

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

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Abstract

A new female specimen of the genus *Volanoceras* Geyssant, from the lower Zitteli Zone of the section Cerro Granito-I (southern Neuquén Basin, Argentina) is described as *V. krantzense* Cantú-Chapa. This specimen shows the sequence of ornamental stages (prosocline ribs with pseudo-furcations – periumbilical and ventrolateral tumid tubercles – periumbilical tubercles and ventrolateral clavi) as is known from the holotype (upper Zitteli Zone), but with slightly different timing and reaching a larger adult size. The large size and tumid sculpture of the present specimen are indicative of an early transient of the species, yet retaining these features closely similar to its ancestor *Volanoceras aesinense* (Meneghini). The male of the species from the Zitteli Zone of Pampa Tril is refigured, showing the expected complete identity of its phragmocone with that of the female at comparable diameter.

Keywords: Neuquén Basin, Phyletic evolution, Sexual dimorphism, *Volanoceras krantzense*.

INTRODUCTION

This paper is the second in a series planned to publish the results of our study of the stratigraphy and ammonites of the Tithonian outcrops along the transect Cerro Lotena-Cerro Granito of the Neuquén Basin (Fig. 1). The ammonites of the Family Himalayitidae Spath, 1925 were the subject of the first paper of the series (Parent & Garrido, 2021).

In this paper we present the description of the ammonites of the Family Simoceratidae Spath, 1924 from our bed-by-bed collection.

GEOLOGIC AND STRATIGRAPHIC FRAMEWORK

Four sections were studied (Fig. 2), namely Cerro Lotena (CL) and Cerro Granito I, II and III (CG-I, CG-II, and CG-III). The geologic framework, including the lithostratigraphical profiles and the biostratigraphy of the study area, has already been described in the first paper of

this series (Parent & Garrido, 2021). The chronostratigraphic scheme adopted (Fig. 3) includes the following recent refinements presented in Parent (2022):

- (1) the introduction of the Malarguensis (standard) Zone, replacing the unviable Mendozanus Zone,
- (2) the introduction of the *internispinosum-beta* Hz., which was designated as the base of the Fascipartita Subzone (Internispinosum Zone) and thus becomes a standard subzone, and
- (3) the standardization of the Zitteli, Alternans and Koeneni zones by defining their bases by the designation of faunal horizons as them.

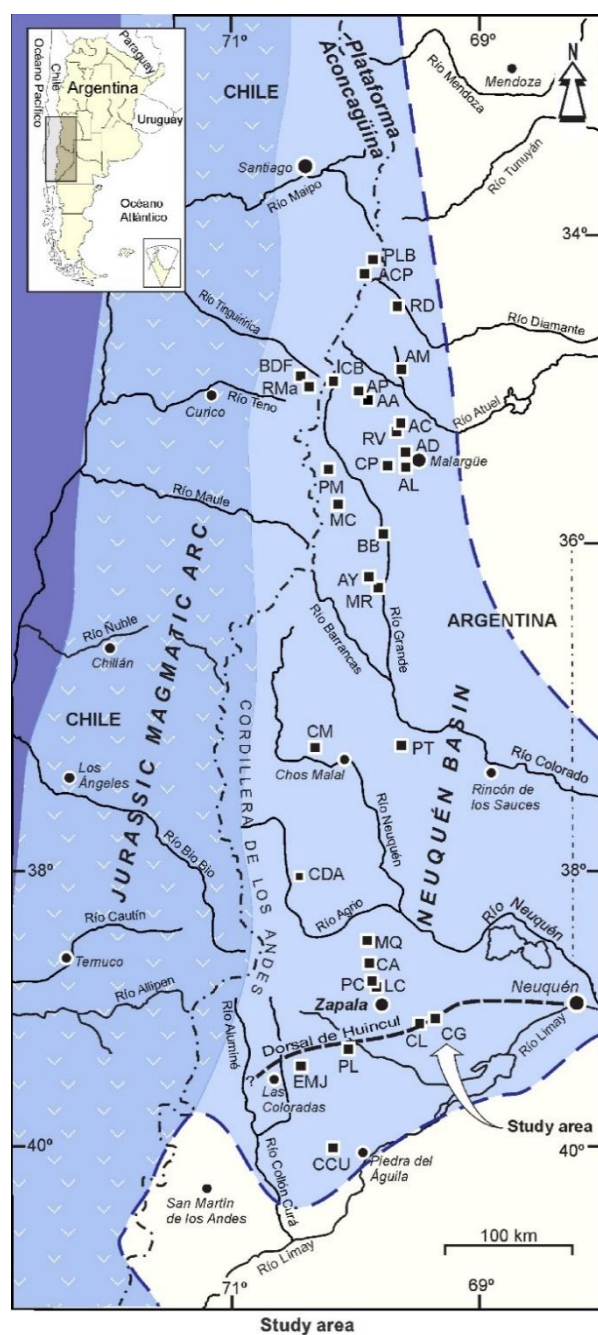
In the local ammonite successions, there are several associations of morphotypes of different species which can be used to define new biohorizons and contribute to refine the zonal chronostratigraphic subdivision of the Andean Tithonian. However, this task must be relegated after the main body of the remaining ammonite fauna will be described, which is a work still in progress.

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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.

Fig. 1. The Neuquén Basin with indication of the localities cited in the text and others showing Upper Jurassic outcrops. Modified from Garrido *et al.* (2018).

SYSTEMATIC PALAEONTOLOGY

Conventions and notation. The herein described material is housed at the Museo Provincial de Ciencias Naturales “Prof. Dr. Juan A. Olsacher”, Zapala (MOZ-PI). Body-chamber is abbreviated Bc and phragmocone Ph; macroconch female: [M], microconch male: [m]. Measurements: diameter (D), diameter at the last adult septum (D_{ls}) and diameter at adult peristome (D_p).

The sex attribution of macroconchs as females and lappeted microconchs as males follows Klug *et al.* (2015), Parent & Zatoñ (2016), and references therein. The relative adult size of an ammonite solely does not indicate definitely its sex for there is a wide variation of this feature both in females and males (e.g. Matyja & Wierzbowski, 2000; Parent *et al.*, 2008; Schweigert & Kuschel, 2017; Parent *et al.*, 2019). The sex attribution must be based on the peristome of adult specimens, commonly more easily recognizable in males because of the distinct development of lappets there.

Occurrence of the specimens is denoted by the level-number with the prefix of the corresponding section in Fig. 2: CL (Cerro Lotena), CG-I (Cerro Granito I), CG-II (Cerro Granito II) or CG-III (Cerro Granito III).

Family Simoceratidae Spath, 1924

Remarks. The ammonites of this family are typical of the Western Tethys, being especially abundant in the southern region or Mediterranean Province (e.g., Cecca, 1999; Schweigert *et al.*, 2002; Scherzinger *et al.*, 2010; Énay & Howarth, 2019; Sarti, 2020; Nannarone & Bilotta, 2021). In the Neuquén Basin, this family is known by few records of *Volanoceras* Geyssant, 1985 in the Zitteli Zone. There is a specimen from the upper Internispinosum Zone of Los Catutos figured as *Simoceratidae* indet. by Zeiss & Leanza (2010: pl. 6: 5), but it is very poorly preserved hampering a closer classification.

Genus *Volanoceras* Geyssant, 1985

Type species: *Ammonites volanensis* Oppel, 1863; by original designation.

Remarks. The composition of the genus and its synonyms have been recently reviewed by Énay & Howarth (2019). According to the extensive revision of Schweigert *et al.* (2002; see also Santantonio, 1986) the *Volanoceras* lineage consists of a phyletic sequence of rather well-known species with a spatiotemporal distribution restricted to the western Tethys, the Caribbean region and the western South Pacific.

The females of the chronospecies of the *Volanoceras* lineage are very evolute serpenticones with a succession of three main ornamental stages during ontogeny (Schweigert *et al.*, 2002: fig. 5):

(1) inner(most) whorls with simple ribs and occasional pseudo-bifurcations,

(2) middle whorls with simple ribs, occasionally looped, with ventrolateral tubercles or nodes, and

(3) subadult-adult phragmocone whorls with bituberculate ribs bearing clavate ventrolateral tubercles or nodes.

(4) the fourth ornamental stage, developed in the phragmocone and body-chamber of adult females, consists of umbilical and ventrolateral tubercles lacking a connecting rib but with a transverse ventral rib connecting the ventrolateral tubercles.

In some specimens of the lower Ponti/Volanense Zone a strong ventral ribbing in the stage 1 can be observed at $D = 9-10$ mm (Sarti, 2020: pl. 45: 5). The latest ornamental stage 4 can be observed only in the more complete specimens which are rather uncommon. These ornamental stages, mainly the first one, change in duration or time-of-onset through the lineage, producing, within ranges of intraspecific variation, the typical configuration of each species. The main evolutionary pattern of the lineage is a gradual expansion of the early ribbed stage with increase of density towards the middle whorls and an increase of adult size.

The males, currently known only in the two earliest species, are smaller. The adult bodychamber is slender than that of the corresponding female at comparable diameter, and loose the tuberculation; they may bear strong ribs or become smooth. The adult peristome bears a pair of small lappets (Villaseñor et al. 2011; and this study).

In the Neuquén Basin, the genus is known by the following records:

(1) the holotype of *Volanoceras krantzense* Cantú-Chapa, 1990, from Bardas Blancas (Fig. 1), originally described by Krantz (1928: pl. 7: 3) as *Simoceras* aff. *Volanense* (Oppel, 1863),

(2) a male specimen with lappets from Pampa Tril (Fig. 1), discussed below, formerly described as *Mazatepites arredondense* Cantú-Chapa, 1967 by Parent et al. (2015: fig. 43), and

(3) two specimens from the transect Cerro Lotena-Cerro Granito described below.

***Volanoceras krantzense* Cantu-Chapa, 1990**

Fig. 3A-C

v1926 *Simoceras* aff. *Volanense* Oppel – Krantz: 433.

v1928 *Simoceras* aff. *Volanense* Oppel – Krantz: 13, pl. 3: 7 (holotype, female).

v1990 *Volanoceras krantzense* n. sp. – Cantú-Chapa: 43.

v2002 *Volanoceras krantzense* Cantú-Chapa – Schweigert et al.: 9, pl. 2: 1 (holotype refigured), and 2. With extensive synonymy.

v2015 *Mazatepites arredondense* Cantú-Chapa – Parent et al.: 47, fig. 43 (male specimen).

v2021 *Volanoceras krantzense* Cantú-Chapa – Parent & Garrido: 60 (described below).

Material. One well-preserved adult female (macroconch) with the beginning of the body-chamber (MOZ-PI-6857/1), from level CG-I-18. One cf.-specimen (MOZ-PI-8422), a fragment of the end of a female phragmocone, from level CG-III-7.

Description. The specimen is a heavily ornamented and very evolute serpenticone, with subquadrangular whorl section through the phragmocone and beginning of the body-chamber. The innermost whorls are not preserved. From about 30 mm in diameter onwards three ornamental stages can be observed:

(1) at about $D = 20-30$ mm, prosocline ribs with pseudo-furcations.

(2) in the next whorl, from about $D = 30-40$ mm, ventrolateral and periumbilical tubercles connected by a broad rib; the ventrolateral tubercles take the form of clavi; two ribs looped in a clavus at about $D = 35$ mm.

(3) after about $D = 45$ mm the sculpture becomes stouter; the periumbilical tubercles invade a little the umbilical window; the clavi, first well formed, tend to transform in tubercles through the end of the phragmocone and beginning of the body-chamber; the ribs connecting the tubercles fade out, and in the venter appear strong transverse ribs connecting the ventrolateral tubercles through the venter. In the beginning of the body-chamber, at about $D_{1/2} = 120$ mm, the tubercles fade out and are replaced by mild ribs. The maximum preserved diameter is 130 mm.

Remarks and comparison. The specimen in Fig. 3A and the cf.-specimen in Fig. 3B are those listed in Parent & Garrido (2021: 60 and 58, respectively). The fragmentary cf.-specimen corresponds to an adult shell larger than the described female.

The specific assignation is indicated by the sequence of ornamental stages: *V. krantzense* has a more extended stage of ribbing lacking tubercles, up to 10-15 mm (Schweigert et al., 2002: pl. 2), than its direct ancestor *Volanoceras aesinense* (Meneghini, 1885) which bears the earliest tubercles from about 5-7 mm in diameter (e.g. Santantonio 1986: pl. 1: 4).

The dimensions of the whorl section and umbilicus of the specimen are not considered in detail because of the strong and prominent ornamentation; in these strongly ornamented ammonites, special considerations for measurements are needed (see Santantonio, 1986).

The holotype of *V. krantzense* (Krantz, 1928: pl. 3: 7; refigured in Schweigert et al., 2002: pl. 2: 1) is a specimen smaller than the present one, and seems to be a phragmocone with the beginning of its body-chamber. The last whorl seems to show incipient signs of uncoiling in its last portion, suggesting adulthood.

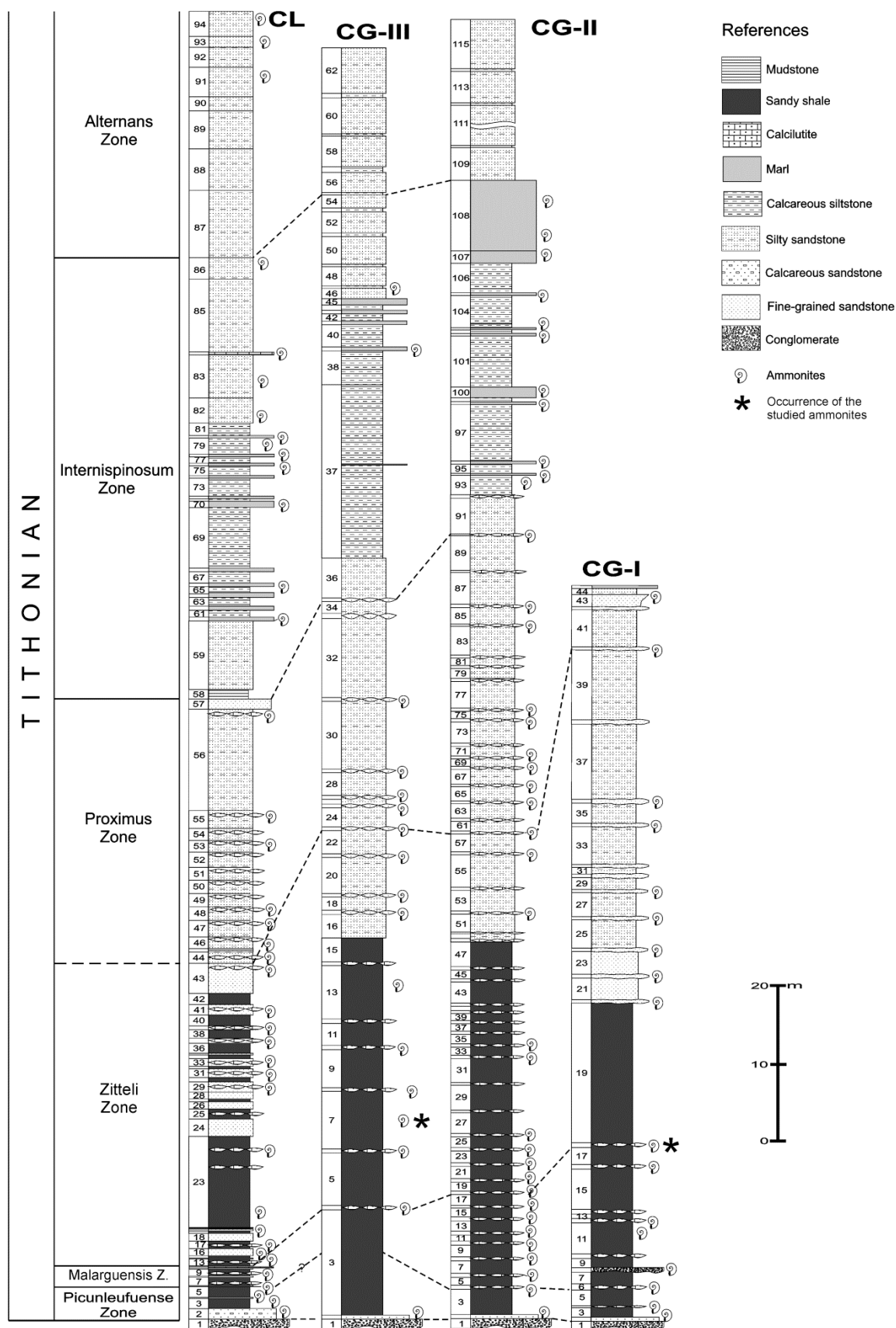


Fig. 2. Studied sections of the Vaca Muerta Fm: Cerro Lotena (CL), Cerro Granito I (CG-I), Cerro Granito II (CG-II), and Cerro Granito III (CG-III). The time-correlation of the sections, according to the scale in Fig. 3, is updated from Parent & Garrido (2021) as explained in the text. The asterisks indicate the occurrences of the studied specimens.

Thus, our specimen corresponds to an individual of larger adult size than that of the holotype, and the tubercles and connecting ribs are tumider. In these respects, our specimen, although being somewhat larger, shows resemblance with *V. aesinense* (e.g. Santantonio, 1986: pl. 1: 2, Schweigert *et al.*, 2002: pl. 1: 2). Considering that the holotype would come from the upper part of the Zitteli Zone (see below) and the present one from the lower part of this zone, this latter would be an early transient of *V. krantzense*, remaining somewhat similar to its direct phyletic ancestor *V. aesinense*.

The Tethyan representatives of *Volanoceras* exhibit periodic and sometimes well-marked constrictions through the ontogeny, whereas those of the Andean region have very few, or no, mild constrictions. Villaseñor *et al.* (2011) indicated that in their studied Mexican specimens the constrictions are subtle and rare in some, while more frequent and marked in others resembling the Tethyan specimens. Constrictions indicate discontinuous growth (Simoulin, 1945; review by Bucher *et al.*, 1996; see also Radtke & Keupp, 2016), and their frequency is most likely an expression of local environmental conditions (e.g., periodic changes in water temperature and/or availability of food) rather than to be genetically determined. Thus, we consider that the differences in prominence and frequency of constrictions of the Andean specimens are merely intraspecific variation, resulting from different environmental fluctuations in the Neuquén Basin, the southernmost region of the known geographical distribution of the genus.

Sexual dimorphism. The only known male specimen of *V. krantzense* is the ammonite figured as *Mazatepites arredondense* Cantú-Chapa, 1967 [m] by Parent *et al.* (2015: fig. 43) from the Zitteli Zone of Pampa Tril; refigured here (Fig. 3C) after removing a false horn, which in fact was the fragment of another ammonite. This specimen actually belongs to *V. krantzense* according to the sculpture of the phragmocone (D_{ls} about 50 mm) which is identical to that of the female specimen of Fig. 3A at comparable diameter. At about $D = 25$ -30 mm (estimation from reconstruction of the spiral) there is a unique pair of ribs looped in the first, small clavus, exactly like in the female described above but placed at a slightly smaller diameter. The peristomatic lappets which indicate the specimen is an adult male, are relatively small, but they could be incompletely preserved.

Villaseñor *et al.* (2011: fig. 3A, C-E) figured several lappeted male *Volanoceras* specimens from Apulco, Mexico, as *Pseudovolanceras aesinense chignahuapense* (Cantú-Chapa, 1990); the specimen in their fig. 3B is an indeterminate impression. We concur with Énay & Howarth (2019) that *Pseudovolanceras* Cecca, 2002 is a junior subjective synonym of *Volanoceras* s.str. and with Schweigert *et al.* (2002) that the holotype of *Volanoceras chignahuapense* Cantú-Chapa, 1990 represents inner whorls of *V. aesinense*. Thus, we consider that the Mexican microconchiate specimens belong to *V. aesinense*. They were collected

together with females and incomplete specimens of *V. aesinense*, along with other ammonites from a short rock interval, forming a loose assemblage of supposed Semiforme Zone age (Villaseñor *et al.*, 2011). The Semiforme Zone is approximately equivalent to the Andean Zitteli Zone (see Schweigert *et al.*, 2002; Parent 2022).

The Mexican male specimens are smaller than the male of *V. krantzense* in Fig. 3C, and their body-chambers show weaker ornamentation, beyond the poor preservation. The sequence of sculptural styles is typical of the genus, but the stages differ in timing: *V. krantzense* [m] retains the fine ribbing with weak or no tubercles up to a larger size (about $D = 20$ mm) than *V. aesinense* [m] ($D = 10$ mm or less). This difference in timing of the successive sculptural stages is exactly as known in the females (see above) at comparable diameter. The lappets of the Andean male specimen are smooth (and shorter, possibly because of incomplete preservation), whereas those of the Mexican specimens have falcate growth lines or riblets. For explanation of the differences in the adult size of the males of these two species the occurrence of developmental heterochronies could be studied, but the adult size of the females is unknown, precluding comparison. Thus, we could not decide if the difference is originated from, for instance, different environmental conditions, or from different size-at-age sexual differentiation within each species.

Occurrence and distribution. The best-preserved specimen (Fig. 3A) comes from level CG-I-18, which corresponds to the lower Zitteli Zone (Parent & Garrido, 2021; see Figs. 2-3), approximately the same age as the male from Pampa Tril revised above. The fragment (Fig. 3B) comes from level CG-III-7 also belonging to the lower Zitteli Zone.

The holotype of *V. krantzense* was collected at Bardas Blancas (Fig. 1) with few stratigraphic information associated, and was subsequently referred to the Zitteli Zone (see the history in Schweigert *et al.* 2002). The assemblage of ammonites from Bardas Blancas cited and partially described by Krantz (1928: 47) is:

- *Pseudolissoceras zitteli* (Burckhardt, 1903) [as *Haploceras* (*Pseudolissoceras*) *zitteli*]
- *Cieneguiticeras perlaevis* (Steuer, 1897) [as *Oppelia* (*Neochetoceras*) *waageni* Zittel, 1870]
- *Pseudhimalayites steinmanni* (Haupt, 1907) [as *Aspidoceras* (*Pseudhimalayites*) *steinmanni*]
- *Volanoceras krantzense* Cantú-Chapa, 1990 [as *Simoceras* aff. *volanense* (Oppel, 1863)]

P. zitteli ranges through the Malarguensis and Zitteli zones (and could range into the lowermost Proximus Zone; see Parent *et al.*, 2011a, 2011b, 2015; Vennari, 2016; Parent & Garrido, 2021). *C. perlaevis* ranges through the Picunleufuense, Malarguensis and Zitteli zones (Parent *et al.*, 2010, 2015; Parent & Garrido, 2021).

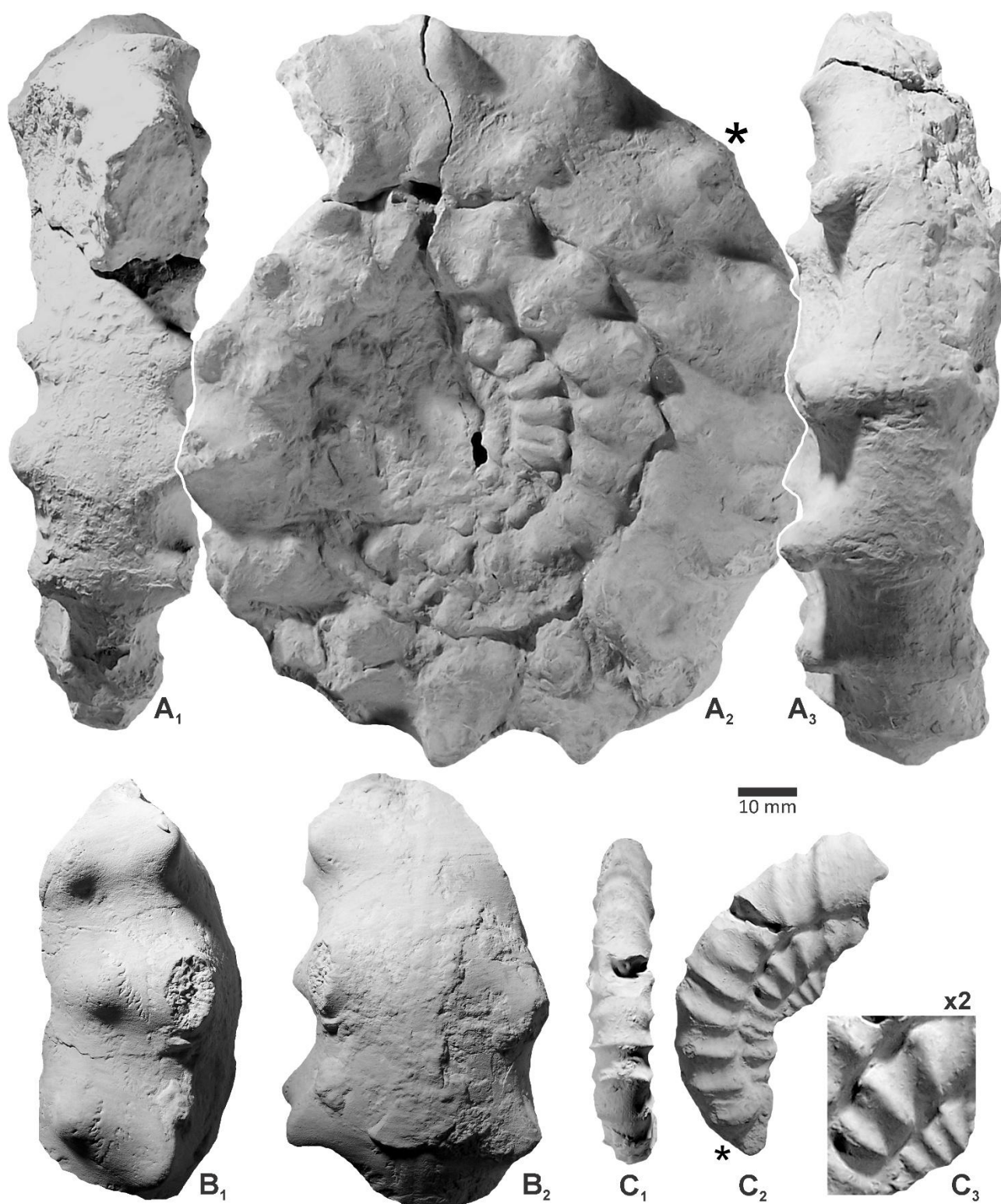


Fig. 3. A: *Volanoceras krantzense* Cantú-Chapa, 1990, adult female phragmocone with part of the body-chamber (MOZ-PI-6857/1), Cerro Granito I, level CG-I-17, lower Zitteli Zone. B: *Volanoceras* cf. *krantzense* Cantú-Chapa, 1990, fragment of a female phragmocone (MOZ-PI-8422), Cerro Granito III, level CG-III-7, lower Zitteli Zone. C: *Volanoceras krantzense* Cantú-Chapa, 1990, adult male (MOZ-PI-7946), Pampa Tril, level PT-11-12, lower Zitteli Zone. Specimen refigured from Parent et al. (2015: fig. 43) after removing the false horn, which in fact was a fragment of another ammonite. – All in natural size (x1) except C3: x2. The asterisk indicates the beginning of the body-chamber.

Pseudhimalayites Spath, 1925 includes at least two species, which in Cerro Lotena cover a range from the upper Zitteli up to the Internispinosum zones. A current study (to be published in a separate paper) of the aspidoceratids listed in Parent & Garrido (2021) shows that *P. steinmanni* is restricted to the Internispinosum Zone, while the occurrences in the interval upper Zitteli-Proximus zones correspond to *Pseudhimalayites andinum* (Leanza & Olóriz, 1987) [M&M]. Out of Argentina, *V. krantzense* is known from Mexico (poor material) and from southern Spain, where well-preserved material is clearly positioned in the Semiforme Zone (see Schweigert *et al.*, 2002). All the additional specimens of *V. krantzense* known in the Andes come from levels of the Zitteli Zone (Fig. 4). We can conclude from the narrowest possible concurrent range inferred that the holotype of *V. krantzense* comes from a horizon of the upper part of the Zitteli Zone that is the upper Semiforme Zone as already suggested by the faunal association in southern Spain (Schweigert *et al.*, 2002).

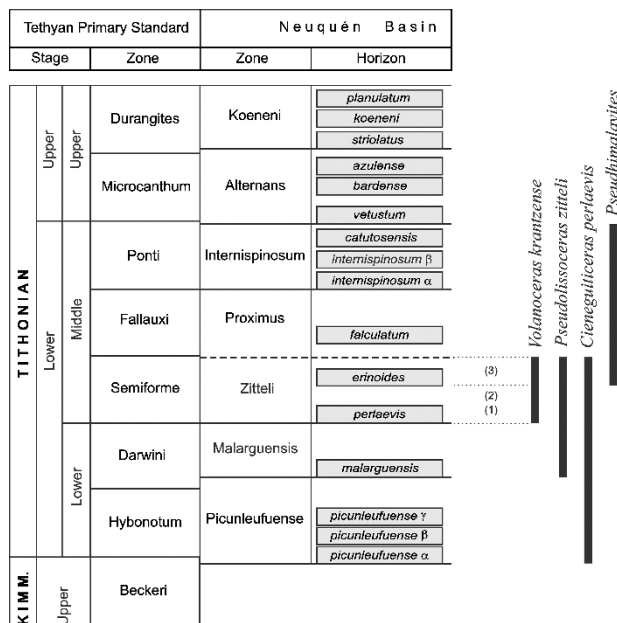


Fig. 4. Chronostratigraphic framework (based on Garrido *et al.*, 2018 updated in Parent, 2022) with the records of *Volanoceras krantzense* Cantú-Chapa, 1990 in the Neuquén Basin. The chronostratigraphic ranges of the species cited as associated with the holotype by Krantz (1926, 1928) in the type locality, are indicated as discussed in the text. Notes: (1): female specimens studied in this paper; (2): male specimen of Pampa Tril in Fig. 4C; (3): holotype (Krantz, 1928: pl. 3: 7).

CONCLUDING REMARKS

The newly described specimens show an early form of *V. krantzense*, heavily ornamented and of large adult size. These specimens come from the lower Zitteli Zone (approximately equivalent to the Semiforme Zone). These records clearly suggest that the genus *Volanoceras*

entered the Neuquén Basin during the early Semiforme Zone, at the evolutionary stage of an early *V. krantzense* or a late *V. aesinense*. The holotype is somewhat younger than the specimens described here; perhaps it was the last representative of the lineage in the basin. During its apparently short range, the local lineage retained the morphology and ornamentation of the main lineage, including the form of the sexual dimorphism. However, the adult size in both sexes seems to have been somewhat larger in the Neuquén Basin than in the Caribbean region and the Tethys.

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