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Article

The Upper Tithonian–Lower Berriasian ammonite succession of Cajón de Almanza (Vaca Muerta Formation, Neuquén Basin, Argentina)

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With 8 figures

Abstract: The exposures of the Tithonian–Berriasian succession of the Vaca Muerta Fm in Cajón de Almanza (Neuquén Basin) are extensively covered by modern material. This condition hampers the bed by bed collection of ammonites which, consequently, have never been sampled as successions of assemblages. The fine preservation and abundance of the local fauna makes of Cajón de Almanza a locality of choice for expanding the knowledge of Tithonian–Berriasian ammonite fauna and its succession in this deep sector of the basin. Recently we have collected small assemblages from three successive horizons within the interval Altenans-Damesi zones (upper Tithonian–upper Berriasian). These ammonites belong to *Catutosphinctes inflatus* (Leanza), *Corongoceras mendozanum* (Behrendsen), *Leonardia almanzaensis* n. gen., n. sp., *Substeueroceras koeneni* (Steuer), and *Subthurmannia boissieri* (Pictet). From this material plus a published list, and a number of few sets of ammonites formerly collected in isolation, we have pieced together a new chronostratigraphic and palaeontologic scheme for the study area, including the confirmation of the stratigraphic position of the holotype of *Pliosaurus almanzaensis* O'Gorman, Gasparini & Spalletti in the upper Alternans Zone.
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Keywords: Andean ammonites; Tithonian; Berriasian; Cajón de Almanza; *Leonardia almanzaensis* n. gen., n. sp.

1 Introduction

The Tithonian ammonite fauna of the Neuquén Basin (Fig. 1A) has been studied since the pioneering works by Behrendsen (1891, 1892), Steuer (1897), and Burckhardt (1900a, 1900b), among others. One of the most interesting derivations from these studies is a fine ammonite-based cronostratigraphic scale (see Leanza 1981; Garrido et al. 2018; Aguirre-Urreta et al. 2019 and Parent 2022 for recent revisions and references). However, few studies have been recently done in the western areas of the basin, the most recent could be the stratigraphic study of the Vaca Muerta Formation in the area of the Cerro Domuyo by Kietzmann & Vennari (2013) where some ammonites were figured.

Preliminary research of the present authors in some western localities (e.g., Cajón de Almanza, La Invernada, Chacay Melehué, Cerro Domuyo, Río Barrancas) has shown that the very thick successions of the Vaca Muerta Fomation there are very rich in ammonites. These are abundant in many levels and well- to exceptionally well-preserved. However, the establishment of sections for detailed stratigraphic study and bed by bed sampling of fossils is very hard because of the extensive tectonic effects and the extensive modern cover over the soft shales and lutites.

The Vaca Muerta Formation in the area of Cajón de Almanza (Fig. 1B), located 16 km southeast of the Loncopué city, is widely exposed but hardly accessible for systematic sampling. The ammonite succession has never been described, only some ammonites were described (see Parent & Garrido 2021), and limited additional information is available from the list given by Leanza & Hugo (1977). During a recent survey in this locality, one of the authors (ACG) has

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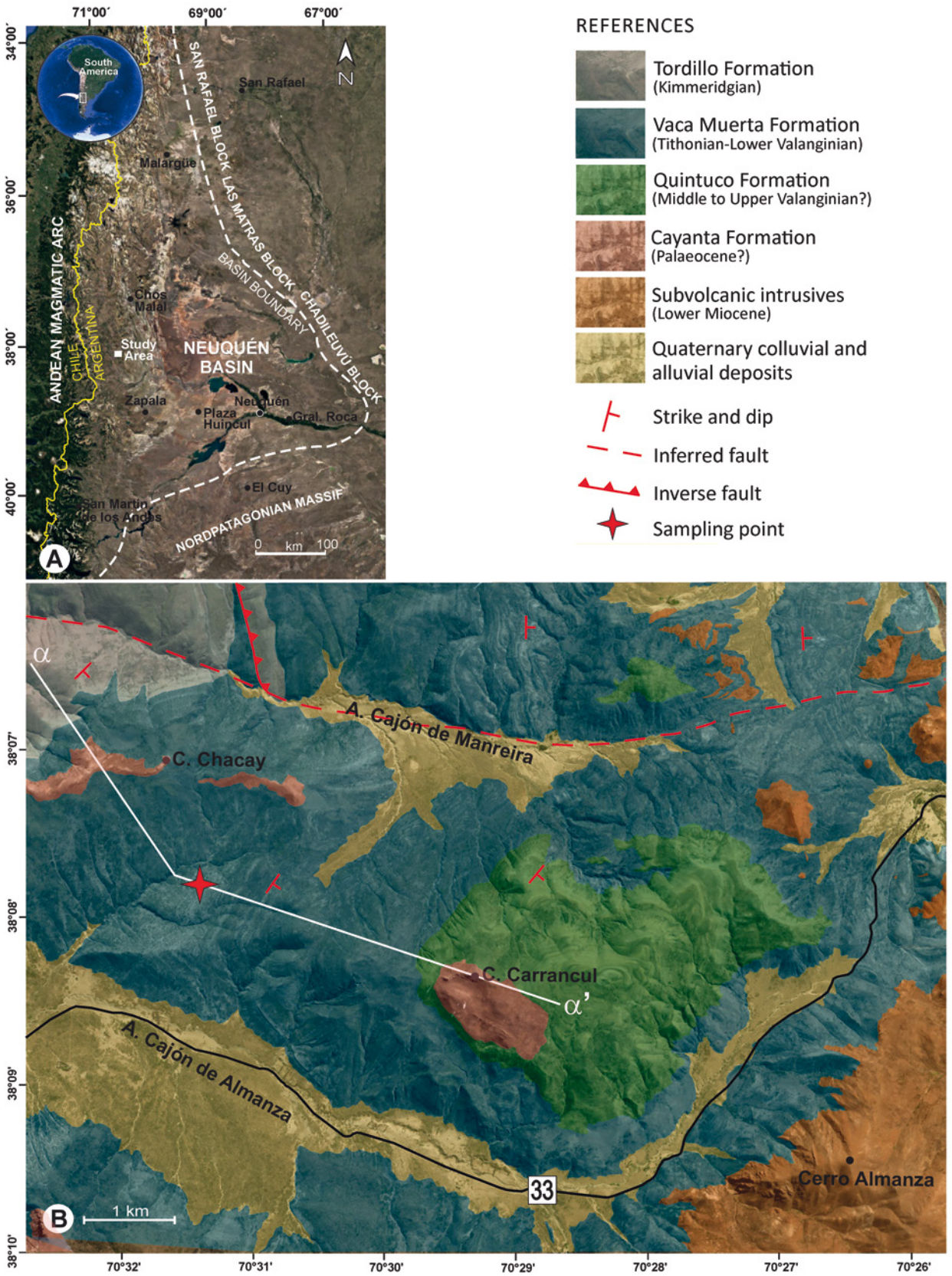

Fig. 1. A – The Neuquén Basin with indication of the study area. **B** – Geologic-topographic map of the study area with indication of the sampling point (red star) and the transect α–α' of Fig. 2.

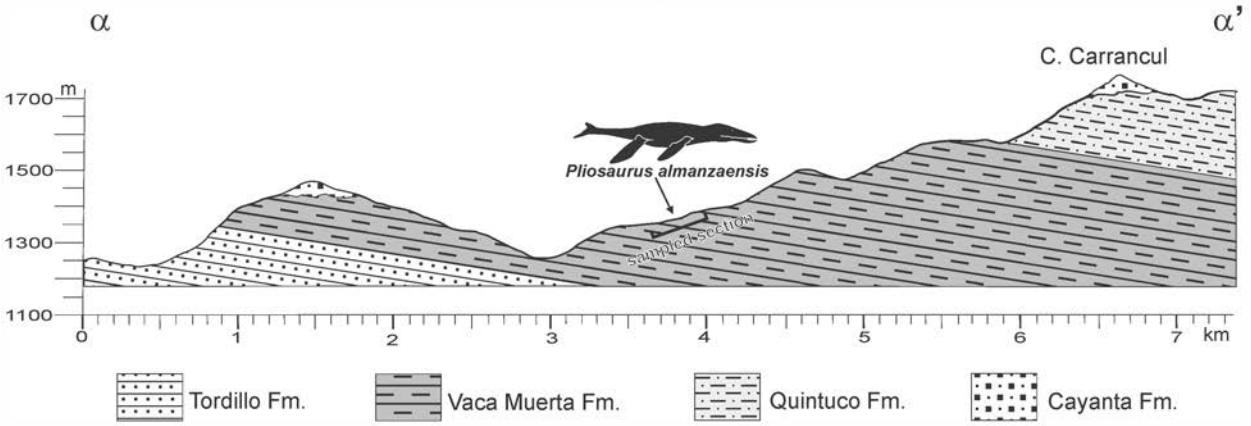

Fig. 2. Transect profile α–α' indicated in Fig. 1B. Note that the holotype of *Pliosaurus almanzaensis* O'Gorman, Gasparini & Spalletti, 2018 was collected 1.6 m below the faunal level 2 of the Koeneni Zone.

collected several ammonites from three successive horizons. The purpose of this report is to describe and date these levels by their ammonites, among which there are interesting representatives of species already known, and two specimens which belong to a new species of a new genus. From these ammonites, plus few other associations formerly collected in isolation, and a revision of the succession listed by Leanza & Hugo (1977), we have worked out a more complete ammonite succession for the interval Upper Tithonian-Lower Berriasian in the locality and the area.

2 Stratigraphic framework

The geology of this area has been described in full or in part by several authors (Holmberg 1973; Leanza 1973; Leanza & Hugo 1977; Rodrigues et al. 2009; Zanettini et al. 2010). Leanza & Hugo (1977: 256) indicated that the Vaca Muerta Fm (with the Quintuco Fm undifferentiated) in the area shows a thickness of about 761 m but its upper part would have been eroded. The succession is monotonous, consisting of black to dark-gray shales and marls.

Along a 5500 m transect between the Chacay and Carrancul hills (Figs. 1B, 2), it is possible to follow an almost complete section of the sedimentary succession comprising the Vaca Muerta and Quintuco formations (sensu Weaver 1931). Unfortunately, a thin layer of Quaternary colluvium masks long stretches of these outcrops. The discovery in this sector of the holotype of *Pliosaurus almanzaensis* O'Gorman, Gasparini & Spalletti, 2018 motivated the need of locating this specimen within a biostratigraphic interval, allowing its dating within a time interval (age) based on the Andean ammonite zonation. Our collection comes from three fossil levels that were sampled, containing the following ammonites which are described below:

Faunal level 1: *Corongoceras mendozanum* (Behrendsen, 1891) and *Catutosphinctes inflatus* (Leanza, 1945). This level is 32.7 m below the *Pliosaurus almanzaensis* level.

Faunal level 2: *Substeueroceras koeneni* (Steuer, 1897) and *Leonardia almanzaensis* n. gen., n. sp. (described below). This level is 1.6 m above the *Pliosaurus almanzaensis* level.

Faunal level 3: *Subthurmannia boissieri* (Pictet, 1867). This level is 25.4 m above the *Pliosaurus almanzaensis* level.

3 Systematic palaeontology

The studied specimens are housed in the collection of the Museo Provincial de Ciencias Naturales "Prof. Dr. Juan A. Olsacher", Zapala, Provincia del Neuquén (MOZ-PI).

Abbreviations and symbols: [M]: macroconch (female), [m]: microconch (male). Bc: body-chamber, Ph: phragmocone. Dimensions (in millimetres): shell diameter at a given point (D), at last septum (D_{ls}), and at peristome (D_p); umbilical width (U), width of whorl section (W), height of whorl section (H_1), and aper-

tural or ventral height of whorl section (H_2), mostly given as ratios to *D*. Number of primary (*P*) and ventral (*V*) ribs per half whorl.

We consider that the female in Jurassic ammonite species is represented by the macroconch, and the male by the microconch. However, in many groups the adult size variation in both sexes can be so broad as to widely overlap between each other (see Scherzinger et al. 2018; Parent et al. 2019; and Klug et al. 2015 for a general review). For female specimens that became adult in a relatively early ontogenetic stage and thus remained smaller than normal macroconchs, the term mesoconch was introduced by Chandler (2019); see also Parent et al. (2008) and Scherzinger et al. (2018) for the case of some aspidoceratids. This overlap is frequently overlooked until the species are well known from complete adult specimens, thus, as we are dealing with several different genera and families of ammonites, we use, herein, mostly the morphologic terms macro- and microconch.

Order Ammonitida Haeckel, 1866
Suborder Ammonitina Fischer, 1882
Superfamily Perisphinctoidea Steinmann, 1890
Family Torquatisphinctinae Tavera, 1985

Genus *Catutosphinctes* Leanza & Zeiss, 1992

Type species: *Catutosphinctes rafaeli* Leanza & Zeiss, 1992, by original designation.

Catutosphinctes inflatus Leanza, 1945
Fig. 3C

Material: Two well-preserved, complete adult microconchs/males (MOZ-PI-11552-11553) from faunal level 1.

Dimensions:
MOZ-PI-11552 (Fig. 3C)
D_p = 41 mm: *U/D* = 0.39, *W/D* = 0.29, *P* = 13, *V* = 23, *V/P* = 1.8
D_{ls} = 32 mm: *U/D* = 0.31, *W/D* = 0.31, *P* = 10, *V* = 18, *V/P* = 1.8

MOZ-PI-11553
D_p = 55 mm: *U/D* = 0.44, *P* = 12, *V* = 20, *V/P* = 1.7

Description: The smaller specimen (Fig. 3C) is a complete adult microconch with one of its lappets preserverd. The phragmocone is moderately evolute, round-whorled, with widely spaced sharp primary ribs, bifurcated in the upper half of the flank. The body-chamber is more evolute, with compressed suboval whorl section; ribbing rather irregular, the primary ribs bifurcate but one single intercalates each one or two of the bifurcates; ventral ribbing uninterrupted and evenly spaced. The body-chamber is 210 ° in angular length. Peristome with small subtriangular lappets.

Remarks: The two specimens show the body-chamber uncoiled, indicating they are adults. The non-figured specimen is somewhat larger, by about one half-whorl, with strong and more widely spaced ribs in the body-chamber. These differences with respect to the smaller specimen show this latter has matured somewhat earlier, at a smaller size, and grew faster. This variation among males has been noted, and even more marked, in other ammonite species (e.g., Scherzinger et al. 2018; Parent et al. 2019). Females also show this kind of variation (e.g., Parent et al. 2008; Scherzinger et al. 2018).

The macro- and microconchs of the successive species of the *Catutosphinctes* lineage are rather well known (see Parent et al. 2011a, 2011b, 2015, 2017b; Garrido et al. 2018; cf. Zeiss & Leanza 2008). Macroconchs of *C. inflatus*, other than the holotype (Leanza 1945: pl. 1, fig. 1), have been described in detail from Arroyo Cieneguita and Pampa Tril (Parent et al. 2011b, 2015), ranging the upper Internispinosum up to the Alternans Zone. A recent collection from Pampa Tril (to be published elsewhere) includes several adult microconchs from the *azulense* Horizon (Alternans Zone) which perfectly match the present specimens.

Family Himalayitidae Spath, 1925

Remarks: This family has been fully reviewed by Énay & Howarth (2019). However, some changes originated in new discoveries and corrections should be introduced as discussed at some length in Parent & Garrido (2021) and Parent et al. (2025). The family comprises several lineages originated, during the Ponti-Micracanthum/Internispinosum-Alternans zones, from different ataxioceratid perisphinctids (mainly of the subfamily Torquatisphinctinae Tavera, 1985) along the borders of the Gondwana and in the Tethys Ocean (see Olóriz 1978; Tavera 1985; Enay et al. 1998a, 1998b; Parent et al. 2011b, 2015, 2017b,

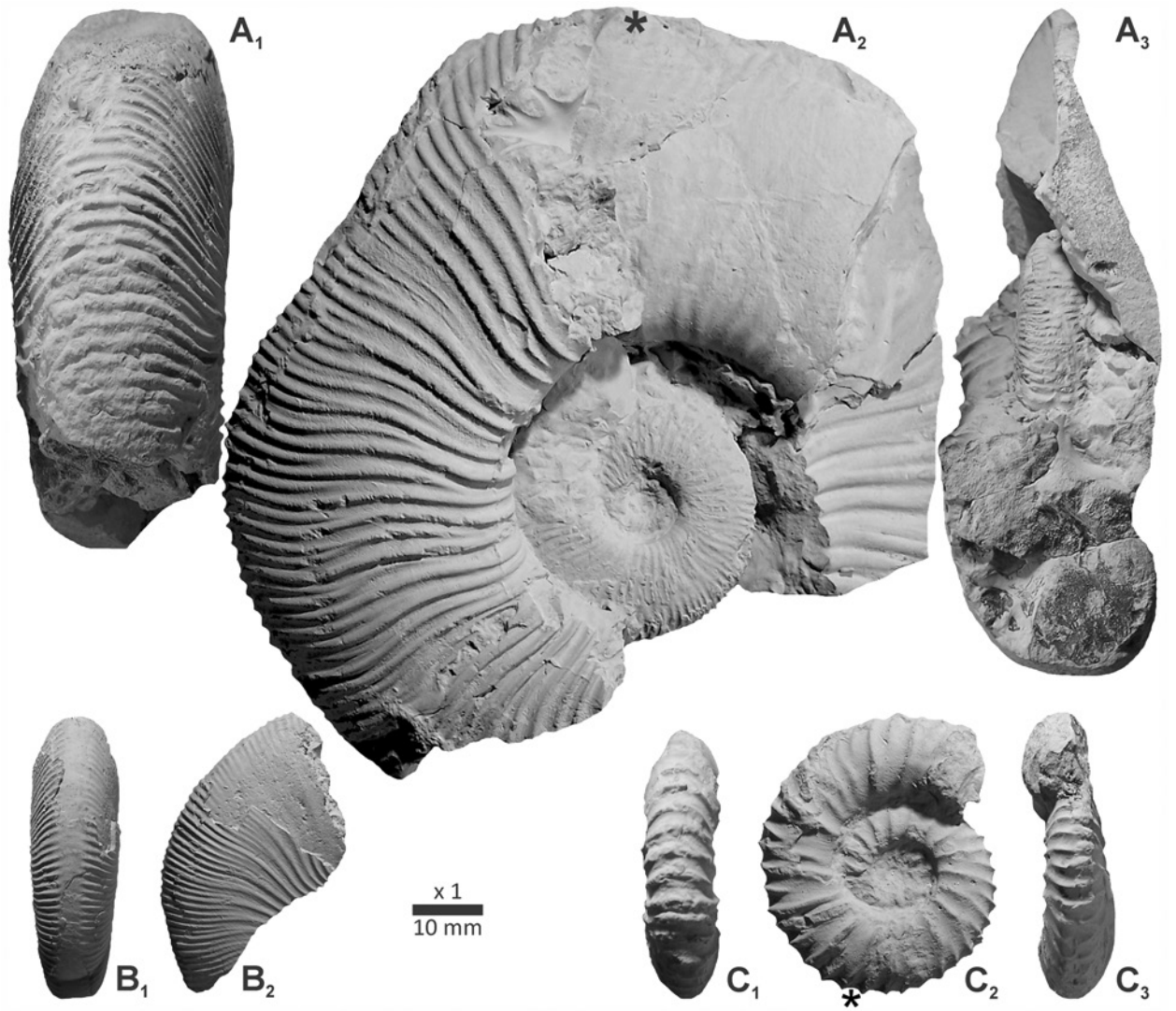

Fig. 3. A – *Subthurmannia boissieri* (Pictet, 1867), faunal level 3, Damesi Zone, Cajón de Almanza; adult macroconch with beginning of the body-chamber (MOZ-PI-11549). **B** – *Substeueroceras koeneni* (Steuer, 1897), faunal level 2, Koeneni Zone, Cajón de Almanza; portion of phragmocone (MOZ-PI-10959). **C** – *Catutosphinctes inflatus* (Leanza, 1945), faunal level 1, Alternans Zone, Cajón de Almanza; complete adult microconch with lappets (MOZ-PI-11552). – All natural size (×1). Asterisk indicating the last septum.

2025; Bulot et al. 2014; Frau et al. 2015, 2016; Parent & Garrido 2021, and references therein).

Genus *Corongoceras* Spath, 1925

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

Remarks: This genus is a typical himalayitid, originally taken by Spath (1925: 144) as one of the core genera of the family. We have the same concept which follows the classification of Énay & Howarth (2019). Bulot et al. (2014) separated many of the Tethyan partial homoeomorphs of *Corongoceras* that had been described (e.g., Tavera 1985) by introducing the genus *Ardesciella* Bulot, Frau & Wimbledon, 2014.

We have studied the origin and evolution of the Andean lineage of *Corongoceras* in detail based on material from all over the Neuquén Basin, from northern Mendoza up to southern Neuquén (see Parent & Garrido 2021 with the references therein). *Corongoceras* seems to have been originated from the latest representatives of *Catutosphinctes proximus* (Steuer, 1897) in the late Proximus or early Internispinosum

Zone. Intermediate forms have been described, in the cited paper as *Corongoceras* aff. *huarpense* Parent & Garrido, 2021.

The himalayitid genera *Corongoceras* and *Steueria* Parent, Scherzinger & Schweigert, 2011b can be easily differentiated based on their different sculpture ontogeny and sexual dimorphism (Parent et al. 2011b; Énay & Howarth 2019). However, since the confussion between both genera yet persists, misplacing, e.g. the typical *Steueria alternans* (Gerth, 1921) in *Corongoceras* (e.g., Salazar & Stinnesbeck 2015; Vennari & Aguirre-Urreta 2019; Aguirre-Urreta et al. 2019), it is important to review the differences between both genera. The specimen in Fig. 4A illustrates a typical adult female macroconch of *Steueria alternans* (Gerth, 1921). This specimen is part of a formerly collected association from the Alternans Zone of Cajón de Almanza (discussed below), further including *Corongoceras mendozanum* (Behrendsen, 1891) and *Pseudoparodontoceras dezai* Parent, Garrido, Scherzinger, Schweigert & Főzy, 2015. This large adult female specimen of *Steueria alternans* illustrates the remarkable morpho-sculptural differences with respect to *Corongoceras mendozanum*:

(1) the phragmocone ribbing of *Steueria* tends to be dense to very dense (see Parent 2001: fig. 9D holotype of the type species, and Parent et al. 2011b: fig. 29A, D), but sharper and more widely spaced in *Corongoceras* (e.g. Fig. 4B),

(2) in *Steueria* the lateral and ventral tubercles are bullae (base of spines) occurring each three to five primary ribs (Fig. 4A), while in *Corongoceras* they are spiniform swellings in almost every bifurcation point and, in the venter of the phragmocone, at every rib ending (e.g. Fig. 4B),

(3) the adult females of *Steueria* are larger and with more inflate body-chamber than those of *Corongoceras* (see Parent et al. 2011b: fig. 33B),

(4) adult males of *Steueria* have densely ribbed body-chamber up to the lappeted peristome (see Parent et al. 2013: fig. 17C), while in *Corongoceras* they remain strongly ribbed with lateral and ventrolateral spiny tubercles, showing no significant differences with respect to the female at comparable size (Parent et al. 2011b: fig. 34B, D).

Corongoceras mendozanum (Behrendsen, 1891)
Fig. 4B

Material: Two well-preserved macroconchs (MOZ-PI-4234/1-2) with the beginning of the body-chamber, from faunal level 1.

Remarks: The species has already been revised in detail recently (Parent et al. 2011b; Parent & Garrido 2021). This species includes several morphotypes; the present specimens perfectly match the most frequent of them (e.g., Parent et al. 2011b: fig. 33B at comparable diameter, and fig. 34E) which includes the holotype of the species.

C. mendozanum is currently known from the Alternans Zone (Leanza 1981; Parent et al. 2015; Parent & Garrido 2021), north of the Huincul High and reaching the northernmost ends of the basin. South of the Huincul High, in the Austral sector of the Neuquén Basin (Garrido & Parent 2017) or Picún Leufú Subbasin, the genus is represented by *Corongoceras lotenoense* Spath, 1925 in coeval horizons (see Parent & Garrido 2021). These two forms seem to be separate species and not merely geographic variants of a single one. The genus seems to have originated from *Catutosphinctes proximus* (Steuer, 1897) with an early *Corongoceras* (*C.* aff. *huarpense* Parent & Garrido, 2021) in the late Proximus Zone.

Both species would have originated from *Corongoceras huarpense* Parent & Garrido, 2021 during the late Internispinosum Zone (Parent & Garrido 2021: fig. 26). *C. lotenoense* remained confined living in the Picún Leufú Subbasin, whereas early forms of *C. mendozanum* soon migrated north of the Huincul High evolving into the well known type morphotype of the species and spreading towards the northernmost regions of the basin (see e.g., Salazar & Stinnesbeck 2016).

Dimensions:
MOZ-PI-4234/1 (Fig. 4B)
D_{max} (Bc) = 48 mm: *U/D* = 0.38, *W/D* = 0.33, *P* = 12, *V* = 19, *V/P* = 1.6
D (Ph) = 37 mm: *U/D* = 0.32, *W/D* = 0.34, *P* = 11, *V* = 20, *V/P* = 1.8

Genus *Leonardia* nov.

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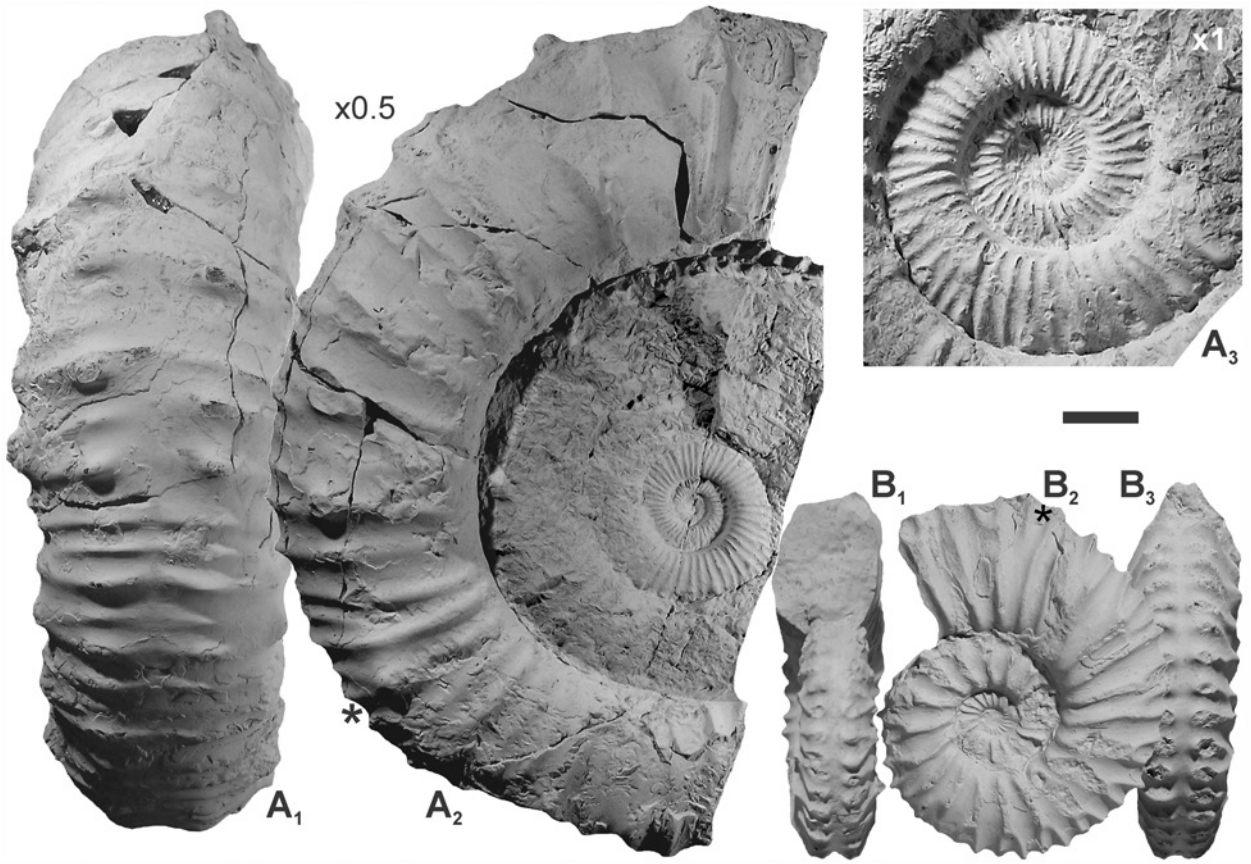

Fig. 4. A: *Steueria alternans* (Gerth, 1921), Alternans Zone, Cajón de Almanza (former collection); almost complete adult macroconch, left face (modified from Parent et al. 2013: fig. 16); A_1–A_2 half size (×0.5), A_3: inner whorls of the right face (×1). **B** – *Corongoceras mendozanum* (Behrendsen, 1891), natural size (×1), faunal level 1, Alternans Zone, Cajón de Almanza; almost complete small macroconch (MOZ-PI-4234/1). Asterisk indicating the last septum. The bar represents 10 mm length, but 5 mm for A_1–A_2.

Etymology: After Dr. Pedro Alejo Leonardi (geologist, 1925–2020), university professor, who for several decades was able to transmit his geological and paleontological knowledge in different academic institutions of the República Argentina.

Type species: *Leonardia almanzaensis* n. gen., n. sp.

Diagnosis: Female (macroconch). Serpenticonic, evolute, whorl section suboval to subrectangular. In the inner whorls single ribs alternate with ribs bifurcated from a small tubercle and looped to a ventral tubercle. Adult phragmocone with regularly bifurcated ribs only. The body-chamber tends to be smooth. Male (microconch) unknown.

Species included: *Berriasella steinmanni* Krantz, 1926 (Alternans Zone) and *L. almanzaensis* n. gen., n. sp. (Koeneni Zone).

Remarks and comparison: The diagnostic morpho-sculptural ontogeny of *Leonardia* n. gen. is not known in any other Andean ammonite. The tuberculate inner and middle whorls, the looped ribs, and the general stout serpenticonic shape of the shell strongly suggest *Leonardia* n. gen. belongs to the Himalayitidae. The number of primary ribs per half whorl increases abruptly up to $D = 20$ mm, then decelerates and becomes rather constant throughout the adult phragmocone (Fig. 5C).

Steueria Parent, Scherzinger & Schweigert, 2011 has similarly sculptured inner whorls but with no looped ribs, and the outer whorls have a different sculpture, retaining the lateral and ventral tubercles; additionally the adult size of the macroconchs is larger. *Wichmanniceras* Leanza, 1945 (Alternans Zone) bears looped ribs and ventral tubercles but the ribs are simple throughout the ontogeny up to the body-chamber. *Corongoceras* (Internispinosum to Alternans

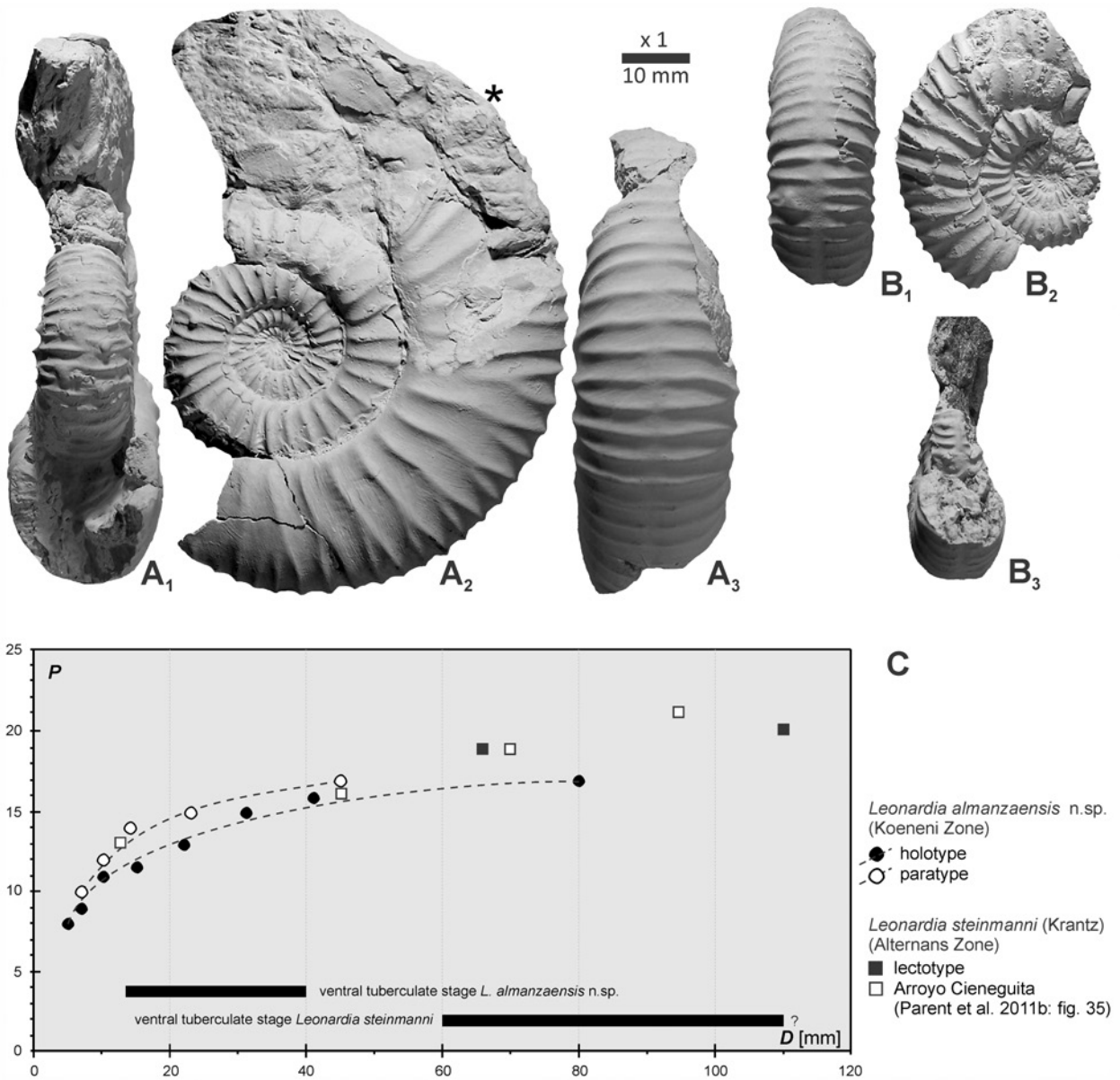

Fig. 5. *Leonardia almanzaensis* n. gen., n. sp., faunal level 2, Koeneni Zone, Cajón de Almanza. **A** – Holotype (MOZ-PI-10958), adult macroconch with beginning of the body-chamber. **B** – Paratype (MOZ-PI-10957), phragmocone. **C** – Plot of *P* (number of primary ribs per half whorl) with respect to *D* and comparison with *Leonardia steinmanni* (Krantz, 1926); the *D*-axis is in natural scale (×1). – All natural size (×1). Asterisk indicating the last septum.

zones) and *Ardesciella* Bulot, Frau & Wimbledon, 2014 (Microcanthum to Durangites zones) differ from *Leonardia* n. gen. by having sharper ribbing with more prominent, regular, and peristent tuberculation, and no looped ribs.

Leonardia n. gen. shows superficial resemblance to some *Catutosphinctes*. Nonetheless, the resemblance is confined to the basic perisphinctoid shell-shape (whorl section and involution). The primary ribs in *Catutosphinctes* show a diagnostic mild to strong swelling in the point of bifurcation (see Parent et al. 2011a, 2011b, 2015), whereas in the new genus the ribs are slightly swollen in the lower flank and then weaken in the point of bifurcation. Furthermore, the inner and middle whorls of *Leonardia* n. gen. have a completely different style of ribbing with lateral spines and ventrolateral or ventral tubercles. Among thousands specimens of *Catutosphinctes* throughout "all" the Tithonian studied by the authors, there has never been found a single one with

tubercles in any part of the ontogeny, only swelling in the points of bifurcation or in the ending of interrupted ribs in the venter, but nothing even comparable with those in the venter with "parabolic" aspect, or the spines in the points of furcation in *Leonardia* n. gen.

Leonardia almanzaensis n. gen., n. sp.
Fig. 5

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Etymology: After the name of the type locality Cajón de Almanza. Almanza derives from the Arabian "almansa", meaning the house.

Material: Two specimens from faunal level 2: (1) the holotype (Fig. 5A), a well-preserved macroconch with incomplete body-chamber (MOZ-PI-10958), and (2) the only paratype (Fig. 5B), a well-preserved phragmocone (MOZ-PI-10957).

Type locality and horizon: Cajón de Almanza, Neuquén Province. Koeneni Zone, Upper Tithonian.

Dimensiones of the holotype:
D_{ls} = 80 mm: *U/D* = 0.50, *W/D* c. 0.28, *P* = 17, *V* c. 35, *V/P* c. 2.1

Description: The holotype (Fig. 5A) is the most complete specimen (maximum *D* = 86 mm), an adult macroconch preserving the whole phragmocone and the beginning of the body-chamber.

The inner and middle whorls, about *D* = 5–50 mm, are evolute with wider than high (W/H_1 about 1.4), suboval whorl section. The sculpture consists of single and bifurcated primary ribs, with small tubercles in the point of furcation in the upper half of the flank. Most secondary ribs are irregularly looped in pairs into a ventral tubercle. The ventral tubercles are not paired in venter but they alternate forming a zigzag pattern.

The outermost whorl of the phragmocone (*D* = 60–80 mm) remains evolute but the whorl section becomes rather subrectangular, with similar height and width. The ribbing consists of rather sharp primary ribs, originated in the upper umbilical wall, regularly bifurcating in the upper half of the flank. The ventral ribs are evenly spaced and equal in strength as the primaries, weakened in the mid-ventral line. Close to the end of the phragmocone there is a singular primary rib joined, at the umbilical shoulder, to a normal bifurcate.

The body-chamber begins at *D* = 80 mm; only the beginning is preserved, poorly, and shows no sculpture. The adult size at peristome is estimated in 120–130 mm, with a body-chamber of three-quarters of a whorl long. There are no constrictions in the whole ontogeny.

The paratype (Fig. 5B) is an incomplete phragmocone. The exposed inner whorls show the ventral pattern of sculpture at *D* = 15–20 mm (Fig. $5B_3$), consisting of ribs interrupted by a smooth ventral band, some of them ending in a small tubercle.

Remarks and comparison: *Berriasella steinmanni* Krantz, 1926 (Alternans Zone) was tentatively assigned to *Corongoceras* in Parent et al. (2011b). However, according to its shell-shape and sculpture it can be assigned to *Leonardia* n. gen., representing a species older than the type species. The last whorl of the lectotype (Fig. 6) is almost wholly septated as indicated by the well-preserved siphuncle. *L. steinmanni* is slightly more compressed than *L. almanzaensis* n. gen. n. sp., and the ribs ending looped in ventral tubercles persist in the adult phragmocone (Fig. 6), whereas in the latter they fade-off in the juvenile phragmocone (Fig. 5).

Family Neocomitidae Salfeld, 1921
Subfamily Berriasellinae Spath, 1922

Genus *Substeueroceras* Spath, 1923

Type species: *Odontoceras koeneni* Steuer, 1897, by original designation.

Remarks: Recent studies (Parent et al. 2015, 2017b; Garrido & Parent 2017) have revealed that the genus forms a lineage through the Alternans–Noduliferum zones composed, at least by *Substeueroceras* n. sp. A (as *Substeueroceras*? sp. A in Parent et al. 2015), Alternans Zone – *Substeueroceras koeneni*, upper Alternans to Koeneni zones – *Substeueroceras permulticostatum* (Steuer, 1897), Noduliferum Zone.

Substeueroceras koeneni (Steuer, 1897)
Fig. 3B

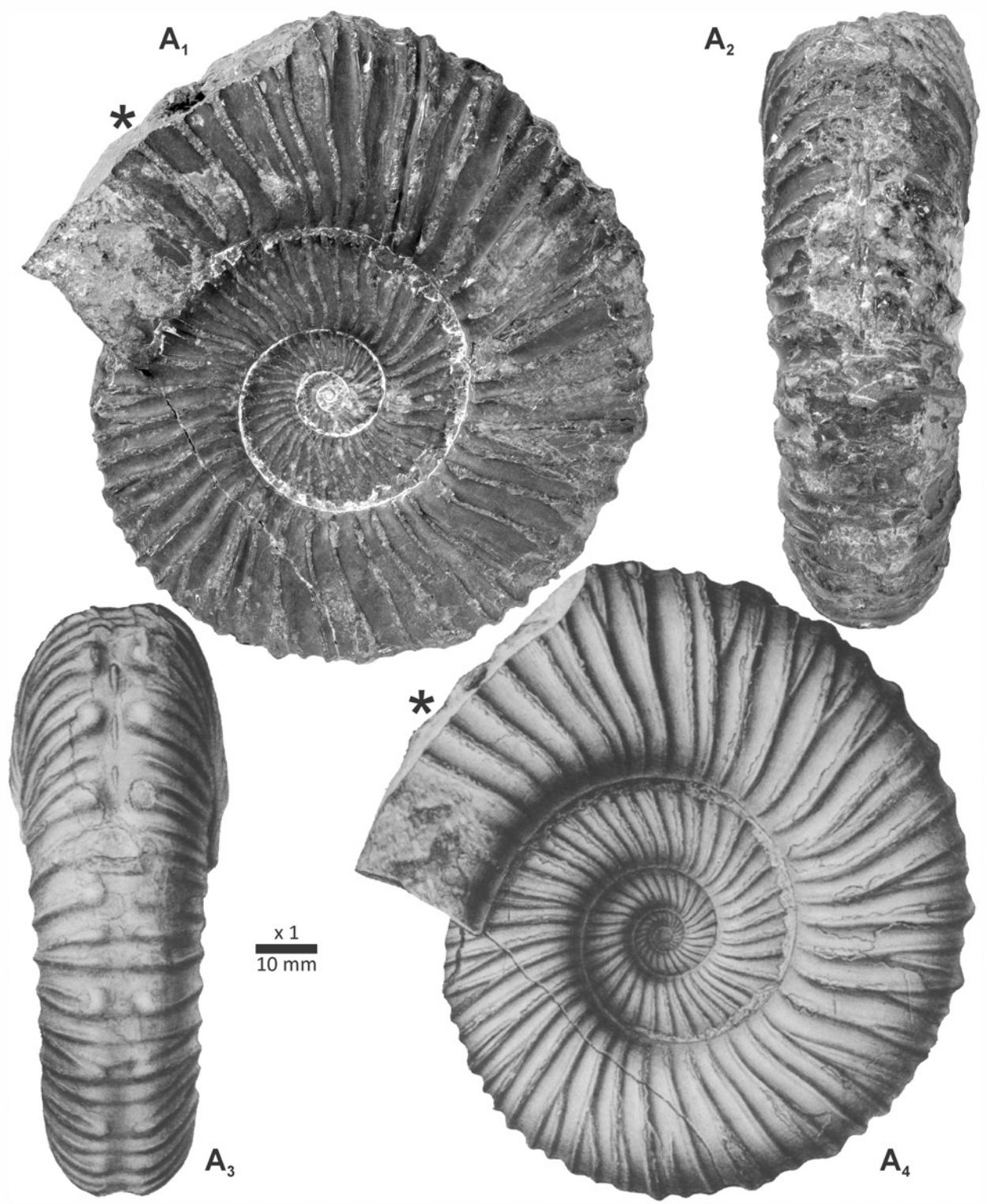

Fig. 6. *Berriasella steinmanni* KRANTZ, 1926, lectotype; assigned to *Leonardia* n. gen. Photographic refiguration (**A**$_1$–**A**$_2$) and original figuration (KRANTZ 1926: pl. 14, figs. 3–4; 1928: pl. 1, fig. 3) (**A**$_3$–**A**$_4$). Adult macroconch with the beginning of the body-chamber, Arroyo de la Manga. Specimen IGPB-Krantz-13 in the collection of the Institut for Geosciences, Section Palaeontology, University of Bonn. – All natural size (×1). Asterisk indicating the last septum.

Description: A single specimen, consisting of a fragmentary phragmocone, from the faunal level 2. The estimated diameter of the specimen is about *D* = 50 mm. The configuration of the radial angles of the ribs indicate a relatively narrow umbilicus. The whorl section is subrectangular, higher than wide, with slightly convex flanks and flattish venter. The ribbing is fine and flexuous; the primaries originate deep in the umbilical wall, and from the lower flank many split irregularly in sheaves, and some again in the middle part of the flank, producing the gently flexuous and dense polyschizotomic ribbing which is diagnostic of the genus (especially important for differentiation from *Parodontoceras* Spath, 1923). All the ribs reach the ventrolateral shoulder evenly spaced where they end leaving a smooth band in the venter.

Remarks: The specimen shows the diagnostic sculpture of *S. koeneni*, perfectly matching, at comparable diameter, the typical specimens figured by Leanza (1945: pl. 7: 4) and Parent et al. (2011b: fig. 23D). *S. koeneni* is characteristic of the Koeneni Zone but the earliest occurrences are known in the upper Alternans Zone (Gerth 1925: 126; cf. Parent et al. 2015).

It is remarkable that the known specimens of this species are macroconchs, or juvenil phragmocones. There is one ammonite which could be a lappeted-microconch, the specimen figured by Romero et al. (1995: pl. 18, fig. 2) as *Berriasella broggi* Rivera, 1951 from the upper Tithonian of Puente Inga Fm at Cerro Candela, Perú. The flexuous, polyschizotomic ribbing and tight involution of this latter specimen are not characteristic of *Berriasella* Uhlig, 1905 but of *Substeueroceras.*

Subfamily Neocomitinae Salfeld, 1921
Genus *Subthurmannia* Spath, 1939

Type species: *Subthurmannia fermori* Spath, 1939, by original designation.

Remarks: The concept and scope of the genus follows Tavera (1985: 284) and Wright et al. (1996), in which *Fauriella* Nikolov, 1966 and *Strambergella* Nikolov, 1966, and in the latter also *Tirnovella* Nikolov, 1966, are included as junior synonyms.

Subthurmannia may show some resemblance with *Substeueroceras* in female adult size, whorl section and involution, but the sculpture shows important differences, and the former is stratigraphically younger. In *Substeueroceras* there are never umbilical tubercles or swellings, the ribs born deep in the umbilical wall and gently pass the shoulder twisted backward and then forward toward the flank; in *Subthurmannia* the ribs born in the umbilical shoulder, from a tubercle/bulla or swelling where most of them already bifurcate from. At least in the Andean representatives, the adult female body-chamber of *Subthurmannia boissieri* (Pictet, 1867) is rather inflated (see description below), whereas in *S. koeneni* is compressed with a narrow ventral area (see Parent 2022: fig. 25A).

Subthurmannia boissieri (Pictet, 1867)
Fig. 3A

Material: Two well-preserved adult macroconchs with the beginning of the body-chamber (MOZ-PI-11548-11549) from faunal level 3.

Remarks: This species has been recorded in abundance from the upper Noduliferum Zone up to the Damesi Zone in Pampa Tril where different morphotypes occur (see Parent et al. 2015, 2017b for description and detailed discussion). These morphotypes mainly differ in the density of the ribbing from a shell diameter of 20–30 mm. The present specimens from Cajón de Almanza match the most finely and densely ribbed of the two morphotypes recorded from Pampa Tril (e.g., Parent et al. 2017b: fig. 8) from the Damesi Zone; the resemblance is the closest with the specimen in the figure 8B of that paper, showing even the same wide, subtrapezoidal whorl section at the end of the adult phragmocone.

The larger specimen (not figured) has the phragmocone identical to the specimen in Fig. 3A, and a quarter of whorl of the body-chamber preserved, more inflate than the phragmocone. From the end of the phragmocone the primary ribs become stronger, and in the preserved part of the body-chamber they are undivided and widely spaced.

The wide, Tethyan and peri-Gondwanian distribution of this species has been discussed in Parent et al. (2015), considering figured specimens from, besides the European Tethys and the material in Spath (1939), Argentina, Perú, México, and India, and can be added New Guinea (Spath 1952; Matsumoto & Skwarko 1993).

4 Biostratigraphic chronostratigraphy of the studied succession

The chronostratigraphic classification of the studied succession of ammonites is based on the age of similar ammonites and the occurrence of similar associations, especially of comparable morphotypes described from well studied sections. The studied succession fits tightly with what is well known in the basin.

The chronostratigrahic ammonite-zonation adopted herein follows Leanza (1981) modified by Parent et al. (2011a, 2011b, 2015) and Garrido et al. (2018), reviewed and updated in Parent (2022), mainly based on ammonite biohorizons. This zonation is very similar to that discussed by Vennari (2016) and Aguirre-Urreta et al. (2019) but differs, mainly, in terminology.

4.1 Faunal level 1

Catutosphinctes inflatus has been recorded in the uppermost part of the Internispinosum Zone and through most of the Alternans Zone (Leanza 1945, Parent et al. 2011a, 2011b, 2015, 2017b, Garrido et al. 2018). Identical microconchs were recently collected (to be published elsewhere) in Pampa Tril from the *azulensis* Hz. of the Alternans Zone.

Corongoceras mendozanum is a typical species of the Alternans Zone (Leanza 1981; Parent et al. 2011b, 2013, 2015), recorded only north of the Huincul High (Parent & Garrido 2021).

The association of the present morphotypes of these two species has been recorded in Pampa Tril, further associated with *Parodontoceras calistoides* (Behrendsen, 1891), *Pseudoparodontoceras dezai*, and *Blanfordiceras vetustum* (Steuer, 1897). This assemblage defines the *vetustum* Hz. in the lower Alternans Zone, with type locality in Pampa Tril (level PT-36 in Parent et al. 2015). Thus, a definite Alternans Zone age is assigned to the faunal level 1.

4.2 Faunal level 2

Substeueroceras koeneni ranges the standard Koeneni Zone, from its basal horizon, the *striolatus* Hz, and at least the lower part of the Noduliferum Zone of the Andean lower Berriasian (Gerth 1925; Leanza 1945; Parent et al. 2011b, 2015; Parent 2022). Our fragmentary specimen is closely comparable with the paralectotype (refigured in Parent et al. 2011b: fig. C in App. 2) but the ventral smooth band in the internal mold is wider, thus matching the macroconch from Chacay Melehué figured in Parent et al. (2011b: fig. D). Strong support for a Koeneni Zone age is provided by the fact that the faunal level 2 is sandwiched between Alternans Zone beds (faunal level 1) and Damesi Zone beds (faunal level 3).

Leonardia almanzaensis n. gen., n. sp., does not contribute to date this level, for the specimens here described are the only known at present. Himalayitids are known to occur within the range Internispinosum–Koeneni zones in the Andean region.

4.3 Faunal level 3

Subthurmannia boissieri is known to range, in the Neuquén Basin, the upper Noduliferum Zone and the Damesi Zone (Windhausen 1918; Parent et al. 2015, 2017b). The perfect match with the morphotype/transient of the Damesi Zone of Pampa Tril (discussion above), strongly suggests this age for the faunal level 3.

5 A composite ammonite succession of Cajón de Almanza

As noted above the ammonite fauna of the Vaca Muerta Fm in the area of Cajón de Almanza is poorly known. Currently, the data available are: (1) the ammonite succession described above, (2) some few ammonite associations formerly collected with no stratigraphic information of succession (Fig. 7), and (3) the faunal list of Leanza & Hugo (1977: 256). A composite-succession from these sources is shown in Fig. 8 and discussed below.

5.1 The succession of Leanza & Hugo (1977)

The ammonites listed by Leanza & Hugo (1977: 256) are interpreted as follows (from below):

Virgatosphinctes cf. *choicensis* (Burckhardt, 1903). – Although sometimes yet cited in the Andes, the genus *Virgatosphinctes* Uhlig, 1910 has no representatives in the Andean region – it is a typical genus of the Indo-Madagascan region including eastern Africa (see Enay & Cariou 1997; Enay 2009; Parent et al.

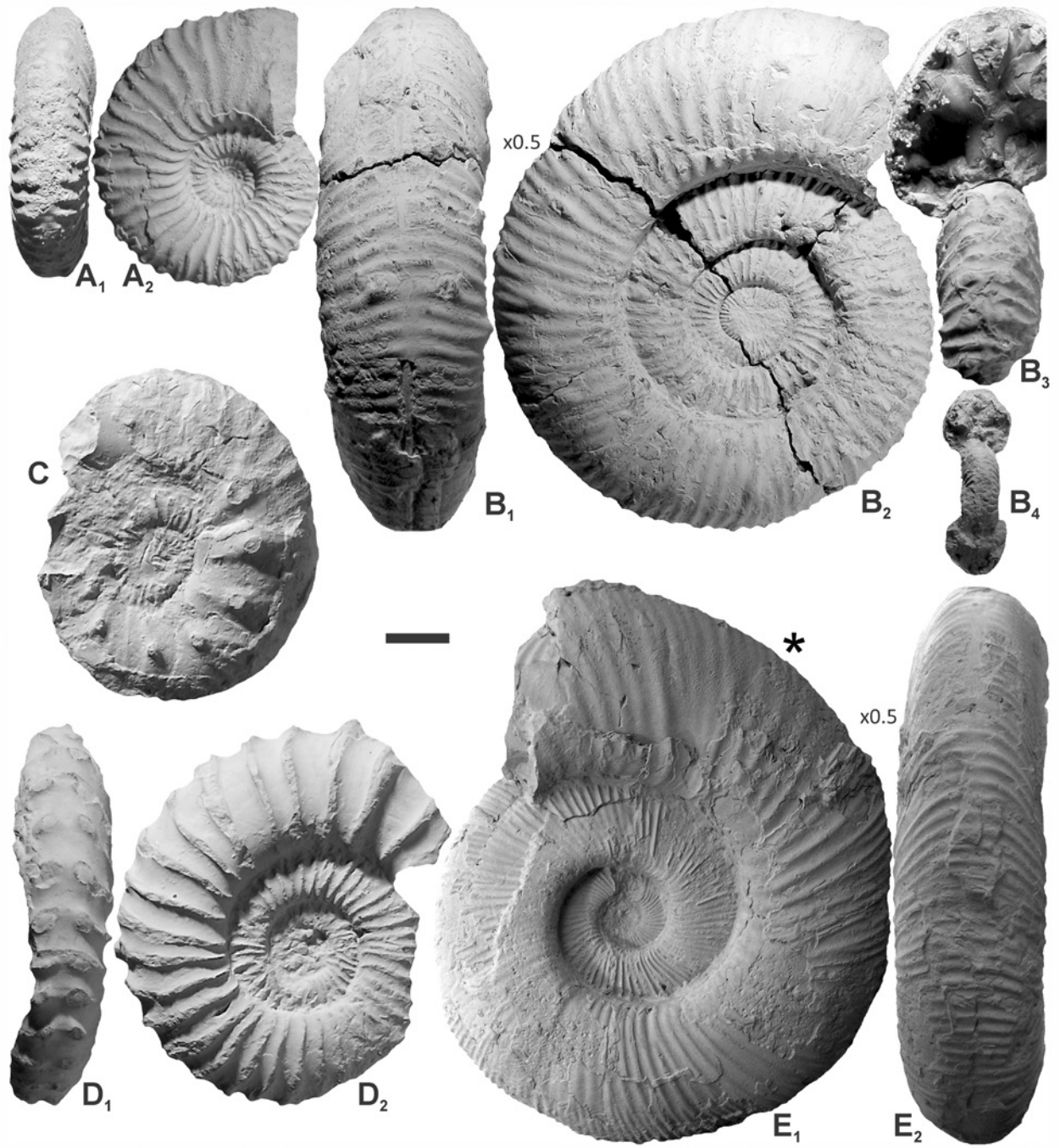

Fig. 7. Ammonites from Cajón de Almanza (former collections), here assigned to the Alternans Zone (A–B) and to the upper Alternans–Koeneni zones (C–E). **A** – *Pseudoparodontoceras dezai* Parent, Garrido, Scherzinger, Schweigert & Főzy, 2015, macroconch phragmocone (×1) (MOZ-PI-4238). **B** – *Steueria alternans* (Gerth, 1921) morph spinulosa, adult macroconch phragmocone (modified from Parent et al. 2011b); $\mathbf{B_1}$–$\mathbf{B_2}$ (×0.5); $\mathbf{B_3}$ (×1) at *D* = 50 mm; $\mathbf{B_4}$ (×1) at *D* = 25 mm. **C** – *Himalayites* cf. *treubi* Boehm, 1904, macroconch phragmocone (×1) (modified from Parent & Garrido 2021). **D** – *Lotenia* aff. *neuquensis* (Zeiss & Leanza, 2008), adult phragmocone (×1) (modified from Parent & Garrido 2021). **E**: *Choicensisphintes striolatus* (Steuer, 1897), adult macroconch with beginning of body-chamber (×0.5) (modified from Parent 2022). – Asterisk indicating the last septum. Scale bar is 10 mm (×1) for all except for B_1–B_2, and E (20 mm, ×0.5).

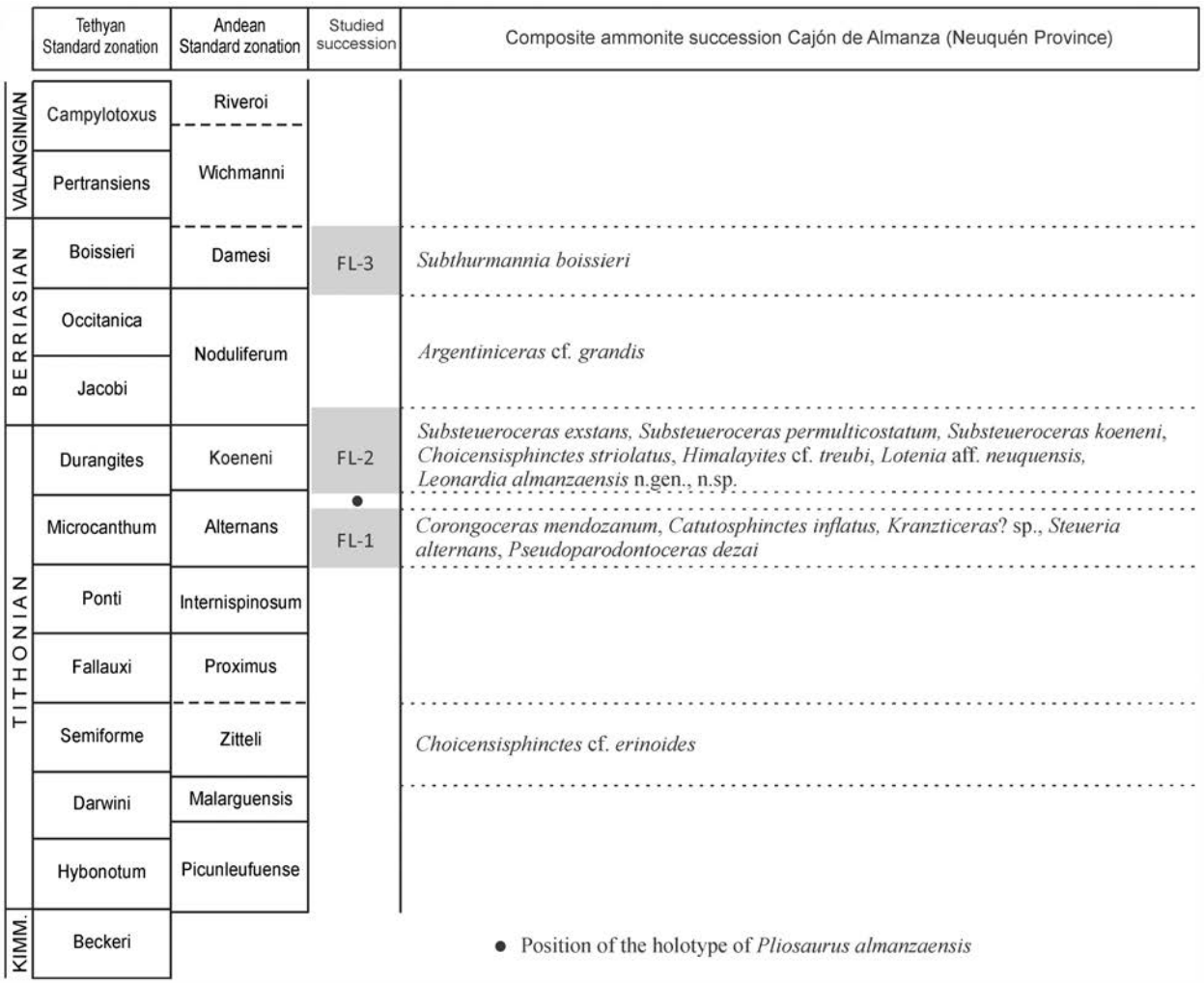

Fig. 8. Chronostratigraphy of the ammonite succession of Cajón de Almanza, referred to the Andean (Leanza 1981; Garrido et al. 2018; Parent 2022) and Tethyan (Cariou & Hantzpergue 1997; Reboulet et al. 2011; Schweigert 2015) ammonite standard zonations. This succession is a composite from the ammonites listed by Leanza & Hugo (1977) with updated taxonomy (see text), former collections in the MOZ, and the material described in this report. The gray boxes indicate the most probable intervals within which the three faunal levels (FL) studied would be included. Solid lines at the base of standardized Andean zones, broken lines for non-standard zones. The stratigraphic position of the holotype of *Pliosaurus almanzaensis* indicated by a bold dot.

2011b, 2015, 2017a). On the other hand, *Perisphinctes choicensis* is the type species of *Choicensisphintes* Leanza, 1980, and subjective synonym of *Choicensispinctes erinoides* (Burckhardt, 1903). The holotype of *C. choicensis* was figured by Burckhardt (1903: pl. 5, figs. 10–11); it is a macroconch from the Zitteli Zone (see Parent et al. 2011b, 2015) of the area between Cajón del Burro and the valley of Río Choicas. Vennari (2016: 111) designated a neotype, but unfortunately it is a microconch and from an unknown horizon.

Thus, the citation of *V.* cf. *choicensis* is here interpreted as *Choicensisphinctes* cf. *choicensis/erinoides*, indicating some horizon within the interval Malarguensis-Zitteli zones (see Parent 2022).

Berriasella sp. This citation cannot be elaborated.

Virgatosphinctes aff. *transitorius* (Oppel, 1865). – This citation suggests an ammonite showing affinity with *Paraulacosphinctes transitorius*, a southern Tethyan species typical of the Microcanthum Zone. However, *Paraulacosphinctes* Schindewolf, 1925 does not seem to occur in the Andean basins. Several ammonites from the Neuquén Basin have been attributed to this genus (e.g., Krantz 1926, 1928; Parent

2003), but they are currently assigned to the Andean genus *Krantziceras* Parent, Scherzinger & Schweigert, 2011 whose phragmocones are to some point homoeomorphs. *Krantziceras* has a long stratigraphic range through the Tithonian and lower Berriasian, with successive species not all known in detail yet (see Parent et al. 2017a). The most similar *Krantziceras* to *P. transitorius* is *K. azulense* (Leanza, 1945) from the Alternans Zone. Thus, considering that the ammonite cited by Leanza & Hugo (1977) occurs below levels with several ammonites attributed to *Substeueroceras*, known from the interval Koeneni to Noduliferum zones (see below), it is reasonable to assign an Alternans Zone age to that.

Substeueroceras permulticostatum (Steuer, 1897). – This species has been revised recently (Garrido & Parent 2017) from the holotype (a macroconch refigured by Salazar 2012: fig. 4.60a–b) and a complete macroconch from the Noduliferum Zone of Mallín Quemado associated with *Groebericeras bifrons* Leanza, 1945. *S. permulticostatum* evolved from *S. koeneni* with little morphologic change in the macroconch, being more evolute and with a marked ventral groove through the adult phragmocone (see above). *S. permulticostatum* has been cited by Leanza & Hugo (1977) from the Koeneni Zone of the studied locality, as well as from Mallín de los Caballos and Huncal. Thus, it seems that early morphotypes transitional from *S. koeneni* may occur already in the upper Koeneni Zone.

Substeueroceras striolatissimum (Steuer, 1897). – The lectotypes of *Reineckeia striolata* Steuer, 1897 and *Reineckeia striolatissima* are ammonites moderately involute which only differ because the latter is more densely and finely ribbed (Parent 2003: fig. 9A–D). There are complete gradational series from single horizons, from one to another in terms of rib-density, whereas the shell shape remains almost invariable (e.g. Leanza 1945, Parent et al. 2011b, 2015), so that they must be considered synonyms. Gerth (1925: 82) and Leanza (1945: 31) assigned, provisionally, *R. striolatissima* to *Substeueroceras*, and Leanza (1945: 24) *R. striolata* to *Pectinaties* Buckman, 1922 with doubts. However, the sexual dimorphism, the inner whorls, and the style of ribbing indicate both species belong to *Choicensisphinctes* (see Parent et al. 2011b, 2015). Beyond the known occurrences in the Koeneni Zone (e.g., Gerth 1925; Leanza 1945; Leanza 1981), a collection of several adult macroconchs in succession from a single section of Pampa Tril, has shown that the earliest occurrences of *C. striolatus* are in the Alternans Zone (Parent et al. 2015) as already recorded in Arroyo del Yeso by Leanza (1945: 89).

Substeueroceras exstans Leanza, 1945. – This poorly known species was based on two specimens from the Koeneni Zone of Arroyo del Yeso. Since no holotype was designated in the original description, we designate the specimen figured by Leanza (1945: pl. 7, figs. 1–2) as lectotype of *S. exstans*. The lectotype is an incomplete ammonite, just portions of two consecutive whorls, apparently adult because of the strong variocostation and apparent uncoiling. The visible portion of the inner whorl is indistinguishable from *S. koeneni* [M] at comparable diameter, but the outer portion of whorl (apparently end of the phragmocone and beginning of the body-chamber) is very different from the adult whorls of *S. koeneni* (see Parent et al. 2011b: figs. 23F and 24). We consider this species, based on insufficient material, has an uncertain systematic position.

Himalayites cf. *grandis* (Steuer, 1897). – *Reineckeia grandis* was based on the holotype only. This holotype was collected from the level Cieneguita V of Steuer (1897: 21) with the following ammonites: *Krantziceras ellipsostomum* (Steuer, 1897), *Krantziceras*? sp. [*Odontoceras theodorii* (Oppel, 1863, with interrupted ribbing in the tabulate venter], *Hemispiticeras steinmanni* (Steuer, 1897), and *Lytoceras* cf. *sutile* (Oppel, 1863). This assemblage seems to belong to the lower Berriasian Noduliferum Zone, although the paralectotypes and the lectotype of *H. steinmanni* seem to come from the Alternans Zone (Parent & Garrido 2021). The shell shape and the ontogeny of the sculpture suggest *R. grandis* could be an evolute representative of *Argentiniceras* Spath, 1924 as already suggested by Leanza (1945: 92), close to *Argentiniceras bituberculatum* Leanza, 1945 from the Noduliferum Zone of Arroyo del Yeso.

5.2 Additional records of isolated associations

These are two records corresponding to former collections of groups of ammonites from isolated levels in the outcrop of the Vaca Muerta Fm in Cajón de Almanza.

Association 1 – Alternans Zone:
Pseudoparondontoceras dezai, a single specimen (Fig. 7A),
Steueria alternans, several large adult female macroconchs (Figs. 4A and 7B)
Corongoceras mendozanum, several more or less incomplete, but typical specimens, exactly identical to the specimen in Fig. 4B.

Association 2 – upper Alternans–lower Koeneni zones:
Choicensisphinctes striolatus, a large adult female (Fig. 7E)

Lotenia aff. *neuquensis* (Zeiss & Leanza, 2008), a well-preserved, adult phragmocone (Fig. 7D). The inner whorls match the holotype of *L. neuquensis* at comparable diameter, but the outermost whorl differs by having more widely spaced ribs ending in well differentiated ventral tubercles which are the bases of spines.

Himalayites cf. *treubi* Boehm, 1904 (Fig. 7C), a moderately well-preserved phragmocone, indistinguishable from the specimens described from the *koeneni* Hz. (base of the Koeneni Zone) from Pampa Tril (Parent et al. 2015).

6 Final remarks

As noted above in Cajón de Almanza the modern cover makes hard the fixation of sections for detailed stratigraphic and palaeontologic sampling. However, the ammonites described and the composite succession obtained here is an important advance showing, on the other hand, that the area is very promisory for bed-by-bed collection for high-resolution chronostratigraphy.

Five faunal levels have been recognized, distributed in the Zitteli, Alternans, Koeneni (Tithonian), and Noduliferum and Damesi (Berriasian) zones (Fig. 8).

The species described are represented in the study area by morphotypes which mostly do not show differences with respect to those described from other localities. Only in some few cases there are some differences whose significance remains to be assessed from larger samples. The two female specimens of *Subthurmannia boissieri* show a larger adult size than in Pampa Tril. The female morphotype of *Corongoceras mendozanum* is identical in Arroyo Cieneguita but more compressed than the dominant morphotype in Pampa Tril.

The holotype of *Pliosaurus almanzaensis* comes from beds of the upper part of the Alternans Zone of the Late Tithonian.

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