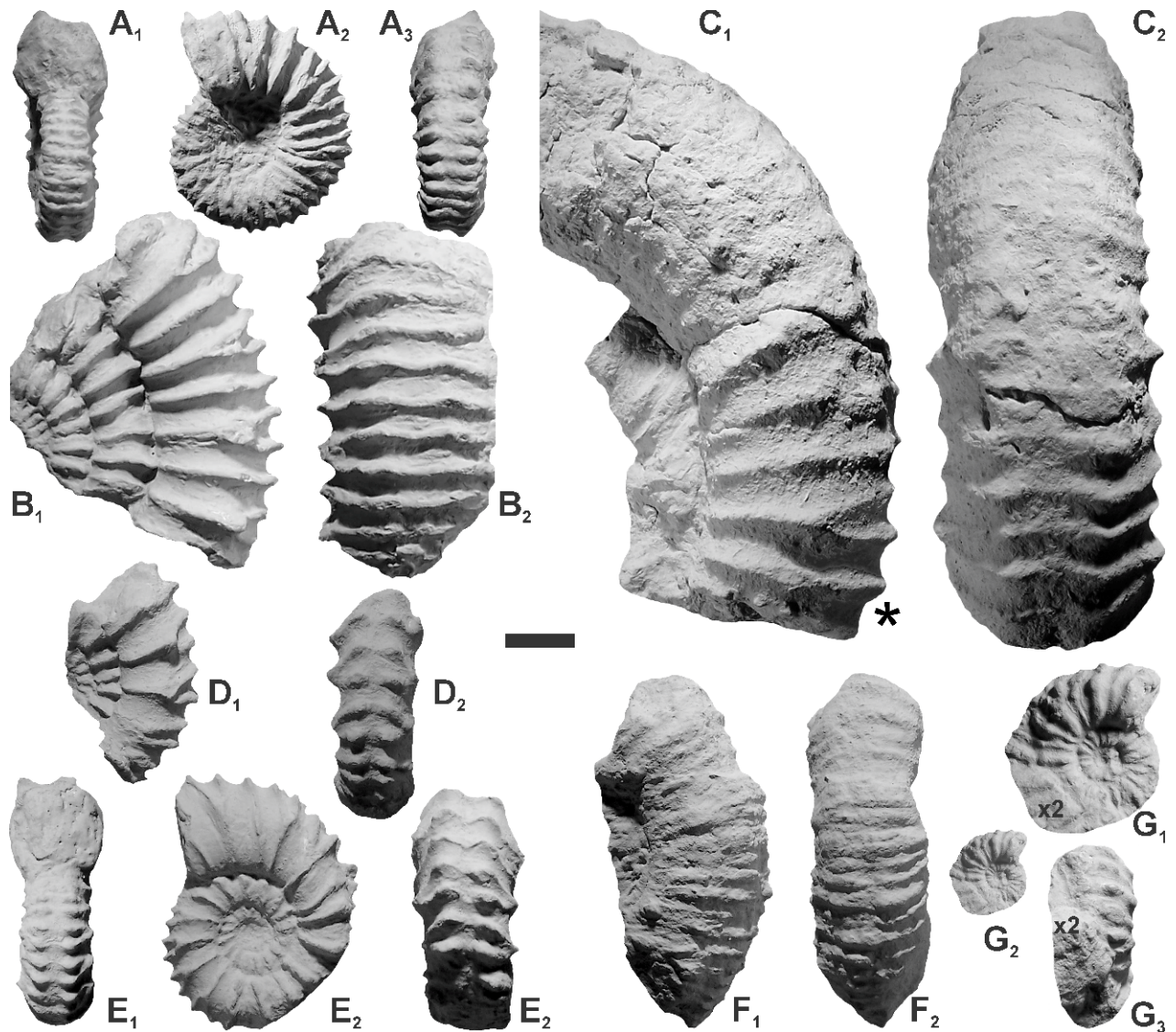   (holotype), non 7d-e

Figure 23. A-E: *Corongoceras lotenoense* Spath, 1925. Cerro Lotena, Alternans Zone. A-B: phragmocones (MOZ-PI-7647, 7646/1), level CL-94. C: incomplete adult macroconch bodychamber with remains of phragmocone (MOZ-PI-7646/2), level CL-91. D-E: adult ?microconchs with beginning of bodychamber (MOZ-PI-7646/3, 707), level CL-91. **F-G**: *Steueria* cf. *alternans* (Gerth, 1921), Cerro Lotena, Alternans Zone. F: portion of phragmocone (MOZ-PI-9355), level CL-91. G: inner whorls, loose from the interval of levels CL-89-94; G_1 and G_3: double size (x2), G_2: natural size (x1). - All natural size (x1) except G_1 and G_3: x2. Asterisk at last septum.

1925 *Corongoceras lotenoense* n. nov. [recte: n. sp.] – Spath: 144
1931 *Berriasella koellikeri* Opp. – Windhausen: pl. 29: 7
* 1957 *Corongoceras lotenoense* Spath – Arkell et al.: L356, fig. 468(6)
? 1979 *Corongoceras* cf. *lotenoense* Spath – Thomson: 30, pl. 6: g
n 1980 *Corongoceras lotenoense* Spath – Leanza: 45, pl. 6: 6
n 1983 *Corongoceras lotenoense* Spath – Matsumoto & Sakai: 79, pl. 8: 2
n 1992 *Corongoceras lotenoense* Spath – Westermann: pl. 81: 4
? 1996 *Corongoceras* cf. *lotenoense* Spath – Enay et al.: 227, 230
* 2001 *Corongoceras lotenoense* Spath – Parent: 32, fig. 9A-C [photographic refiguration of the holotype]
n 2008 *Corongoceras lotenoense* Spath – Riccardi: fig. 9.18-19
2009 *Corongoceras* cf. *lotenoense* Spath – Shome & Bardhan: 2, pl. 1: a, d-c
? 2013 *Steueria* aff. *alternans* (Gerth) – Parent et al.: 25, fig. 19
* 2019 *Corongoceras lotenoense* Spath – Énay & Howarth: 103, fig. 2a-c

Material. 1 incomplete adult [M] from level CL-91, 2 adult [m?] from level CL-91, 4 phragmocones [M] from level CL-94 (MOZ-PI-7646/1-3, 7647/1-2); several incomplete fragmentary specimens.

Description. Macroconch (Fig. 23A-C): Although the specimens are incomplete, they overlap sufficiently to allow most of the ontogeny to be composed.

Inner whorls (about $10 < D < 35$-40 mm) moderately involute to evolute with subrectangular whorl section. Ribbing strong and sharp, moderately dense; the primaries born in the
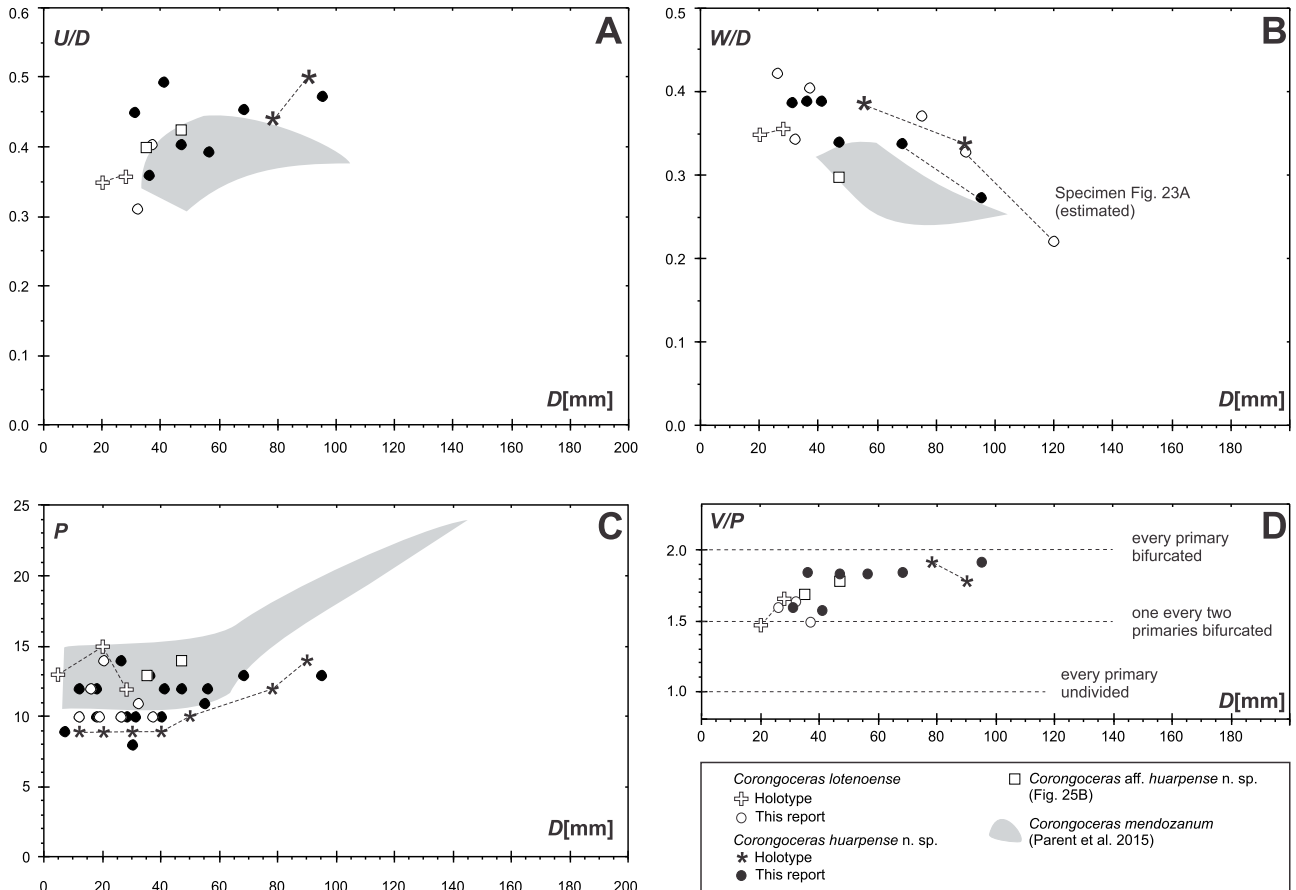
Figure 24. Biometric characterization of the ontogeny of shell-shape and ribbing of *Corongoceras* aff. *huarpense* n. sp., *Corongoceras huarpense* n. sp. and *Corongoceras lotenoense*, compared with *Corongoceras mendozanum* (gray area from data from Parent et al. 2015). **A**: relative umbilical width versus diameter. **B**: relative whorl width versus diameter; all the species become consistently more compressed through the ontogeny. **C**: number of primary ribs per half-whorl versus diameter; the number of ribs, although rather variable, remains constant through the ontogeny around a mean of $P = 10$, lower than *C. mendozanum*. **D**: ratio of ventral to primary ribs per half-whorl versus diameter.

umbilical seam, and cross the flanks radially; most of them bifurcate from a lamellar swollen or spiny tubercle in the upper flank; the secondary and intercalatory ribs reach the ventro-lateral shoulder unchanged then forming a small elongated tubercle in the margins of the venter. All ribs cross the venter, sometimes slightly weakened, forming tubercles in the ventro-lateral shoulder. These tubercles, evenly spaced, produce the aspect of a mid-ventral concavity.

The outer whorls of the phragmocone ($40 < D < D_{ls} = 80\text{-}90$ mm) retain the style of ribbing and tubercles, but the whorl section becomes slightly wider than high, suboval to subrectangular.

Bodychamber (only known the first half-whorl): whorl section and sculpture rather unchanged. Peristome unknown.

The microconch seems to be represented by relatively small specimens (Fig. 23D-E), with beginning of bodychamber uncoiled and strongly varicostate from $D = 20\text{-}25$ mm.

Remarks and comparison. The holotype of *C. lotenoense* is a juvenile phragmocone. The new material shows that the adult phragmocone and bodychamber of the species are quiet different.

C. lotenoense (Alternans Zone) differs from *C. huarpense* n. sp. (lower Internispinosum Zone) mainly by the sculpture of the

ventral area: ribs ending in lamellar tubercles and a furrow in the latter species (Fig. 21) whereas in the former they are uninterrupted between two elevations produced by sharp elongate tubercles or bullae (Fig. 23A-C). Additionally, *C. huarpense* n. sp. has more rounded whorl section throughout the ontogeny.

The little doubted microconchs (Fig. 23D-E) are strongly variocostate in the adult bodychamber, with strong, sharp and distant primary ribs with tubercles in the points of furcation and in the ventro-lateral shoulder endings The more complete of these specimens (Fig. 23E) shows clear signs of incipient uncoiling indicating it is an adult. These spiny-tuberculate specimens are very similar to the phragmocones of *C. huarpense* n. sp. and *C. mendozanum*.

The large macroconch from the Alternans Zone of Portada Covunco, described as *Steueria* aff. *alternans* (Gerth, 1921) by Parent et al. (2013a: 25, fig. 19), could be a late representative or a derived species from *C. lotenoense* n. sp. according to the here described ornamental style, whorl section, and stratigraphic position.

The specimen from Río Diamante, Mendoza Province, figured in Westermann (1992: pl. 81: 4; refigured by Riccardi 2008: fig. 9.18-19) has typical shell-shape (serpenticonic with subcircular whorl section) and ribbing of *Catutosphinctes*, with

some occasional points of furcation with a weak swollen in the form of an incipient spine. This specimen must be assigned to *Catutosphinctes inflatus* (Leanza, 1945), a species from the Alternans Zone, well known from Pampa Tril, Arroyo del Yeso, and Arroyo Cieneguita (see Leanza 1945, Parent et al. 2011b, 2015).

The fragment from Alexander Island (Antarctica) figured by Thomson (1979: pl. 6: g) as *C*. cf. *lotenoense* certainly seems to belong to *Corongoceras*, but can not be attributed safely to any species in particular; the aspect of this specimen is more closely comparable to *C. huarpense* n. sp., however. The same considerations can be advanced to the case of the fragmentary specimen from La Caja Fm at El Verde, northeastern Mexico figured as *Corongoceras* sp. by Zell et al. (2016: fig. 3e), but here the ribs cross the venter, resembling *C*. cf./aff. *lotenoense*. The specimen figured as *C. lotenoense* by Matsumoto & Sakai (1983: pl. 8: 2) from Muktinath, Nepal has shell-shape and ornamentation comparable to *C. huarpense* n. sp. but differing from that of *C. lotenoense*; however, the specimen was collected loose in the scree so that no meaningful comparison can be advanced.

Age and distribution. Present material comes from Cerro Lotena, levels CL-91-94, Alternans Zone. The holotype has an uncertain stratigraphic position in the succession of Cerro Lotena (Haupt 1907: 187, 201-202); however, the practically identical specimen (Fig. 23A) from level CL-94 and the rather narrow local stratigraphic range of the species, indicate that the holotype most likely come from this level in the type locality and section.

The species has been cited from different localities through the Neuquén basin (Haupt 1907, Krantz 1928, Suero 1951, Leanza & Hugo 1977 with references, among others), but according to published specimens (see synonymy) it seems to be confined to the Alternans Zone in the southern Neuquén Basin, possibly only in the lower part of the zone. The pattern of distribution of *C. lotenoense* in the south and *C. mendozanum* in the north of the Huincul High (Fig. 26) was already pointed out by Windhausen (1931: 261).

The stratigraphic position of *C. lotenoense* has been misunderstood to be in the Internispinosum Zone of Cerro Lotena, and so it has been taken as the reference for many records of the species in stratigraphic surveys in the Neuquén Basin. Nevertheless, this assumption is based on reference to the material of Haupt (1907) and Windhausen in 1912 (described by Leanza 1980), all collected without stratigraphic information as pointed out by Haupt (1907: 187) and Leanza (1980: 6). The specimens described herein indicate that *C. lotenoense* occurs in the Alternans Zone, since they occur (1) above the uppermost recorded occurrence of *W. internispinosum*, (2) associated with *Steueria* cf. *alternans* (Gerth, 1921), one of the guide species of the Alternans Zone, and (3) the Internispinosum Zone occurrences of *Corongoceras* actually correspond to *C. huarpense* n. sp. and *C*. cf./aff. *lotenoense* as demonstrated above (see Fig. 4).

Enay et al. (1996) have recorded *C*. cf. *lotenoense* from the Upper Tithonian of the Chicama Basin, western Peru. The associated ammonites suggest the interval Alternans-Koeneni zones, but those identified with greater certainty clearly point to the Alternans Zone, especially the *Parodontoceras*, the so-called *Chigaroceras gerthi* (Krantz, 1926), and *Blanfordiceras bardense* (Krantz, 1926). These two latter species have been reviewed by Parent et al. (2011b), documenting a well defined stratigraphic position of the holotypes and additional material in the Alternans Zone.

Collignon (1960: pl. 175: fig. 754) figured under *Himalayites microcanthus* (Oppel, in Zittel, 1868) a Hollandi Zone Madagascan specimen almost indistinguishable from the adult phragmocone of *C. lotenoense*. According to the ammonites figured by Collignon (1960) from the Hollandi Zone
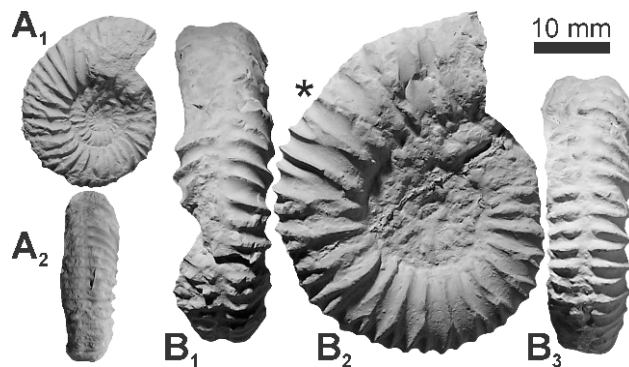

Figure 25. *Corongoceras* aff. *huarpense* n. sp., upper Proximus Zone. **A**: phragmocone (MOZ-PI-8337) from Cerro Lotena, level CL-56. **B**: Adult ?microconch with part of the bodychamber (MCNAM-24431), Arroyo Cieneguita, level AC-8; refigured after additional preparation from Parent et al. (2011b: fig. 33A). - Natural size (x1). Asterisk at last septum.

it seems this zone correlates with the interval Ponti-Durangites/Andreaei zones of the Tethyan zonation, approximately correlative of the interval Internispinosum-Koeneni zones of the Andean zonation (Fig. 4). The ammonite assemblage of the *vetustum* Hz., lower Alternans Zone, has been recognized among the Madagascan ammonites described by Collignon (1960) within the Hollandi Zone (Parent et al. 2011b).

Two specimens from Kutch figured as *C*. cf. *lotenoense* by Shome & Bardhan (2009: pl. 1: a, c-d) closely match to the specimens described herein.

Origin and evolution of the genus *Corongoceras* and relationships with *Ardesciella*

The evolution of *Corongoceras* in the Neuquén Basin is represented in Fig. 26 as a spatio-temporal model according to the above discussion, considering all the specimens published with stratigraphic control. This phylogenetic scheme emerges naturally from the stratigraphic sequence of the species, slowly changing in morphology and sculpture. The sexual dimorphism is included only partially because of the insufficient information about microconchs.

In the upper Proximus Zone of Arroyo Cieneguita occurs an ammonite figured as *Corongoceras*? sp. A in Parent et al. (2011b: fig. 33A) which has an intermediate shell-shape and sculpture between late representatives of *Catutosphinctes proximus* and *C. huarpense* n. sp. It is herein refigured after additional preparation in Fig. 25B, labelled as *C*. aff. *huarpense* n. sp., besides a similar specimen (Fig. 25A) from the level CL-56, uppermost Proximus Zone. These specimens show significant similarities to *C. huarpense* n. sp. in shell shape and sculpture but still retaining similarity to *C. proximus*, thus appearing as the earliest form assignable to *Corongoceras*. *C*. cf. *cordobai* could be an intermediate form but it is not clear because of its conspicuous shell shape and lateral ribbing, appearing as somewhat divergent from the pattern of the mentioned species. However, the specimen in Verma & Westermann (1973: pl. 54: 2) has a good intermediate morphology and ornamentation between *C*. cf. *cordobai* and *C. huarpense* n. sp.

C. lotenoense must have evolved from *C. huarpense* n. sp. via *C*. cf./aff. *lotenoense* through little morpho-ornamental changes.

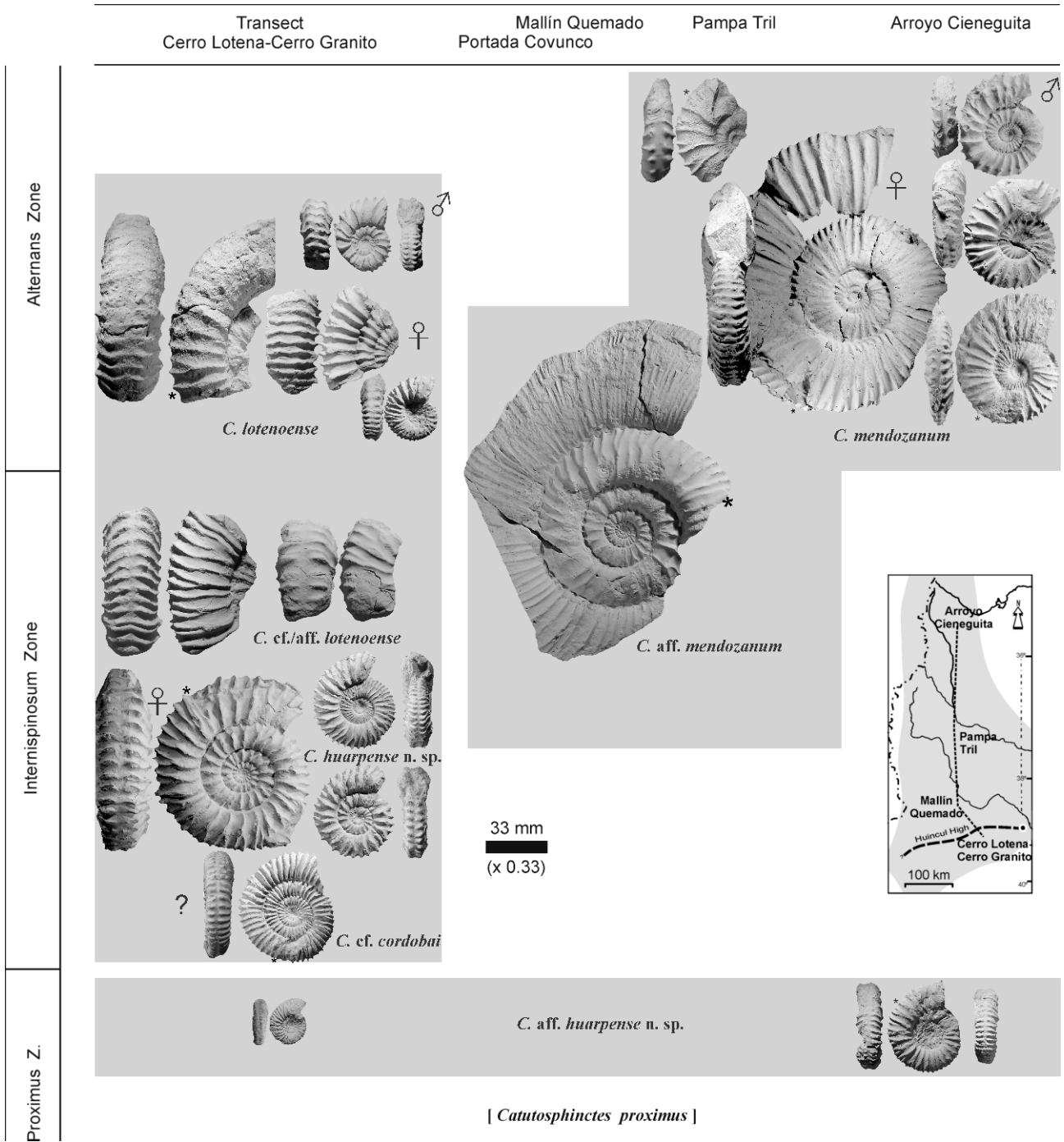*C. mendozanum* seems to form part of a differentiated

Figure 26. Phylogenetic scheme of the evolution of the genus *Corongoceras* in the Neuquén Basin based on the geographical and chronostratigraphic ranges (gray rectangles) of the material studied herein and from Portada Covunco, Mallín Quemado, Pampa Tril, and Arroyo Cieneguita discussed in text.*C.* cf. *cordobai* is not clearly an intermediate form because of its conspicuous morphology and sculpture. *C. mendozanum* from Pampa Tril (Parent et al. 2015) and Arroyo Cieneguita (Parent et al. 2011b). *C.* aff. *mendozanum* from Mallín Quemado (Garrido et al. 2018). *C.* aff. *huarpense* (see Fig. 25). All reduced x0.33. Some specimens flipped. The asterisk indicates the last septum.

lineage, developed in deeper areas of the basin, north of the Huincul High, recorded even north of Arroyo Cieneguita (Fig. 26). *C.* aff. *mendozanum* from Mallín Quemado and Pampa Tril has a phragmocone barely distinguishable from that of the somewhat older *C. huarpense* n. sp. and later *C. mendozanum*, but more compressed, and apparently differing significantly in the bodychamber. *C. mendozanum* is considered as derived from *C.* aff. *mendozanum* as indicated by their stratigraphic relationships and high morpho-ornamental resemblance. The record from Portada Covunco-Cerrito Caracoles gives good support to this hypothesis: (1) the ?microconchiate specimens from the Internispinosum Zone of Portada Covunco (Parent et al. 2013a: fig 13C-D). These specimens were figured as *Catutosphinctes* cf. *rafaeli*, but actually the best match is to *C.* aff. *mendozanum*. (2) typical *C. mendozanum* occurs somewhat higher in these sections, in the Alternans Zone.

Out of the Neuquén Basin, a large number of ammonites have been attributed to *Corongoceras*. Most of the nominal species have been defined in the Submediterranean and Mediterranean regions of the Tethys, and the Madagascan and Indian regions (see Collignon 1960, Olóriz 1978, Tavera 1985, and references in these papers). Parent et al. (2011b) excluded the Mediterranean and Submediterranean species from the genus, which was thus restricted to few Andean and Caribbean forms. According to significant morphologic and palaeobiogeographic differences between the "Tethyan *Corongoceras*" and the Andean *C. mendozanum* and *C. lotenoense*, it was created, with type species *Himalayites rhodanicus* Mazenot, 1939, the genus *Ardesciella* Bulot, Frau & Wimbledon, 2014 (non "*Ardesciella* Wimbledon et al., 2013", p. 451).

The type species of *Ardesciella* Bulot et al., 2014 is similar in shell-shape and adult macroconch size to *C. huarpense* n. sp. and *C. lotenoense*, but showing a set of significant differences: (1) consistent occurrence of evenly distributed undivided primaries, intercalated one-by-one with bifurcates, (2) less frequent and unevenly distributed ventral bullae/spines, and (3) the inner whorls are stout and involute with prosocline ribs (similar to *C. mendozanus*). In this genus can be allocated most of the Tethyan ammonites described as *Corongoceras* (see Parent et al. 2011b, Bulot et al. 2014, Énay & Howarth 2019). Besides the diagnostic differences mentioned, the general resemblance of the sculptural elements, adult macroconch size and shell shape suggest *Ardesciella* could have originated from *Corongoceras*, perhaps from the yet poorly known *C*. cf./aff. *lotenoense*.

Genus *Steueria* Parent, Scherzinger & Schweigert, 2011

Type species. *Berriasella alternans* Gerth, 1921; by original designation.

***Steueria* cf. *alternans* (Gerth, 1921)**
Fig. 23F-G

Material. One fragmentary specimen (MOZ-PI-9355) from level CL-91; a nucleus from the interval levels CL-89-94, Alternans Zone.

Description and remarks. The two fragmentary specimens show clearly the features of the genus, and match to typical material of *S. alternans* at comparable diameter (see Parent et al. 2011b), but they are very incomplete for a definite specific assignation.

The species was introduced by Gerth (1921) but described later (Gerth 1925), although before the formal introduction of the classification rules in 1930 (see details in Parent et al. 2011b). The species has been described by Leanza (1945) under different names, and recently reviewed in detail in Parent et al. (2011b).

CONCLUSION

The family Himalayitidae is well represented in the Tithonian succession of the Cerro Lotena-Cerro Granito transect of the Picún Leufú Subbasin. In this study the following genera were recorded in the interval upper Proximus-Alternans zones: *Corongoceras*, *Windhauseniceras*, and *Steueria*. Among many hundreds of ammonites collected, *Lotenia* has not been found.

W. internispinosum has a fine record in the study area allowing to study its origin from *C. proximus* and its evolution in greater detail than in any other of the localities where it was recorded up to today. The phyletic evolution of the species can be described as a succession of five transients. The evolutionary

pattern observed from their succession shows an increasing mean macroconch adult size and rib density in the adult phragmocone-bodychamber but reverted in the latest transient, and a progression of the coronate stage towards larger diameters. The range of shell shape variation of the macroconchs shows a spectrum of evolute and serpenticonic shells towards others more compressed suboxyconic-platyconic, and more involute and finely ribbed. The sequence of ornamental stages is unchanged, the variations are produced by changes in the duration of these stages. This intraspecific variation occurs in the same mode within and between transients. Unfortunately, the material available, although abundant and well preserved does not include sufficient a number of complete adult macro- and microconchs for a quantitative description of these patterns and processes.

Corongoceras must have originated from *C. proximus* through *C*. aff. *huarpense* n. sp. In the Picún Leufú Subbasin the genus is composed by the succession *C*. aff. *huarpense* n. sp. (upper Proximus Zone), *C. huarpense* n. sp. (lower-middle Internispinosum Zone), *C*. cf./aff. *lotenoense* (middle-upper Internispinosum Zone), and *C. lotenoense* (Alternans Zone). In the northern domains of the basin the genus is represented by a different sequence: *C*. aff. *huarpense* n. sp., *C*. aff. *mendozanus* (middle-upper Internispinosum Zone and possibly lower Alternans Zone) and *C. mendozanus* (Alternans Zone).

If *C. proximus* is the root of the genera *Windhauseniceras* and *Corongoceras*, the *Catutosphinctes* lineage has been a seeding lineage in times of the late Proximus Zone.

Steueria occurs as a form very similar to *S. alternans*, but is very scarce for a better characterization.

Hybridization and the consequence of reticulated evolutionary scenarios, must have played a central role in the configuration of the complex modes and ranges of variation observed in many groups of ammonites which are usually organized in phylogenetic schemes of improbable complexity. The record of rare forms associated with early *W. internispinosum* and close forms seem to be the result of this phenomenon.

The detailed characterization of the successive transients of *Windhauseniceras* and *Corongoceras* and the ammonite assemblages to which they belong, will surely be an efficient biostratigraphic-based chronostratigraphic tool for refining the chronostratigraphy based on the current ammonite zonation. The refinement should be based on the identification of time-planes as ammonite biohorizons represent. These biostratigraphic units, which are the link between bio- and chronostratigraphy, provide the highest time-resolution possible, far beyond the radiometric numerical datings.

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Appendix 1

Ammonite biostratigraphy of the study area. List of recorded species from the studied sections CL, CG-III, CG-II, and CG-I (Fig. 3) of the transect Cerro Lotena-Cerro Granito (Fig. 2). This list includes only the ammonites collected for the present study. The specimens considered are mostly complete or moderately complete, and well preserved.

Section Cerro Lotena (CL)

CL-2

Indansites picunleufuense (Parent et al., 2011a) transient alpha [M]

CL-3

Indansites picunleufuense tr. alpha
Catutosphinctes guenenakenensis Parent et al., 2011a

CL-4-6

Indansites picunleufuense [M&m]
Choicensisphinctes platyconus Parent et al., 2011a. Small and coarsely ribbed morphotype
Choicensisphinctes cf. *platyconus* [M]. Medium and large suboxyconic, involute macroconch phragmocones
Catutosphinctes windhauseni (Weaver, 1931) [m?]
Catutosphinctes aff. *windhauseni* [M]. A large complete macroconch with the inner whorls coarsely ribbed as in *C. windhauseni* and outer whorls resembling *C. guenenakenensis*. It is a stratigraphically and morphologically intermediate form between these two species
Pseudolissoceras cf. *pseudoolithicum* (Haupt, 1907) [M]. Several specimens whose phragmocone is indistinguishable from that of *P. pseudoolithicum*. However, a definite assignation is doubtful since the holotype (by monotypy) of this species consists of the inner whorls of an apparently macroconchiate specimen. The stratigraphic position of the holotype given by Haupt (1907) is speculative, based on the matrix of the ex-situ specimen, set as associated with *P. zitteli*. The specimens could also be assigned by morphology and stratigraphic position, below typical *Pseudolissoceras zitteli* (Burkchardt, 1903), to *Pseudolissoceras rasile* (Zittel, 1870) [M], a species of the Darwini Zone of the southern Tethys (Olóriz 1978, Cecca & Santantonio 1988; discussion in Parent 2001). However, the morphotype can persist into the Semiforme Zone

CL-7

Indansites cf. *picunleufuense*
Choicensisphinctes erinoides [M&m] tr. alpha. Medium-sized macroconch with coarsely ribbed adult phragmocone and smooth, compressed adult bodychamber. Microconch one-half to one-third in adult size, very evolute with coarse lateral and fine ventral ribbing in the adult bodychamber; widely rounded lappets
Choicensisphinctes windhauseni (Weaver, 1931) [M&m]. Probably a compressed and densely ribbed morphotype of *C. erinoides* tr. alpha (see Parent et al. 2011a)
Physodoceras? sp. A [m]
Pseudolissoceras zitteli (Burckhardt, 1903) [M]
Parastreblites? sp. A
Cieneguiticeras perlaevis [m]

CL-8

Choicensisphinctes erinoides [m] tr. alpha
Cieneguiticeras perlaevis (Steuer, 1897) [m]
Pseudolissoceras zitteli [M]

CL-9
Choicensisphinctes aff. *platyconus* [M]
Aspidoceratinae indet. (large laevaptychus)
Pseudolissoceras zitteli [M]

CL-11
Choicensisphintes erinoides tr. alpha [M]

CL-12
Choicensisphintes erinoides tr. beta [M&m]

CL-13
Choicensisphinctes erinoides tr. beta [M&m]. Macroconchs of small to large (maximum D = 400-450 mm) adult size; extremely variable from evolute-inflate platycones to compressed-involute suboxycones. Adult phragmocone more or less evolute (inflate platyconic morphotypes) to involute and densely ribbed (suboxyconic morphotypes). The adult microconchs are one-tenth to one-third the size of the adult macroconch, but there is correspondance between the ratio according to the morphotypes; moderately involute and finely ribbed adult bodychamber (the smaller morphotypes) to more evolute with well marked primary ribs divided in bunchs of secondaries (larger morphotypes). The larger microconchs correspond to *Virgatites mendozanus* Burkchardt, 1911 which, after a long nomenclatorial history, was assigned to *Virgatosphinctes* Uhlig, 1910 by Spath (1936); later (Parent et al. 2011a, b, 2015, 2017a) demonstrated the undoubted sexual dimorphic correspondence with the macroconch of *C. erinoides*. According to its stratigraphic position (associated with the lectotype of *Virgatites mendozanus*) and morpho-sculptural ontogeny, the holotype of *C. erinoides* (Burckhardt 1900a: pl. 25: 1) can be assigned to this transient
Aspidoceras cf. *casitense* Imlay, 1939 [M]
Toulisphinctes rafaeli (Oppel, 1863) [M]
Pseudolissoceras zitteli [M]
Pasottia andina Parent et al., 2008 [M&m]
Cieneguiticeras perlaevis [M&?m]
Semiformiceras? sp. A [M]

CL-14
Choicensisphinctes erinoides tr. beta [M&m]

CL-15
Choicensisphinctes erinoides tr. beta

CL-17
Choicensisphinctes erinoides tr. beta [M]

CL-23
Choicensisphinctes erinoides tr. gamma [M&m]. Macroconchs large to very large (maximum recorded D > 1000 mm) in adult size; similar patterns of intraspecific variation and sexual dimorphism of transient beta. The holotype of *Choicensisphinctes limits* (Burckhardt, 1930) is a large macroconch assignable to this transient
Catutosphinctes n. sp. aff. *guenenakenensis* [M]
Physodoceras? n. sp. A [M&m]. Macroconch small to medium-sized, compressed, involute, and smooth from the inner whorls. Microconch one-third to one-half the size of the macroconch
Pseudolissoceras zitteli [M&m]

CL-25
Physodoceras? n. sp. A [m]
Pseudolissoceras zitteli [M&m]

CL-27-28
Choicensisphinctes erinoides tr. gamma [m]
Pseudolissoceras zitteli [M]

CL-29
Catutosphinctes n. sp. aff. *guenenakenensis* [M&?m]

CL-31
Catutosphinctes n. sp. aff. *guenenakenensis* [M]
Pasottia andina [M]

CL-32
Catutosphinctes n. sp. aff. *guenenakenensis* [M]
Pseudolissoceras zitteli [M]

CL-33
Pseudolissoceras zitteli [M&m] (with aptychus in the bodychamber)
Cieneguiticeras perlaevis [m]

CL-37
Catutosphinctes cf. *proximus* (Steuer, 1897) [M]
Pseudolissoceras cf. *bavaricum* Barthel, 1962 (with aptychus in the bodychamber)

CL-39
Indansites n. sp. aff. *picunleufuense* [m?]. This species was illustrated in Parent et al. (2017a: fig. 2E-F).
Catutosphinctes cf. *proximus* (Steuer, 1897) [M]
Pseudolissoceras zitteli [M]

CL-41
Indansites n. sp. aff. *picunleufuense* [M&m].
Choicensisphinctes cf. *erinoides*
Catutosphinctes cf. *proximus* (Steuer, 1897) [M&m]
Pseudolissoceras cf. *zitteli-bavaricum* [M]
Pseudhimalayites cf. *subpretiosus* (Uhlig, 1878) [M]

CL-43
Indansites n. sp. aff. *picunleufuense* [M&m]
Choicensisphinctes? sp. A (inner whorls)
Catutosphinctes proximus [M&m]
Catutosphinctes cf. *proximus* (Steuer, 1897) [M&m]
Physodoceras? n. sp. B [m]. Phragmocone of the macroconch evolute, with smooth subquadratic whorls. Microconch evolute, with subquadratic whorls; bodychamber with mild falcate ribblets and a lateral groove. This species could correspond to "*Hildoglochiceras*" *wiedmanni* Leanza, 1980 which occur much older strata.
Pseudhimalayites cf. *subpretiosus* (Uhlig, 1878) [M]
Toulisphinctes cf. *rafaeli* [M]
Pseudolissoceras cf. *zitteli*

CL-44
Indansites n. sp. aff. *picunleufuense* [M&m]
Choicensisphinctes n. sp. A [M&?m]
Catutosphinctes proximus [M&m]
Catutosphinctes cf. *proximus* (Steuer, 1897) [M&m]

CL-45
Catutosphinctes cf. *proximus*
Physodoceras? n. sp. B [M?&m]

CL-47
Indansites n. sp. aff. *picunleufuense* [M?&m]
Choicensisphinctes n. sp. A [M]
Catutosphinctes proximus
Catutosphinctes cf. *proximus*
Physodoceras? n. sp. B
Cieneguiticeras? sp. (lamellaptychus)

CL-49
Catutosphinctes cf. *proximus*

CL-52
Catutosphinctes proximus [M&?m]

CL-53
Catutosphinctes proximus [M]
Aspidoceras sp. A [M]
Toulisphinctes cf. *rafaeli* [M]

CL-55
Indansites n. sp. aff. *picunleufuense* [M&m]
Catutosphinctes cf. *proximus*
Catutosphinctes cf. *rafaeli* Leanza & Zeiss, 1992 [M] ["*Mapuchesphinctes*"]
Toulisphinctes cf. *rafaeli* [M]

CL-56
Catutosphinctes proximus (late transient)
Aspidoceras euomphalum Steuer, 1897 [M]
Physodoceras? sp. B [M]
Pseudhimalayites subpretiosus [M]
Toulisphinctes cf. *rafaeli* [M]
Windhauseniceras internispinosum (Krantz, 1926) [M&m], earliest representatives
Corongoceras aff. *huarpense* n. sp.
Cieneguiticeras falculatum (Steuer, 1897) [M]

CL-58
Choicensisphinctes n. sp. A [M]
Windhauseniceras internispinosum [M] tr. alpha

CL-60
Pseudhimalayites subpretiosus [M]
Windhauseniceras internispinosum [M] tr. alpha
Windhauseniceras? sp. A
Corongoceras cf. *cordobai* Verma & Westermann, 1973

CL-62
Catutosphinctes rafaeli Leanza & Zeiss, 1992 [M&m]. The corresponding microconch is *Perisphinctes colubrinoides* Burckhardt, 1903 (reviewed and refigured in Garrido et al. 2018).
Windhauseniceras internispinosum [M] tr. alpha
Corongoceras huarpense n. sp. [M]

CL-64
Catutosphinctes araucanensis Leanza, 1980 [M]
Corongoceras huarpense n. sp. [M&?m]

CL-66
Catutosphinctes cf./aff. *proximus* [M]
Corongoceras huarpense n. sp. [M&?m]

CL-68
Windhauseniceras internispinosum [M&m], tr. beta. In this level and CL-70 the largest macroconchs (D_p up to 600 mm) were collected.

CL-70
Catutosphinctes araucanensis Leanza, 1980 [M&m]
Mazatepites? n. sp. A [M?] (loose)
Windhauseniceras internispinosum [M] tr. beta
Corongoceras huarpense n. sp. [M&?m]

CL-74
Windhauseniceras internispinosum [M] tr. beta
Corongoceras cf./aff. *lotenoense* Spath, 1925 [M]

CL-79
Toulisphinctes? sp. A [m] in Parent et al. (2011b: fig. 37D), a microconch ("*Sutneria*") with lateral ribs and two rows of tubercles, ending in a long lappet.

CL-80
Catutosphinctes cf. *araucanensis* [M]
Aspidoceratinae indet (laevaptychus)
Windhauseniceras internispinosum [M] tr. beta
Corongoceras cf./aff. *lotenoense* [M]

CL-82
Catutosphinctes n. sp. B [M&?m] ["*Mapuchesphinctes*"]

CL-84
Catutosphinctes aff. *rafaeli* [M] [= *Aulacosphinctoides* aff. *hundesianus* (Uhlig, 1910) in Leanza 1980]
?*Catutosphinctes* n. sp. B [M]
Simoceratidae? indet.
Windhauseniceras internispinosum [M&m] tr. beta
Zapalia cf. *fascipartita* Leanza & Zeiss, 1990 [M]

CL-86
Krantziceras? n. sp. A
Catutosphinctes araucanensis Leanza, 1980 [m?]
Windhauseniceras internispinosum [M] tr. beta and latest representatives
Zapalia cf. *fascipartita* [M]

CL-88
Catutosphinctes n. sp. B [M] ["*Mapuchesphinctes*"]

CL-91
Aspidoceratinae indet. (laevaptychus)
Corongoceras lotenoense [M&?m]
Steueria cf. *alternans* (Gerth, 1921) [M?]

CL-94
Corongoceras lotenoense [M&?m]

Section Cerro Granito III (CG-III)

CG-III-2
Indansites picunleufuense tr. alpha

CG-III-4
Indansites cf. *malarguensis* [m]
Choicensisphinctes erinoides tr. alpha/beta [M&m]
Pseudolissoceras zitteli [M]
?*Pseudolissoceras zitteli* [M] (large lamellaptychus)

CG-III-7
Choicensisphinctes erinoides tr. alpha/beta
Volanoceras cf. *krantzense* Cantú-Chapa, 1990 [M]

CG-III-10
Choicensisphinctes erinoides tr. beta [M]
Pseudolissoceras zitteli [M]

CG-III-13
Choicensisphinctes erinoides tr. gamma [M]

CG-III-17
Cieneguiticeras perlaevis [m]

CG-III-23
Pseudolissoceras zitteli [M]

CG-III-29
Choicensisphinctes n. sp. A [M]

CG-III-31
Choicensisphinctes n. sp. A [M]

CG-III-37
Platydiscus beresii Parent et al., 2011b [M]

CG-III-39
Windhauseniceras internispinosum [M] transient beta
Aspidoceras euomphalum [M]

CG-III-45
Windhauseniceras internispinosum [M] transient beta
Aspidoceras euomphalum [M]

CG-III-48
Choicensisphinctes n. sp. A [M] (late transient)

Section Cerro Granito II (CG-II)

CG-II-2
Indansites picunleufuense tr. alpha [M]
Choicensisphinctes cf. *platyconus* [M]

CG-II-4
Indansites malarguensis (Spath, 1931) [M]
Choicensisphinctes platyconus [M]

CG-II-6
Indansites cf. *malarguensis* [M]
Indansites n. sp. A
Choicensisphinctes platyconus-erinoides [M]
Catutosphinctes guenenakenensis-windhauseni [M]
Pseudolissoceras zitteli [M]
Aspidoceras sp. B [M]

CG-II-8
Indansites n. sp. A [M]
Choicensisphinctes platyconus-erinoides [m]
Choicensisphinctes erinoides [m]. This microconch belongs to a conspicuous morphotype with subquadrate whorl section in the bodychamber, already described from Pampa Tril (Parent et al. 2015: fig. 27C).
Catutosphinctes windhauseni [M]

CG-II-10
Indansites n. sp. A, late transient
Pseudolissoceras zitteli [M]

CG-II-18
Pasottia andina [m]

CG-II-26-28
Choicensisphinctes erinoides tr. beta [M&?m]
Catutosphinctes cf. *guenenekenensis*
Pseudolissoceras zitteli [M]
Cieneguiticeras perlaevis [m]
Pasottia andina [M&m]
Taramelliceratinae? n. gen. et n. sp. A [M]
Physodoceras n. sp A [m]

CG-II-32
Catutosphinctes n. sp. aff. *windhauseni* [M], loose from the scree.

CG-II-34
Choicensisphinctes cf. *erinoides*

CG-II-44
Choicensisphinctes erinoides tr. gamma [M&m]

CG-II-50
Choicensisphinctes cf. *erinoides*
Physodoceras n. sp. B [m?]
Pseudolissoceras zitteli [M]

CG-II-56
Physodoceras? n. sp. A

CG-II-58-60
Choicensisphinctes cf. *erinoides*
Catutosphinctes cf. *guenenekenensis*
Pseudolissoceras zitteli [m]
Cieneguiticeras perlaevis [m]
Pasottia andina [m]
Parastreblites? cf. *comahuensis* [M]
Physodoceras cf. *neoburgense* [m]

CG-II-64
Physodoceras cf. *neoburgense* [m]
Pseudolissoceras zitteli [M] with lamellaptychus

CG-II-66
Catutosphinctes cf./aff. *guenenakenensis* [M]

CG-II-74
Indansites n. sp. A [M]
Choicensisphinctes cf. *erinoides* [M]
Catutosphinctes cf./aff. *proximus*

CG-II-76
Indansites n. sp. A?
Choicensisphinctes n. sp. A [m?]
Catutosphinctes proximus-araucanensis [M]

CG-II-84
Catutosphinctes proximus
Toulisphinctes cf. *rafaeli* [M] (large bodychambers)
Windhauseniceras internispinosum tr. alpha [m]

CG-II-86
Catutosphinctes proximus [m]

CG-II-90
Catutosphinctes cf. *rafaeli* [M&m]

CG-II-91
Catutosphinctes cf. *rafaeli*

CG-II-93
Choicensisphinctes n. sp. aff. *striolatus* (Steuer, 1897) [M]
Windhauseniceras internispinosum [M] compressed morphotype (= *Windhauseniceras stipanicici* Zeiss & Leanza, 2010)

CG-II-94
Catutosphinctes cf. *rafaeli*
Platydiscus beresii

CG-II-95
Platydiscus beresii [M]

CG-II-98
Windhauseniceras internispinosum [M] transient CG-II-98

CG-II-99
Catutosphinctes cf. *rafaeli* [M&m]
Windhauseniceras internispinosum [m] transient CG-II-98
Corongoceras cf./aff. *lotenoense* [M&?m]

CG-II-102
Indansites zapalensis Zeiss & Leanza, 2010 [M]
Zapalia cf. *fascipartita* [M]
Windhauseniceras internispinosum [M] tr. beta

CG-II-103
Choicensisphinctes n. sp. aff. *striolatus* [M]
Windhauseniceras internispinosum [M] tr. beta
Aspidoceras cf. *euomphalum* [M]
Aspidoceratinae indet (large laevaptychus)

CG-II-105
Zapalia triplex Zeiss & Leanza, 2010 [M]
Windhauseniceras internispinosum [M] tr. beta
Aspidoceratinae indet (laevaptychus)

CG-II-108
Indansites zapalensis [M]
Choicensisphinctes n. sp. A
Aspidoceras euomphalum [M]
Toulisphinctes cf. *rafaeli* [M]

Section Cerro Granito I (CG-I)

CG-I-2
Indansites picunleufuense tr. beta [M]
Choicensisphinctes platyconus [M]
Choicensph. cf./aff. *platyconus* [M] in Parent et al. (2013a)
Catutosphinctes guenenekenensis [M]

CG-I-4
I. picunleufuense tr. alpha/beta
Choicensisphinctes platyconus [M]
Catutosphinctes cf. *guenenakenensis*

CG-I-6
Indansites n. sp. A
Indansites? sp. A
Catutosphinctes windhauseni (Weaver, 1931) [M&?m]
Cieneguiticeras perlaevis [m]

CG-I-7
Pseudolissoceras zitteli [M]

CG-I-8
Indansites cf. *picuenleufuense*

CG-I-10
Pseudolissoceras zitteli [M]

CG-I-14
Pseudolissoceras zitteli [M]

CG-I-16
Indansites n. sp. A [M&?m]
Choicensisphinctes windhauseni [m]
Pseudolissoceras zitteli [M]
Parastreblites? *comahuensis* Leanza, 1980 [M]

CG-I-18
Choicensisphinctes cf. *burckhardti* (Douvillé, 1910)
Choicensisphinctes erinoides tr. alpha/beta
Volanoceras krantzense [M]

CG-I-22
Choicensisphinctes erinoides tr. beta/gamma [M&m]
Pasottia andina [M&?m] (type horizon)

CG-I-26
Choicensisphinctes erinoides tr. gamma [M&m]
Physodoceras cf. *neoburgense* (Oppel, 1863) [M&?m]. This form seems to be a persistent morphotype of a (probably local) lineage which could be represented from the Picunleufuense Zone in Picún Leufú (see Parent et al. 2019b).
Physodoceras? n. sp. A [M]

CG-I-28
Choicensisphinctes erinoides tr. gamma [M&m]
Choicensisphinctes n. sp. A [M&m]
Pseudolissoceras zitteli [M&m]
Pasottia andina [m]
Cieneguiticeras perlaevis [m]
Physodoceras? n. sp. A [M&m]

CG-I-30
Choicensisphinctes erinoides tr. gamma [M&m]

CG-I-34
Physodoceras cf. *neoburgense* (Oppel, 1863) [M&?m]

CG-I-38/40
Physodoceras? n. sp. A [M] .-