BIFG

Boletín del Instituto de Fisiografía y Geología
ISSN 1666-115X

Volumen 94, 2026

Instituto de Fisiografía y Geología
Facultad de Ciencias Exactas, Ingeniería y Agrimensura
Universidad Nacional de Rosario

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Rosario - 2026 - Argentina

Boletín del Instituto de Fisiografía y Geología

ISSN 1666-115X

Fundado en 1937

Publicado por el Instituto de Fisiografía y Geología
"Dr. Alfredo Castellanos"
FCEIA - UNR - Argentina

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The lower Valanginian ammonite fauna of Puerta Quintuco, Argentina – with description of the new genus *Quintucoceras*

Horacio Parent & **Alberto C. Garrido**

Parent H. & Garrido C.A., 2026. The lower Valanginian ammonite fauna of Puerta Quintuco, Argentina – with description of the new genus *Quintucoceras*. *Boletín del Instituto de Fisiografía y Geología* 94: 1 - 41. Rosario, 14/03/2026. ISSN 1666-115X. [urn:lsid:zoobank.org:pub:7BC45593-2BB7-4DEC-885E-7CB68E722D64]

Abstract. In the Neuquén Basin (Argentina) occur several early Valanginian neocomitid ammonites that have been long assigned, provisionally to *Thurmanniceras* Cossmann, *Neocomites* Uhlig, or *Pseudoblanfordia* Spath. A new collection including adult and well-preserved ammonites from the uppermost Vaca Muerta and Quintuco formations in the type locality of this latter, Puerta Quintuco, is described in this paper. This new fauna, Wichmanni to Riveroi zones in age, shows that a large part of the mentioned neocomitids belong to a single evolving lineage here described as the new genus *Quintucoceras*. It is proposed that *Lissonia* branched from the new genus in the uppermost Wichmanni Zone. The new fauna also includes species of *Lissonia*, *Subthurmannia* Spath, *Sarasinella* Uhlig, and possibly *Kilianella* Uhlig, and *Karakaschiceras* Thieuloy.

According to our lithostratigraphic interpretation, in the studied section the base of the Quintuco Fm in its type locality is marked by the first appearance of a sandy level with tractive structures and intraclasts, strongly contrasting with the lutitic (black shale) domain succession that defines the underlying Vaca Muerta Fm. It is important to note that the lower levels of the Quintuco Fm as defined here are laterally correlated with the Huncal Member, included in the Vaca Muerta Fm by previous authors.

Key words. Neocomitidae, *Quintucoceras* n. gen., mosaic morphology, *Lissonia,* early Valanginian, Vaca Muerta Formation, Quintuco Formation, Argentina.

Recibido 04/01/2026
Aceptado 14/03/2026

Disponible vía Internet
18/03/2026

Editor: A. Greco

Resumen. En la Cuenca Neuquina se presentan numerosos amonites neocomítidos del Valanginiano temprano que han sido asignados provisoriamente a *Thurmanniceras* Cossmann, *Neocomites* Uhlig, ó *Pseudoblanfordia* Spath. En este trabajo se describe una nueva colección de amonites provenientes de las formaciones Vaca Muerta y Quintuco en la localidad tipo de ésta última, Puerta Quintuco. Esta nueva fauna, de edad zonas Wichmanni a Riveroi, muestra que una gran parte de los neocomítidos mencionados pertenece a un linaje evolutivo que aquí se describe como *Quintucoceras* n. gen. Se propone que *Lissonia* se origina en el nuevo género, como una rama independiente, en la parte mas alta de la Zona Wichmanni. La nueva fauna incluye además amonites de los géneros *Lissonia, Subthurmannia* Spath, *Sarasinella* Uhlig, y posiblemente *Kilianella* Uhlig, y *Karakaschiceras* Thieuloy.

De acuerdo a nuestra interpretación litoestratigráfica, en la section estudiada la base de la Formación Quintuco en su localidad tipo es marcada por la primera aparición de un nivel arenoso con estructuras de tracción e intraclastos, contrastando marcadamente con el dominio lutítico que define a la Formación Vaca Muerta que la subyace. Es importante notar que los niveles inferiores de la Formación Quintuco como se define aquí, se correlacionan lateralmente con el Miembro Huncal, incluído en la Formaión Vaca Muerta por autores previos.

Palabras clave. Neocomitidae, *Quintucoceras* n. gen., morfología en mosaico, *Lissonia*, Valanginiano temprano, Formación Vaca Muerta, Formación Quintuco, Argentina.

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INTRODUCTION

The marine lower Valanginian deposits in the depocentral area of the Neuquén Basin (Fig. 1) is mostly represented by black shales and mudstones of the uppermost part of the Vaca Muerta Fm and the Quintuco Fm (Weaver 1931, Groeber 1946, Leanza 1972, Leanza & Hugo 2001, Leanza et al. 2011, Medina et al. 2016). According to Garrido & Parent (2017), in the central sector of the basin the Quintuco Fm is mostly Berriasian in age, and early Valanginian towards northern localities (e.g. Pampa Tril, Parent et al. 2015).

The ammonite fauna of the lower Valanginian in the Neuquén Basin has not received much attention in comparison with that of the upper Valanginian (see Leanza & Wiedmann 1980, Aguirre-Urreta et al. 2005, Aguirre-Urreta & Rawson 2010). It could be due to the fact that in most of the studied localities there were not collected abundant ammonites (e.g. Leanza & Wiedmann 1980, 1989, Aguirre-Urreta & Rawson 1999).

We have studied the outcrops of the upper Vaca Muerta and Quintuco formations in a new section of the locality named Puerta Quintuco (Figs. 1-2). The local succession (Fig. 3) has yielded abundant well-preserved ammonites

which belong to the Family Neocomitidae Salfeld, 1921, but most of them cannot be assigned to any of the known genera. Some of these ammonites were incompletely known from scarce material (Aguirre-Urreta & Rawson 1999, Parent et al. 2015), published under provisional assignations to *Thurmanniceras* Cossmann, 1901, *Pseudoblanfordia* Spath, 1925, or *Lissonia* Gerth, 1925. However, material from Pampa Tril had allowed Parent et al. (2015) to arrange a sequence of these ammonites and to propose a preliminary phylogeny.

In this paper we describe the new early Valanginian ammonite fauna collected from the upper part of the Vaca Muerta Fm and the Quintuco Fm in Puerta Quintuco.

STRATIGRAPHIC FRAMEWORK

The study area is included in the Geological Chart 3969-I-Zapala (1:250.000) elaborated by Leanza & Hugo (2001), later described with some detail by Leanza (2009) and Leanza et al. (2011). Additionally, the are several geological and palaeontological reports of regional studies of localities closely related to our study area (e.g. Behrendsen 1891-1892, 1922, Weaver 1931, Leanza 1972, Leanza & Wiedmann 1980, 1989, Leanza et al. 2002, 2003, Aguirre-Urreta & Rawson 1999, Naipauer et al. 2020).

Garrido & Parent (2017) have revised in detail the definition, lithostratigraphy and chronostratigraphy of the Quintuco Fm at Sierra de la Vaca Muerta sector, indicating clear differences from the underlying Vaca Muerta Fm under strict litholotical criteria. Thus, the lithofacial changes between both lithostratigrapic units respond to the infill evolution of the depositional system itself, gradually transitioning towards shallower marine environments under the influence of the progradation of large deltaic systems.

According to the Código Argentino de Estratigrafía (Comité Argentino de Estratigrafía 1991), and following Weaver (1931) who described and introduced the term Quintuco Formation, it is clear that the type locality of this unit is defined by the outcrops exposed in the eponymous locality: the Quintuco Hill and the Puerta Quintuco Pass (also known as Portezuelo Quintuco; see Fig. 1B). In this sector, Leanza (2009) and Leanza et al. (2011) indicate the presence of the Quintuco Formation, which they note has relatively little development compared to the underlying Vaca Muerta Formation. These authors also recognized the presence of the so-called Huncal Member (Leanza et al. 2002, 2003) which, according to our observations, tends to wedge southwards. Conversely, 15 to 20 km north and northeast of Puerta Quintuco, in the classic profiles of the Huncal, Cerrito Ventana, and Cerro Mulichinco area, the Huncal Member becomes more prominent, while the facies of the Quintuco Formation become difficult to distinguish from the Vaca Muerta Formation. Because of this, in these latter localities several authors have considered the entire Tithonian-lower Valanginian succession under the single term of Vaca Muerta Fm (Leanza, 1972, 1973, Aguirre-Urreta & Rawson, 1999, Naipauer et al. 2020).

It is important to note that, based on the description by Weaver (1931) and the Código Argentino de Estratigrafía (Comité Argentino de Estratigrafía 1991), we establish the base of the Quintuco Fm in the study area. In the local succession the first notable lithofacial change occurs, maintaining there a gradual but constant change with a clear coarsening-upwards trend in the sedimenatry column. Thus, in our profile, the base of the Quintuco Fm is established with the first appearance of a sandy level with tractive structures and intraclasts. This lithology contrasts markedly with the underlying lutitic (black shale) domain succession of the Vaca Muerta Fm (Figs. 2-3). From there, the lithological change continues with an increasing frequency of the repetition of sandy facies (wacky sandstones, calcareous sandstones, and fine to medium-grained sandstones, with a lower porcentage of sandy limestones) interstratifed with pelitic facies (shale and sandy mudstones), until that the latter finally disappears (Fig. 3).

Along with the facial change, there is also a change in the fossil content of the strata. While in the black shale deposits of the Vaca Muerta Fm only ammonites appear alongside a single type of bivalve (*Huncalotis millaini* Damborenea & Leanza, 2016), in the sandy deposits of the Quintuco Fm a wide diversity of bivalves is observed alongside small gastropods. From base to top there is a gradation from a dominance of allochthonous concentrations towards para-autochthonous and autochthonous concentrations.

Finally, based on the definitions and descriptions discussed above, we must highlight that the base of the Quintuco Formation (in its type locality) is laterally correlated with the base of the Huncal Member (Fig. 2) while the basal limit of the Quintuco Formation indicated by Leanza (2009: fig. 13b) corresponds approximately to the base of level PQ-I-63 of our profile (Fig. 3), and in the case of what was indicated by Leanza et al. (2011: fig. 6D) its correlation would be approximately with the base of our level PQ-I-77.

SYSTEMATIC PALAEONTOLOGY

Conventions and notation. Body-chamber is abbreviated as Bc and phragmocone as Ph. Dimensions (in millimetres): shell diameter at a given point (D), at last septum (D_{ls}), at peristome (D_p); umbilical width (U), width of whorl section (W), height of whorl section (H_1), apertural or ventral height of whorl section (H_2), mostly given as ratios to D. Number of primary (P) and ventral (V) ribs, and umbilical (T_U), lateral (T_L) and ventrolateral (T_{VL}) tubercles/spines per half whorl. It is essential to recognize the kind of specimens described, that is juvenile or adult, complete or incomplete, phragmocone or bodychamber, sex. Thus, when possible we note for every specimen studied its condition and growth stage with the terms: (1) inner whorls or the post-embryonic, juvenile ontogeny, (2) middle whorls or the subadult (not fully adult), and (3) outer whorls or the adult portion of the shell (fully grown and developed, sexually mature individual).

In this paper we consider the female of the species is the so-called macroconch [M] and the male the microconch [m], according to the abundant evidence and discussions summarized by Klug et al. (2015, with references) and Parent & Zatoń (2016, with references). 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 and Parent et al. 2019; Klug et al. 2015 for cases and a general review). For example, female specimens that

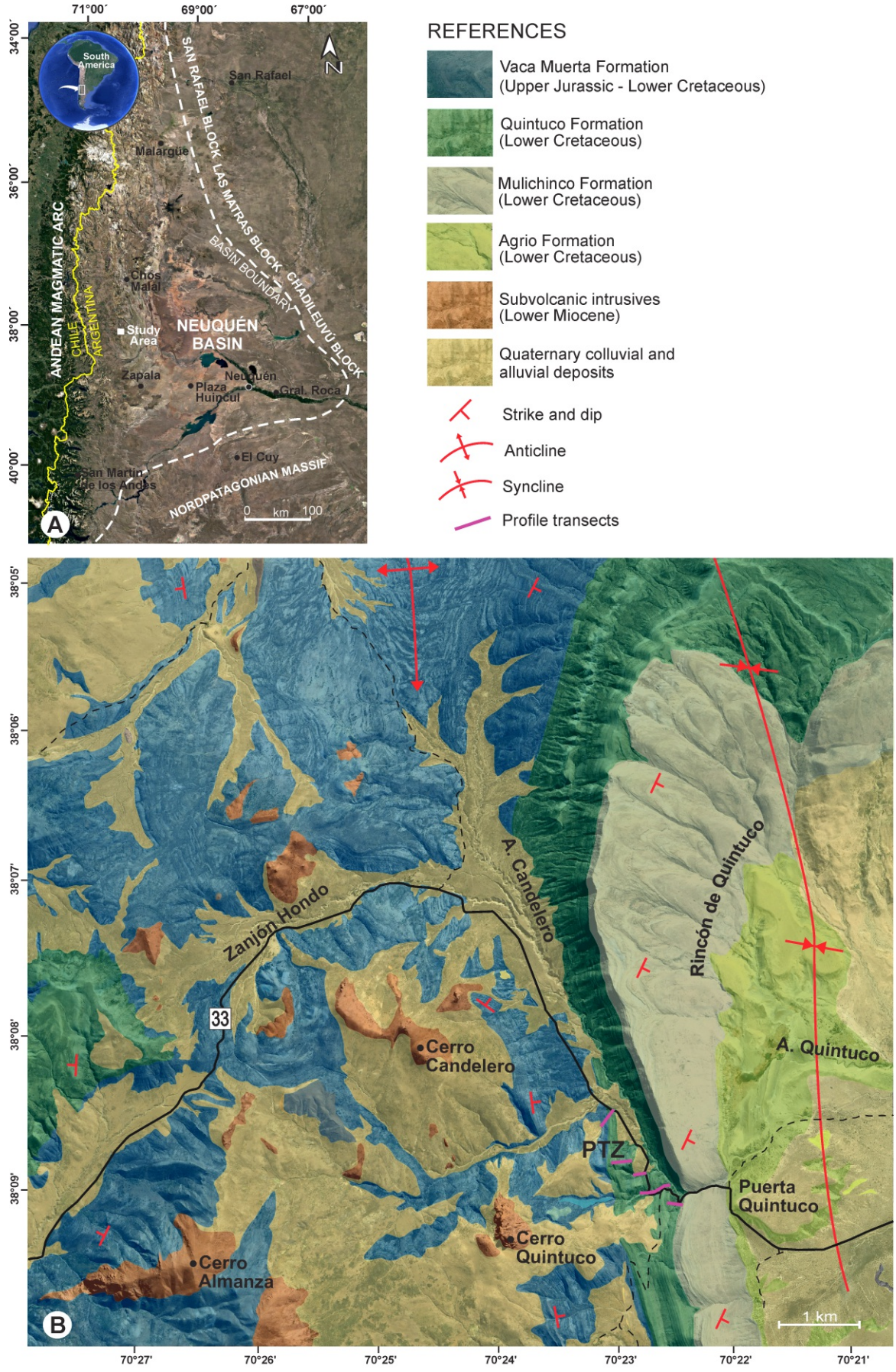

Figure 1. **A**: geographic location of the Neuquén Basin and the study area. **B**: geological map of the study area with indication of the profile transect zone (PTZ).

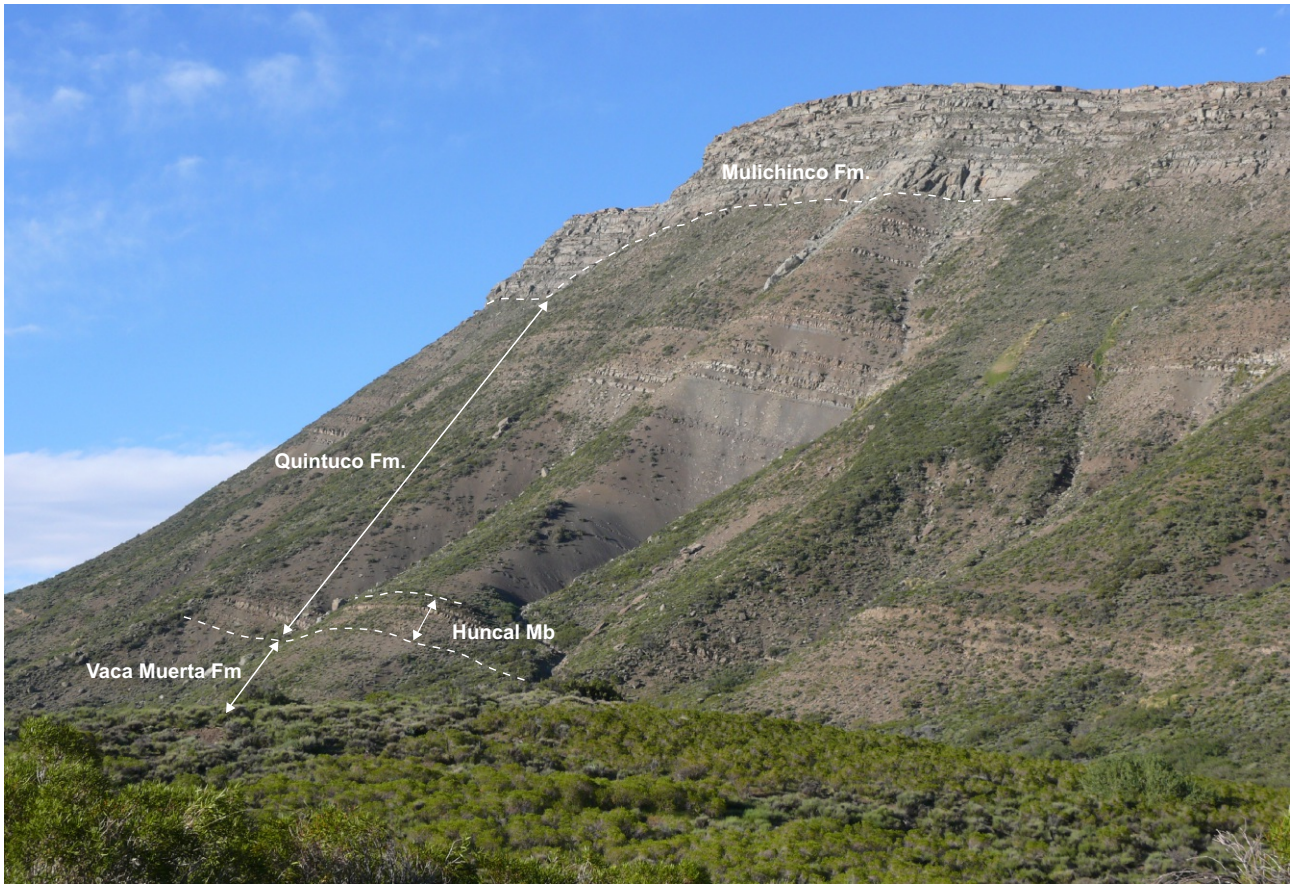

Figure 2. Panoramic view of the studied section at Puerta Quintuco, showing the Vaca Muerta, Quintuco and Mulichinco formations. The Huncal Mb was defined as part of the Vaca Muerta Fm (see text for details).

became adult in a relatively early ontogenetic stage and thus remained smaller than normal macroconch females, the term mesoconch was introduced by Chandler (2019); see also Parent et al. (2008) and Scherzinger et al. (2018).

All the specimens come from the section in Fig. 3, distributed as shown in Fig. 4. The number of the level is preceeded by the name of the studied section of Puerta Quintuco I (PQ-I). All the specimens were collected and photographed by the authors, except those in old collections (see below).

Repositories. The studied material is housed in the Museo Provincial de Ciencias Naturales "Prof. Dr. Juan A. Olsacher" (MOZ-PI), Zapala. We have refigured for comparison some specimens in old collections. Specimens described by Weaver (1931) are in the Burke Museum of Natural History (UWBM_IP), Seattle; photographs courtesy of Ron Eng and Liz Nesbitt. Specimens described by Gerth (1925) are in the Steinmann-Institut, Abteilung Paläontologie & Goldfuß-Museum (Gerth-21-P1080317), Bonn; photograph courtesy of Georg Heumann.

Order Ammonitida Haeckel, 1866
Suborder Ammonitina Fischer, 1882
Superfamily Perisphinctoidea Steinmann, 1890
Family Neocomitidae Salfeld, 1921

Subfamily Neocomitinae Salfeld, 1921

Remarks. In the literature there are many ammonites which show close resemblance, at some size, with the new ammonites studied here, but most of the ontogeny is different. Many of the neocomitid genera described in the literature seem to be mosaics of morpho-sculptural ontogenetic stages, e.g., the earlier or later onset of trituberculation, or the occurrence of a *Neocomites*-like stage. The changes of the position at which typical ontogenetic stages occur and the duration of their expression during growth, produce a phenomenon that has been noted by several authors in different forms, and is present in our material as described in detail below. Nikolov (1977: 107) considered this phenomenon as homoeomorphic similarities during the shell ontogenetic stages. Kemper et al. (1981: 278) interpreted this phenomenon as a recurrence of evolutionary trends. Thieuloy (in Busnardo et al. 1979: 39) noted the "aspect des kilianelle" in the inner whorls of specimens that anyway he decided to include in *Thurmanniceras* because of the lack of tubercles. The differentiation between *Jabronella* Nikolov, 1966 (*sensu* Company 1987) and *Sarasinella* Uhlig, 1905 is based on the earlier onset of the trituberculate stage in this latter with respect to the former (Company 1987: 141). *Clavithurmannia* Thieuloy in Busnardo et al., 1979 is defined by Wright et al. (1996: 58) as large ammonites with

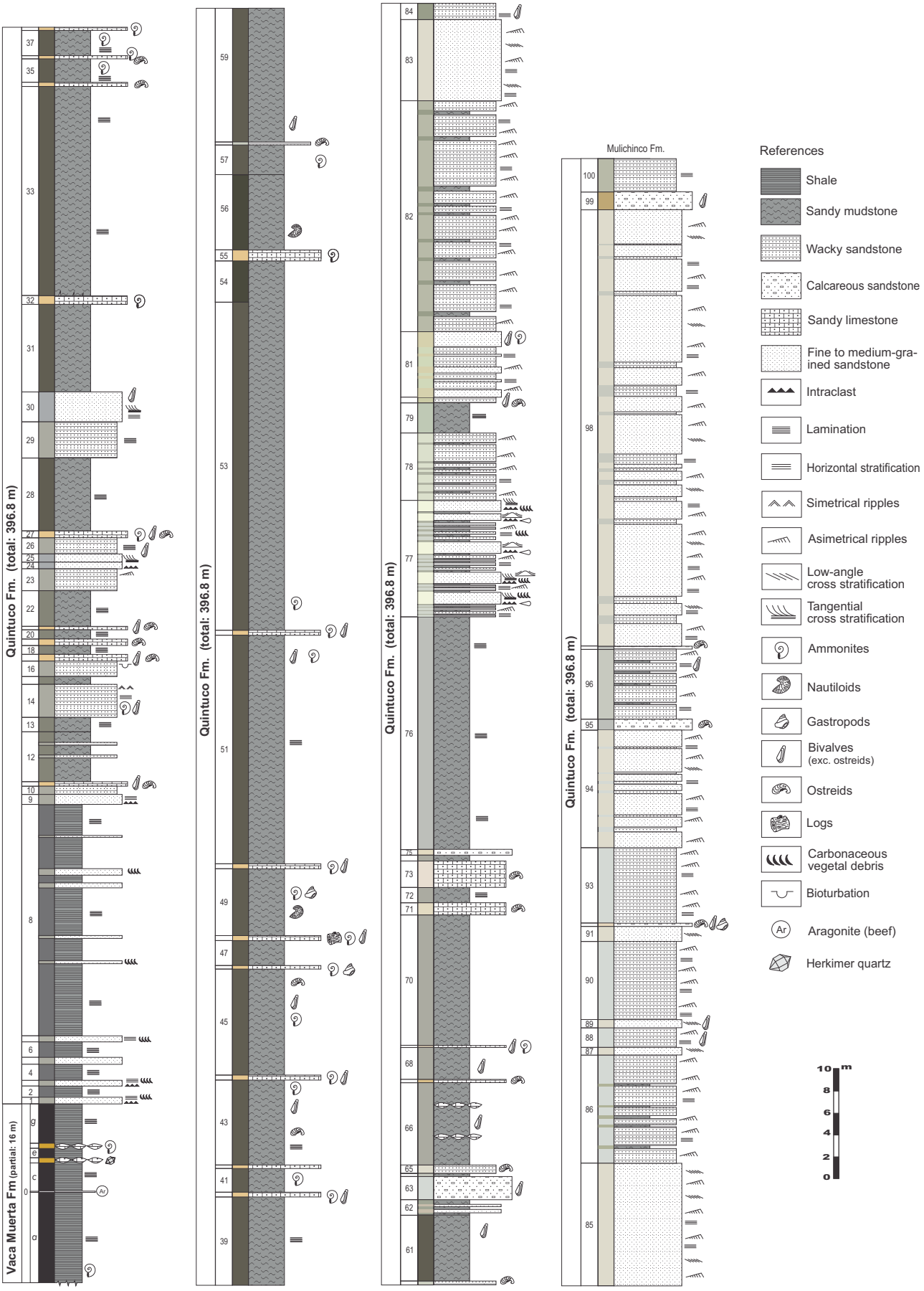

Figure 3. Profile of the studied section in Puerta Quintuco.

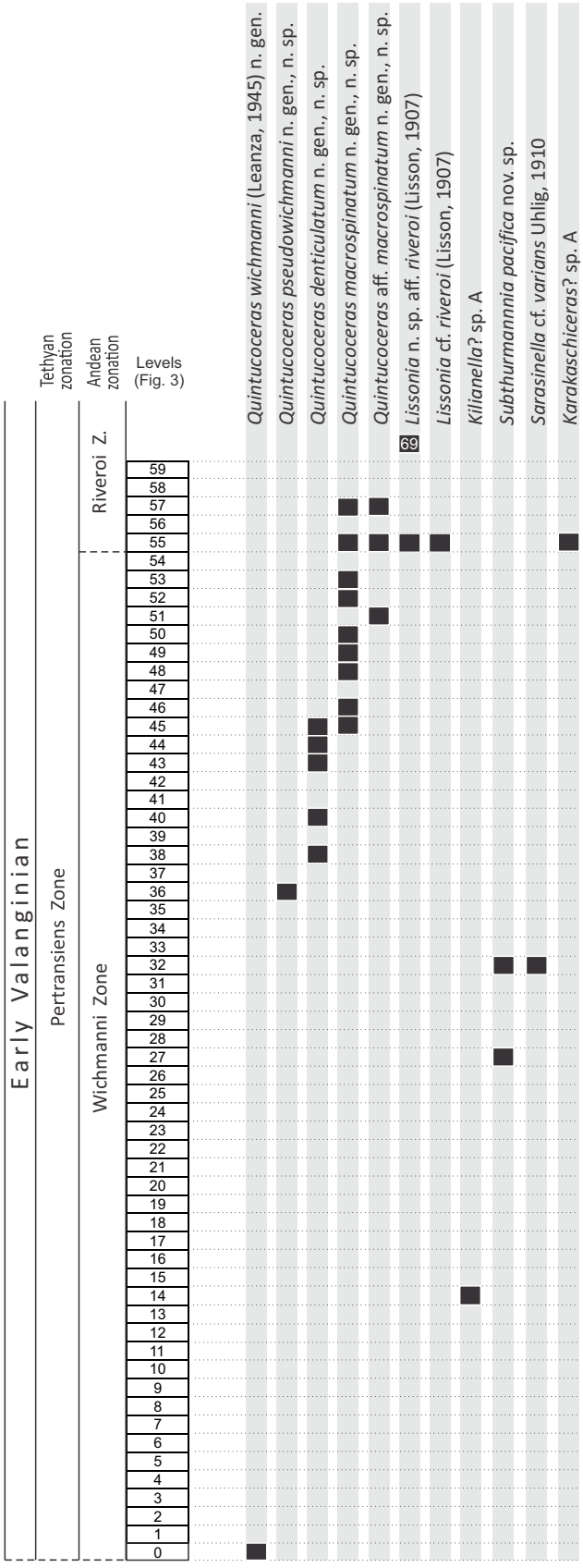

Figure 4. Biostratigraphy of the ammonite fauna and the derived chronostratigraphic classification of the studied section. Levels referred to Figure 3. The occurrences indicated correspond to specimens considered in the descriptions.

middle whorls as in *Thurmanniceras* and last half of outer whorl as in *Neocosmoceras* Blanchet, 1922.

This phenomenon can be described as mosaic morphology, and may be interpreted as the product of variations in the onset and timing of occurrence of morpho-sculptural ontogenetic stages during growth, that is developmental heterochronies. It may appear as intraspecific variation at first, and evolve, even recurrently, as noted by Kemper et al. (1981), what indeed is known in much of the Ammonoidea. Some homoeomorphies produced by the mosaic morphology could have been originated from episodes of hybridization between members of related lineages, in particular in early stages of their differentiation (see Parent & Garrido 2021 for discussion and references).

This variation in the onset and timing of morpho-sculptural ontogenetic stages may be misleading when working with insufficient or poor material, producing taxonomic artifacts without any biological significance. Examples are some of the cases of assumed occurrences of *Neocomites* Uhlig, 1905 and *Thurmanniceras* in the lower Valanginian of the Andean region. Several authors (e.g. Company 1987, Aguirre-Urreta & Rawson 1999) have noted that many of the specimens attributed to these genera are few and incomplete, and that could belong to other genera. We have founded that in fact, some of these ammonites actually belong to a new genus described below. The resemblance between these Andean ammonites with *Neocomites* or *Thurmanniceras* is restricted to some part of the ontogeny, but the comparison of complete adult specimens, mainly females, shows important and significant differences throughout most of their ontogeny.

Genus *Quintucoceras* nov.

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Type species: *Quintucoceras macrospinatum* n. gen., n. sp.

Derivation of the name: After Puerta Quintuco (Fig. 1), the type locality of the type species.

Definition: Female. Large to very large platycone; moderately evolute to involute; whorl section suboval to subrectangular, with flattish venter in the phragmocone, rounded towards the adult bodychamber.

Inner whorls more or less densely ribbed by sharp, more or less flexuous ribs, irregularly bifurcated around the middle of the flank. Middle whorls with strong, wiry primary ribs, most bifurcated into secondaries projected forward; the external ribs end in ventrolateral spines (tubercles in the internal mold) that gradually fade towards the adult bodychamber. A wide to narrow, smooth ventral band occurs irregularly in the phragmocone. A rather short stage of polyschizotomic ribs originated in spines (or swellings) at the umbilical shoulder develops in some part of the phragmocone. Adult bodychamber of early representatives with fine undivided ribs, later with strong distant primaries bearing one or two long lateral spines.

Male. Poorly known. Smaller, with lappets; indistinguishable from the female at comparable diameter.

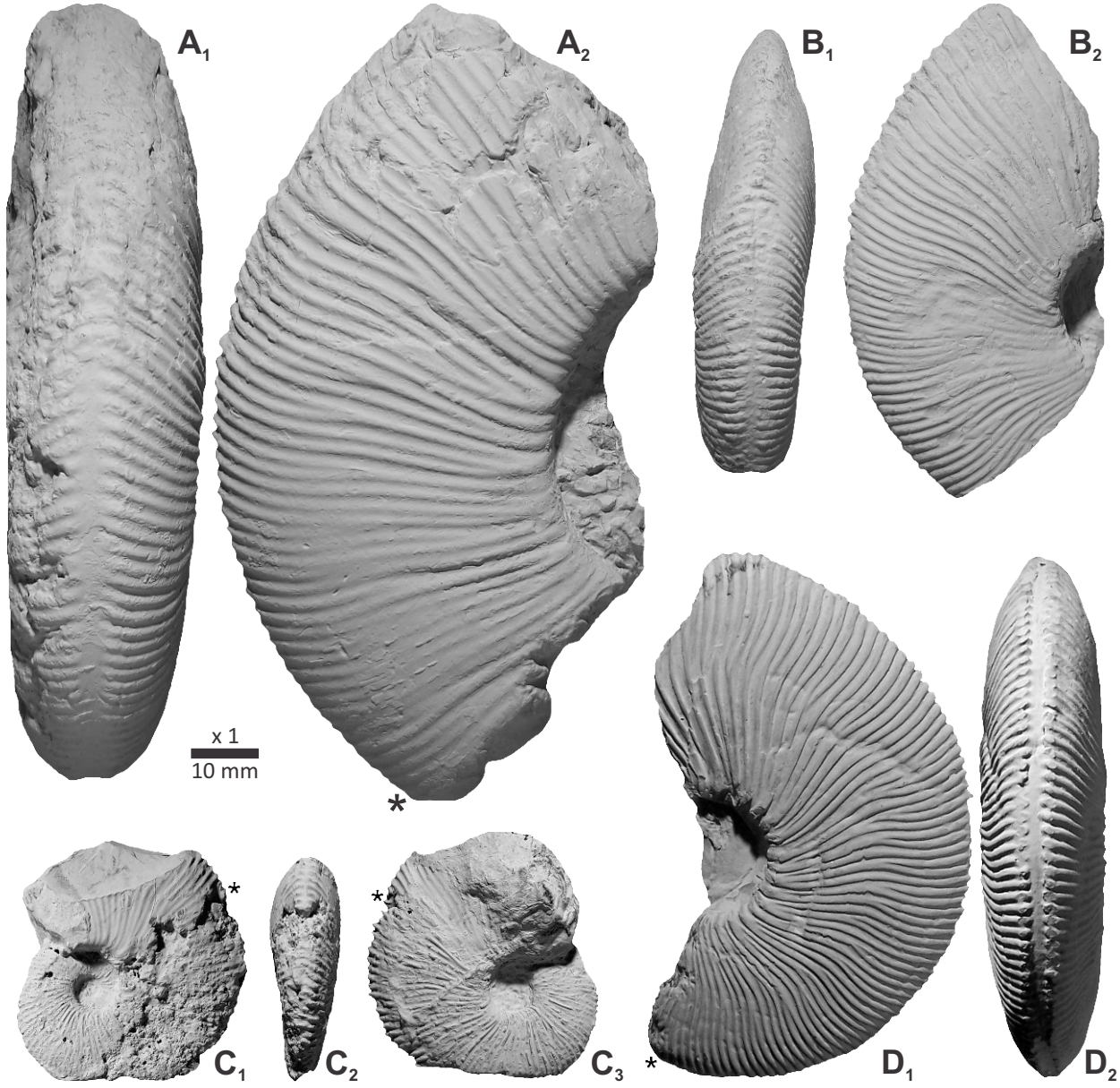

Figure 5. *Quintucoceras wichmanni* (Leanza, 1945) n. gen., Puerta Quintuco, level PQ-I-0, Wichmanni Zone. **A**: adult female bodychamber (MOZ-PI-11708/2). **B**: female phragmocone (MOZ-PI-11708/3). **C**: juvenile female with beginning of bodychamber (MOZ-PI-11708/4). **D**: female phragmocone (MOZ-PI-11708/1). – The asterisk indicates the last septum. All natural size (x1).

Species included (in stratigraphic succession): *Quintucoceras wichmanni* (Leanza, 1945) n. gen.; *Quintucoceras pseudowichmanni* n. gen., n. sp.; *Quintucoceras denticulatum* n. gen., n. sp.; *Quintucoceras macrospinatum* n. gen., n. sp.; *Quintucoceras* aff. *macrospinatum* n. gen., n. sp.

Distribution: Currently lower Valanginian of the Neuquén Basin.

Remarks and comparison: The attribution of the new genus to the Neocomitinae is based on the shell morphology and sculpture of the phragmocone: compressed, high-whorled, moderately involute platycones with flattish venter and dense ribbing with tubercles/spines on the ventrolateral shoulder.

These ammonites as a whole have in common the diagnostic features that led us to include them in a single genus, and their occurrence in close succession in a single area, indicates they conform to a single phylogenetic entity that has evolved in the area during a considerable extension of time (more than an ammonite zone). Thus, the conception of *Quintucoceras* n. gen. is that of a Valanginian evolving lineage composed of a succession of species which show evolutionary changes in different subadult and adult ontogenetic stages, while the juvenile (inner whorls) remains rather unchanged. This series of forms was then segmented in four successive species, delimited according to consistent morpho-sculptural differences.

In the form discussed above as mosaic morphology,

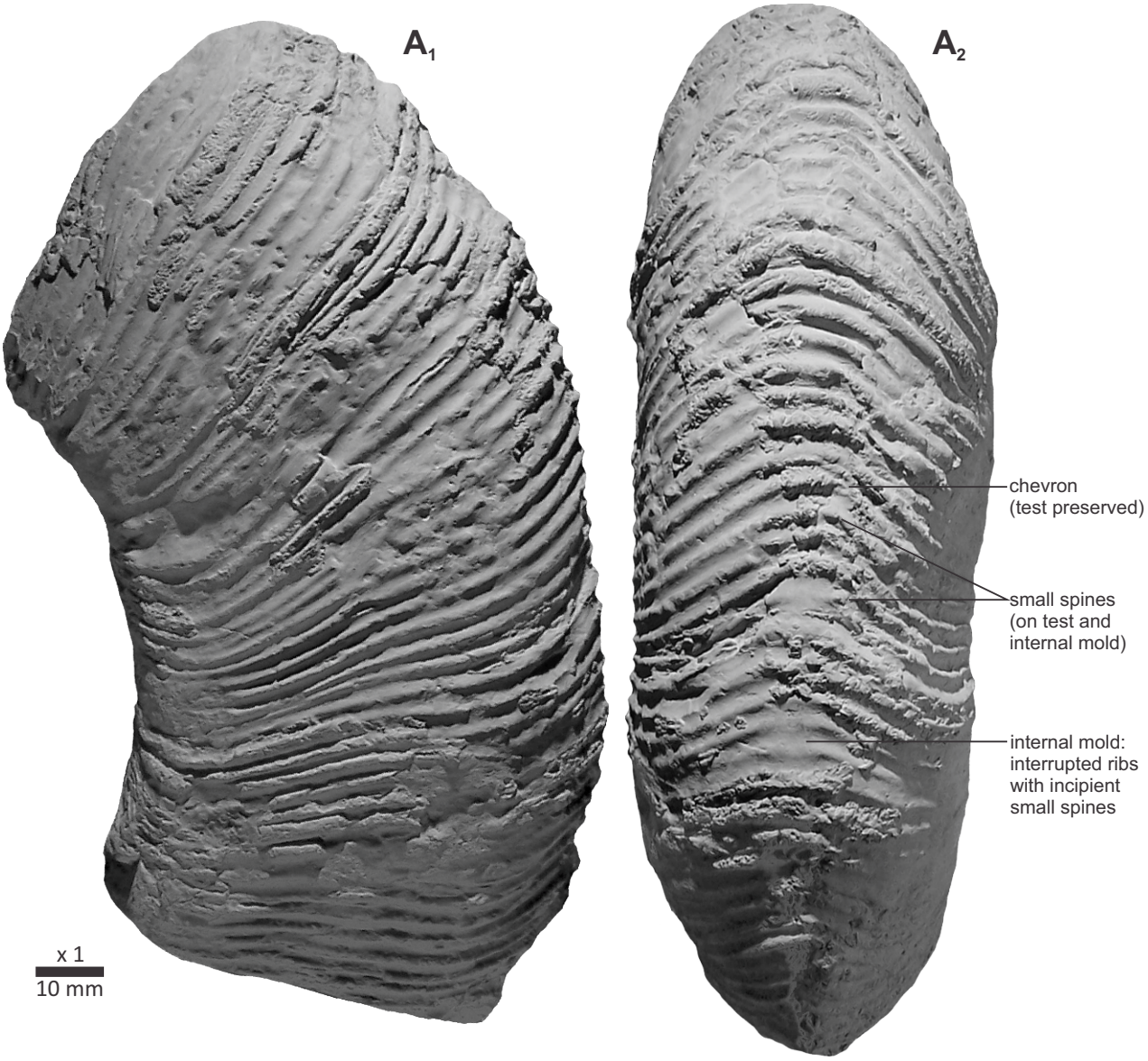

Figure 6. *Quintucoceras wichmanni* (Leanza, 1945) n. gen., Puerta Quintuco, level PQ-I-0, Wichmanni Zone. Incomplete adult female bodychamber (MOZ-PI-11708/5). – Natural size (x1).

there are neocomitid genera which show resemblance with *Quintucoceras* n. gen. at some ontogenetic stage and are more or less coeval.

- *Neocomites* Uhlig, 1905 (= subgenus *Neocomites* sensu Wright et al. 1996: 60) – Early *Quintucoceras* n. gen. are almost indistinguishable, at a short ontogenetic stage, from early forms of this genus (see Company 1987, Reboulet 1996) . The most notable differences are that in *Quintucoceras* n. gen. dominates a regular biplicate ribbing in the phragmocone, with larger adult female size; the sculpture of the bodychamber is composed of densely spaced, fine, undivided and ventrally uninterrupted primary ribs, and the later members with strong lateral ribs with long spines.

- *Thurmanniceras* Cossmann, 1901 and *Hoedemaekeria* Company & Reboulet (in Reboulet et al. 2025) – The phragmocone of *Quintucoceras* n. gen. may be similar, but can be distinguished by the absence of constrictions and the non flexuous, only regularly bifurcated ribbing. Furthermore, the larger adult size, with dense undivided ribbing or with long lateral spines in the bodychamber can be also very distinctive.

- *Tirnovella* Nikolov, 1966 – This is genus is here considered a synonym of *Subthurmannia* Spath, 1939 (*sensu* Wright et al. 1966), since they seem to differ only by the more involute coiling of *Tirnovella*. However, its type species, *Berriasella alpillensis* Mazenot, 1939 (mainly upper Berriasian), has a lateral ribbing very similar to that of *Quintucoceras wichmanni* n. gen. They differ more notoriousy (both holotypes of similar size) in that the phragmocone of *B. alpillensis* is more involute and has more rounded venter where the ribs end producing a narrow groove (cf. Company 1987: 108), whereas in the Andean species the venter is flat and the ribs end in a ventrolateral spine tending to produce a wider smooth band.

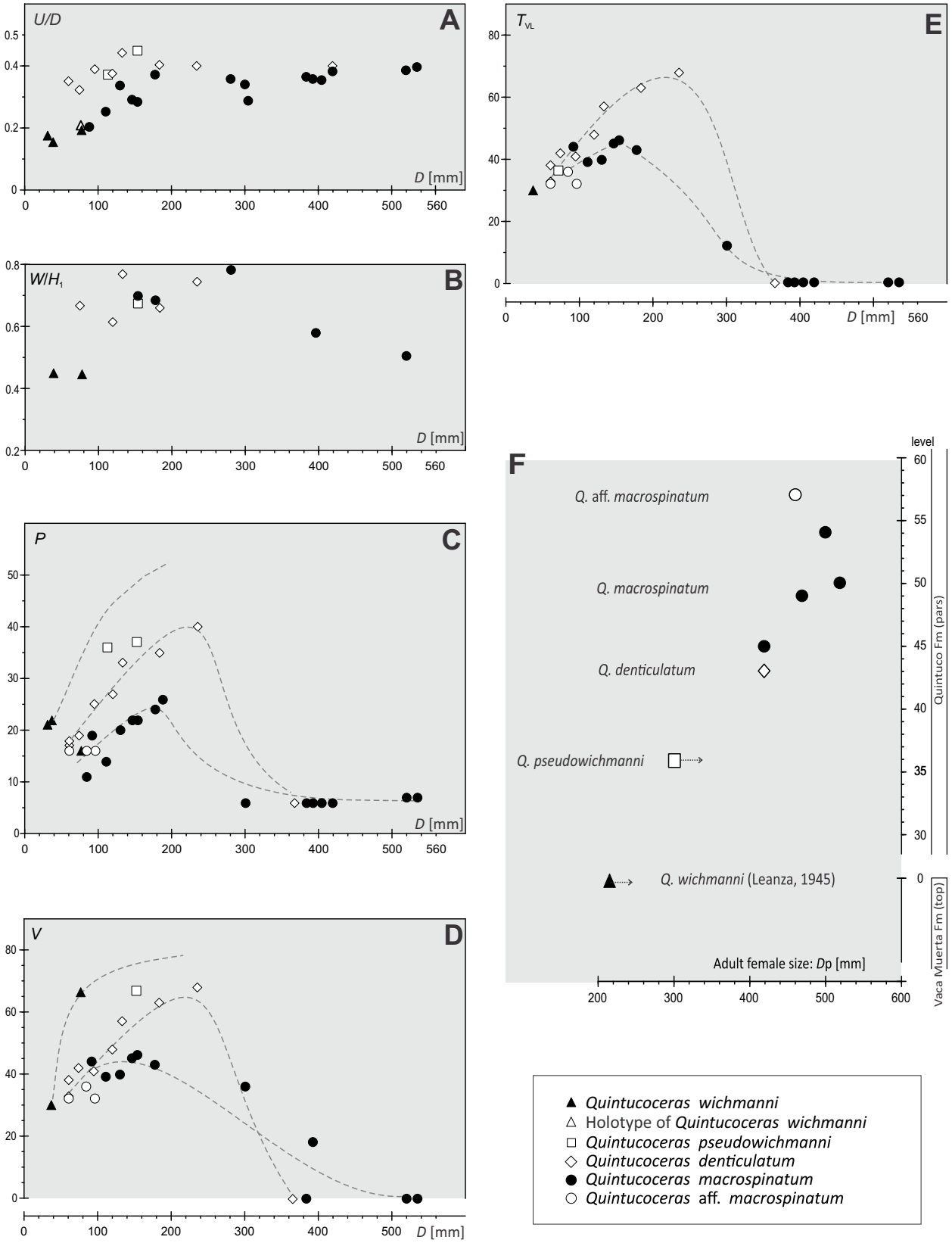

Figure 7. Biometric characterization of *Quintucoceras* n. gen. relative to the diameter (*D*). **A**: involution, relative umbilical diameter. **B**: whorl section, relative width to height of whorl section. **C**: number of primary ribs per half-whorl. **D**: number of ventral (or external) ribs per half-whorl. **E**: number of ventrolateral spines (or tubercles) per half-whorl. **F**: Evolution of the adult female size at peristome. The trajectories in broken lines are merely approximations of main patterns.

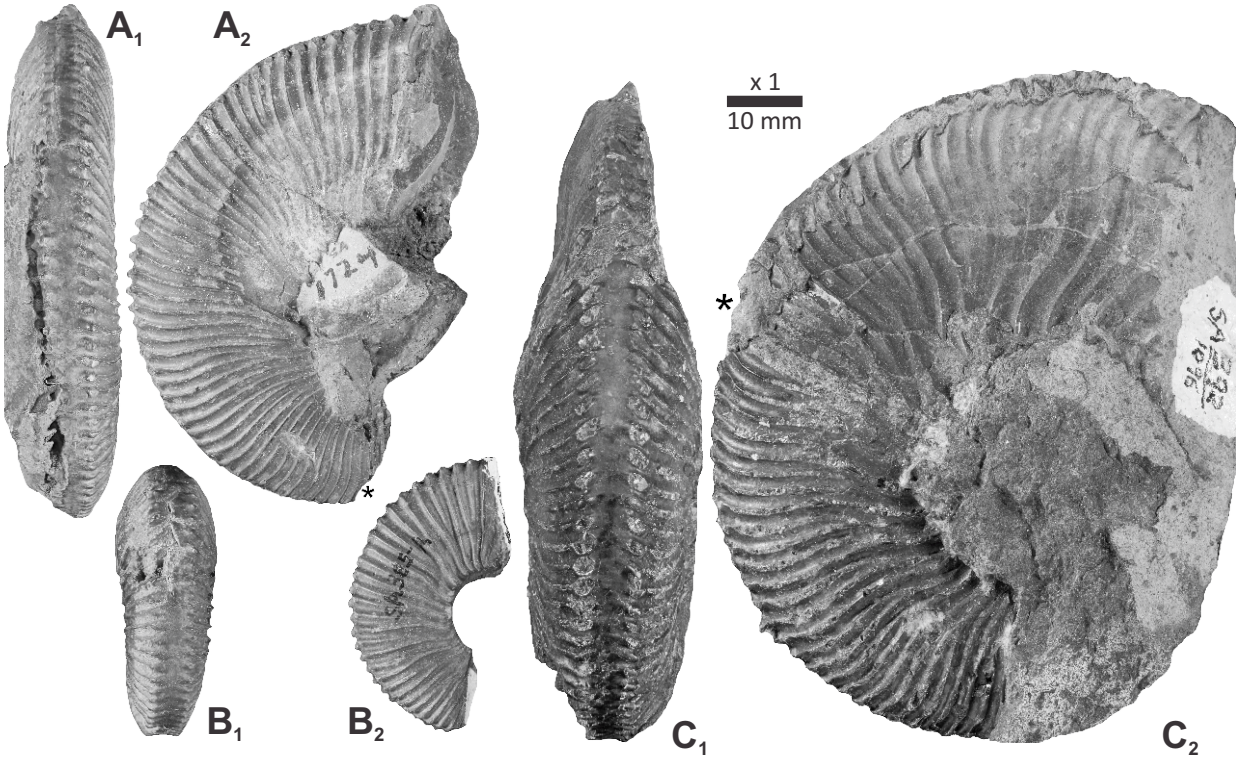

Figure 8. Photographic refigurations of specimens from the Valanginian of the Neuquén Basin described by Weaver (1931). **A**: holotype (UWBM_IP_ S384) of *Thurmannia quintucoensis* Weaver (1931: fig. 358), refiguration (A_2) with addition of the ventral view (A_1). **B**: paratype (UWBM_IP_ 44931) of *Thurmannia quintucoensis* Weaver (1931: fig. 359), refiguration (B_1) with addition of the lateral view (B_2). **C**: paratype (UWBM_IP_ S392) of *Thurmannia salinasensis* Weaver (1931: fig. 353), refiguration (C_1) with addition of the lateral view (C_2). – The asterisk indicates the last septum. Natural size (x1).

- *Varlheideites* Rawson & Kemper, 1978 – The type species of this genus (most likely a synonym of *Neocomites*), *Varlheideites peregrinus* Rawson & Kemper, 1978, is typical of the upper Valanginian of Europe (Kemper et al., 1981; Wright et al., 1996). Adult females of *Quintucoceras* differ in being larger, the division of the ribs only in the mid- or upper-flank, with short stages in the umbilical shoulder; the trituberculation is only known in late representatives. Aguirre-Urreta & Rawson (2018) described a small collection of Valanginian neocomitids as *Neocomites* (*Varlheideites*) cf. *peregrinus* (Cerro Caycayén) and *Neocomites* (*Varlheideites*) sp. nov? (Arroyo Truquicó). These specimens are very incomplete to advance significant comparisons, but the close resemblance with specimens of level PQ-I-51, suggests the very interesting possibility that they correspond to a late development of *Quintucoceras* n. gen. in the Atherstoni Zone.

***Quintucoceras wichmanni* (Leanza, 1945) n. gen.**
(Figs. 5-7)

1945 *Necomites wichmanni* n. sp. – Leanza: 61, pl. 12: 2-3 (holotype).
1970 *Necomites* cf. *wichmanni* Leanza – Imlay & Jones: 49, pl. 14: 1-15.
1970 *Necomites* cf. *neocomiensis* Orbigny – Imlay & Jones: 49, pl. 14: 16.
1970 *Necomites* cf. *neocomiensis* var. premolica Sayn – Imlay & Jones: 50, pl. 14: 17-19.
?1970 *Thurmanniceras jenkinsi* (Anderson) – Imlay & Jones: 49, pl. 13: 1-6.
2005 *Necomites wichmanni* Leanza. – Aguirre-Urreta et al.: fig. 4e-f.
2007 *Necomites wichmanni* Leanza. – Aguirre-Urreta et al.: fig. 10D (same specimen)
2020 "*Neocomites*" *wichmanni* Leanza – Naipauer et al.: fig. 7C

Holotype: The specimen is a phragmocone showing incipient uncoiling (Leanza 1945: pl. 12: 2-3). It was collected by P. Groeber from the level *n* (type horizon) of the section he sampled at Arroyo del Yeso (Mendoza Province), a calcareous bank 0.40 m in thickness.

From this bank there were also collected two specimens that Leanza (1945: 64) assigned to *Thurmanniceras pertransiens* (Sayn, 1907). These specimens (Leanza 1945: pl. 10: 5-7) seem to be adult females as they show a well marked variocostation and uncoiling in the last whorl preserved. The boudary between the Ph and the Bc and the morphology of the ventral area of previous whorls are unknown, they were not described and cannot be assessed from the figures. Both specimens are very similar to the lectotype of the species (Sayn 1907: pl. 5: 10) and to the females figured by Company (1987: pl. 6: 1, 7), but the uncertainties noted and the very weak umbilical bullae, hamper a definitive identification with the Tethyan species. Although we think that the Andean specimens could belong to *T. pertransiens* or a closely related species, they cannot be

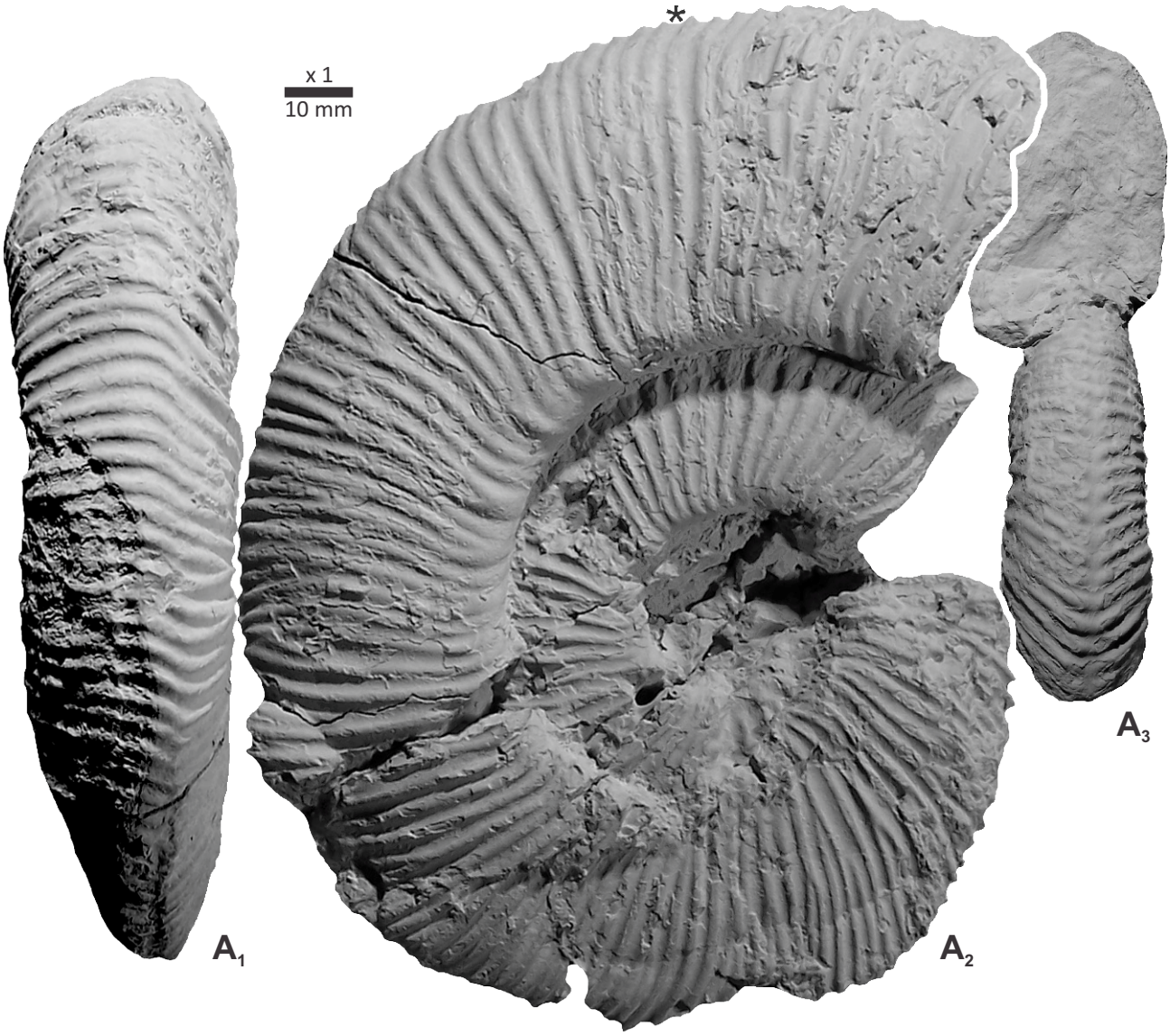

Figure 9. *Quintucoceras pseudowichmanni* n. gen., n. sp., Puerta Quintuco, level PQ-I-36, Wichamnni Zone. Holotype (MOZ-PI-11556), adult female phragmocone with beginning of bodychamber. The ventral area after removing the last part of the last whorl is shown in A_3. – The asterisk indicates the last septum. Natural size (x1).

used in isolation for strong time-correlation tied to the known chronostratigraphic range of this species.

Above the level *n* there are no ammonites recorded. In the next underlying level *m-n* occur specimens (Leanza, 1945: pl. 11: 1-4) assignable to *Subthurmannia boissieri* (Pictet, 1867), indistinguishable from the specimens from Pampa Tril (Parent et al., 2015, 2017). The next underlying level *m* has yielded (Leanza 1945: pl. 17: 4, pl. 20: 7, pl. 22: 1-2) specimens of *Spiticeras damesi* (Steuer, 1897). These ammonites from levels *m* and *m-n* of Arroyo del Yeso strongly suggest the Damesi Zone (see Parent 2022), mostly equivalent to the Boissieri Zone of the late Berriasian (further discussion below). Thus, the age of the holotype of *Quintucoceras wichmanni* n. gen. could be latest Berriasian or earliest Valanginian.

Material: Five specimens from level PQ-I-0. One well-preserved juvenile female with beginning of bodychamber (MOZ-PI-11708/4). Two incomplete phragmocones (MOZ-PI-11708/1, 3). Two portions of adult bodychamber (MOZ-PI-11708/2, 5).

Description: Female. Moderately large platyconic shell, involute and compressed with suboval to subrectangular, higher than wide whorl section throughout the ontogeny.

In the inner whorls, $D = 10$ to 40 mm, the ribbing is fine, dense and slightly flexuous. The primary ribs originate in the umbilical wall, and many bifurcate from the mid-flank; some few bifurcate from the umbilical shoulder and again at the mid-flank. The ventral ribs form a mild ventrolateral swelling and cross the venter weakened.

The subadult phragmocone (cf. the holotype) exhibits the *Neocomites*-like stage: bundles of two-four fine, flexuous ribs originated in umbilical spines, most bifurcating in some part of the middle third of the flank, some few remaining simple. All ribs end in a ventrolateral

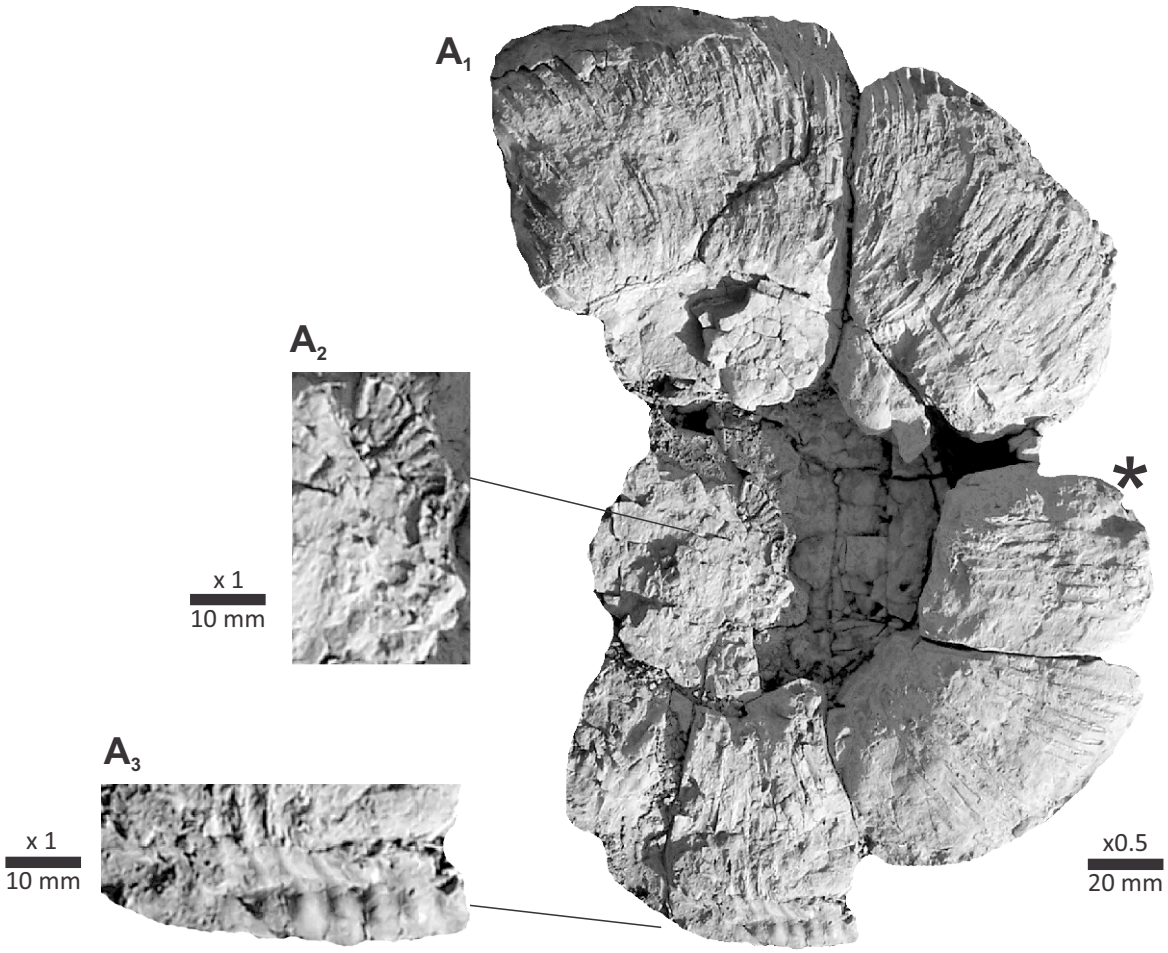

Figure 10. *Quintucoceras pseudowichmanni* n. gen., n. sp., Puerta Quintuco, level PQ-I-36, Wichamnni Zone. Almost complete adult female, not collected (field photograph). A_1: general half-size view of the specimen. A_2: natural size view of the inner whorls. A_3: natural size view of the ventral area with two rows of spines (rounded tubercles internal mold) and a mild ventral groove. – The asterisk indicates the last septum. A1: x0.5, A_2-A_3: natural size (x1).

spine, leaving a smooth ventral band. In the adult phragmocone the ribbing transitions to simple and closely spaced ribs, and the venter is covered by the ribs crossing unchanged.

The beginning of the bodychamber in the specimen in Fig. 5A is roughly estimated as D_{ls} = 110 mm. The largest portion of adult bodychamber available (Fig. 6) has only fine, simple ribs which cross the venter forming a mild chevron. Some ribs form a little spine and cross the venter slightly weakened in the internal mold. Apparently the peristome is not preserved.

Remarks and comparison: The attribution of this species to the genus *Neocomites* has been cast in doubt (e.g. Company 1987, Lehmann et al. 2015). The morphology and sculpture ontogeny of the phragmocone are similar to those of *Neocomites* indeed, but the adult phragmocone and bodychamber show they do not belong to this genus. This species was recorded from the uppermost 10 m of the Vaca Muerta Fm in the studied section, mainly from the concretional bands (Fig. 3) where occurs isolated but in abundance. Further than the collected specimens there were recorded many impressions of specimens at all sizes. The largest impression observed indicates that the species could reach at least D = 300 mm.

Some of the Valanginian neocomitids described by Weaver (1931) show some resemblance with *Quintucoceras wichmanni* n. gen. The holotype of *Thurmannia quintucoensis* Weaver (1931: fig. 358) is herein refigured adding the ventral view (Fig. 8A). It consists of a bodychamber, somewhat similar to the specimen in Fig. 5D, differing by its wider smooth ventral band, the many ribs undivided and others only divided in the lower third of the flank. This specimen comes from the Quintuco Fm of his locality 1724, Cerro Candelero, very close to our section (Fig. 1B). The stratigraphic position is rather loose, indicated by Weaver (1931: 69) as collected from a level of 100 m of rocks yielding a number of early Tithonian to early Valanginian ammonites. The holotype and a paratype of *Thurmannia salinasensis* Weaver, 1931 were illustrated by his figures 352-353. The holotype is lost (Ron Eng, pers. comm. 08/08/2025); the paratype is herein

refigured adding the lateral view (Fig. 8C). Both specimens come from a point 7 km before the mouth of the River Rio Chico (Mendoza Province). The paratype differs from *Quintucoceras wichmanni* n. gen., at comparable diameter, by the wider smooth ventral band, the wider relative umbilicus, and the many ribs bifurcated well above the umbilcal shoulder, like in *Thurmannia salinasensis*. We cannot assess the taxonomic significance of these differences with respect to *Quintucoceras wichmanni* n. gen. because the inner whorls, the bodychamber, and the accurate stratigraphic position of the specimens of Weaver are not known. *T. quintucoensis* and *T. salinasensis* seem to belong to a single species, closely resembling some *Thurmanniceras*, but according to the modular morphology dominant in the subfamily they cannot be assigned definitely.

The Valanginian specimens from southern N America described by Imlay & Jones (1970) under different names (above) could well be assigned to *Quintucoceras wichmanni* gen. n. These specimens have a larger proportion of simple ribs, but as it compares with the inner whorls of some specimens of *Quintucoceras wichmanni* n. gen., it is assumed as intraspecific geographic variation. It is especially interesting the specimen with bodychamber in their pl. 14: 2-4 which is identical, but at smaller size, to the adult female bodychamber in Fig. 6. The specimens described as *Thurmanniceras jenkinsi* (Anderson, 1938) in their pl. 13: 1-6 do not show important sculptural or morphological differences.

Age and distribution: the species has been recorded with figurations from levels assigned to the Wichmanni Zone from several localities of the western border of America: Huncal (Naipauer et al 2020), Puerta Quintuco (this report), Arroyo de Yeso (Leanza 1945; Aguirre-Urreta et al. 2005, 2007), and California, USA (Imlay & Jones 1970).

Quintucoceras paseudowichmanni n. gen., n. sp.
(Figs. 7, 9-10)

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1999 "*Thurmanniceras*" sp. a – Aguirre-Urreta & Rawson: fig. 3I-J.
2015 *Pseudoblanfordia* cf. *australis* (Burckhardt) – Parent et al.: 64, fig. 68A-C.
2020 "*Thurmanniceras*" cf. *keideli* – Naipauer et al.: fig. 7D-E.

Derivation of the name: After the partial resemblance with *Quintucoceras wichmanni* n. gen.

Material: Two specimens from level PQ-I-36. Holotype (MOZ-PI-11556): a rather well-preserved adult with beginning of the adult bodychamber. An adult female with incomplete bodychamber, not collected.

Type locality and horizon: Puerta Quintuco. Quintuco Fm, level PQ-I-36. lower Valanginian, Wichmanni Zone.

Description: Female. Evolute platycone, compressed throughout the ontogeny, with suboval, higher than wide whorl section.

Inner whorls poorly preserved; ribbing fine and slightly flexuous.

Middle worls densely ribbed with ribs originated in the umbilical wall, mostly bifucated in the upper half of the flank, some remain undivided. All ribs reach the ventrolateral shoulder evenly spaced, ending in a ventrolateral spine. In the adult phragmocone, at about D = 120 to 140 mm, the ribs bi- or trifurcate from an umbilical swelling (base of spine) and one of the secondaries bifurcates again in the upper third of the flank; the external ribs are uninterrupted, forming a mild chevron. After this short stage of polyschizotomy the primaries in the bodychamber are all simple, crossing the venter unchanged.

The adult bodychamber begins at D = 150 mm in the holotype and about 200 mm in the not collected specimen. This latter specimen seems to be adult because of the apparent uncoiling in the last whorl; its maximum diameter is about D = 250 mm, suggesting a diameter at peristome of not less than 300 mm (with a bodychamber of three quarters of a whorl). Its adult bodychamber is finely ribbed with simple, slightly curved forward primary ribs. The ventrolateral spines fade from D = 230 mm.

Remarks and comparison: This new species shows close resemblance to *Quintucoceras wichmanni* n. gen., but occurs in a higher stratigraphic position, and differs by the shorter stage of bundled ribs from umbilical spines. This stage is not only shorter but also developed at larger size and with no ventrolateral spines and smooth ventral band (cf. Fig. 5D and 9). The adult female bodychambers are very similar in both species.

The specimen from Cerrito de la Ventana figured by Aguirre-Urreta & Rawson (1999: fig. 3I-J) as "*Thurmanniceras*" sp. a, is directly comparable to the beginning of the last whorl of the phragmocone of the holotype. The specimens from Pampa Tril, figured as *Pseudoblanfordia* cf. *australis* (Burckhardt, 1903) by Parent et al. (2015: fig. 68A-C), are incomplete phragmocones matching the inner whorls of the present new species, and their stratigraphic position is equivalent. The specimens from the section C in the area of Huncal figured as "*Thurmanniceras*" cf. *keideli* Gerth, 1925 by Naipauer et al. (2020), are identical to the specimens from Pampa Tril. These specimens also occur above *Quintucoceras wichmanni* n. gen. and can be assigned to *Quintucoceras pseudowichmanni* n. gen., n. sp.

Age and distribution: the species has been recorded from levels assigned to the Wichmanni Zone from Huncal (Naipauer et al. 2020), Puerta Quintuco (this report), Cerrito de la Ventana (Aguirre-Urreta & Rawson 1999), and Pampa Tril (Parent et al. 2015).

Quintucoceras denticulatum n. gen., n. sp.
(Figs. 7, 11-15)

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2015 *Lissonia* cf. *riveroi* (Lisson) – Parent et al.: 66, fig. 69A-E.

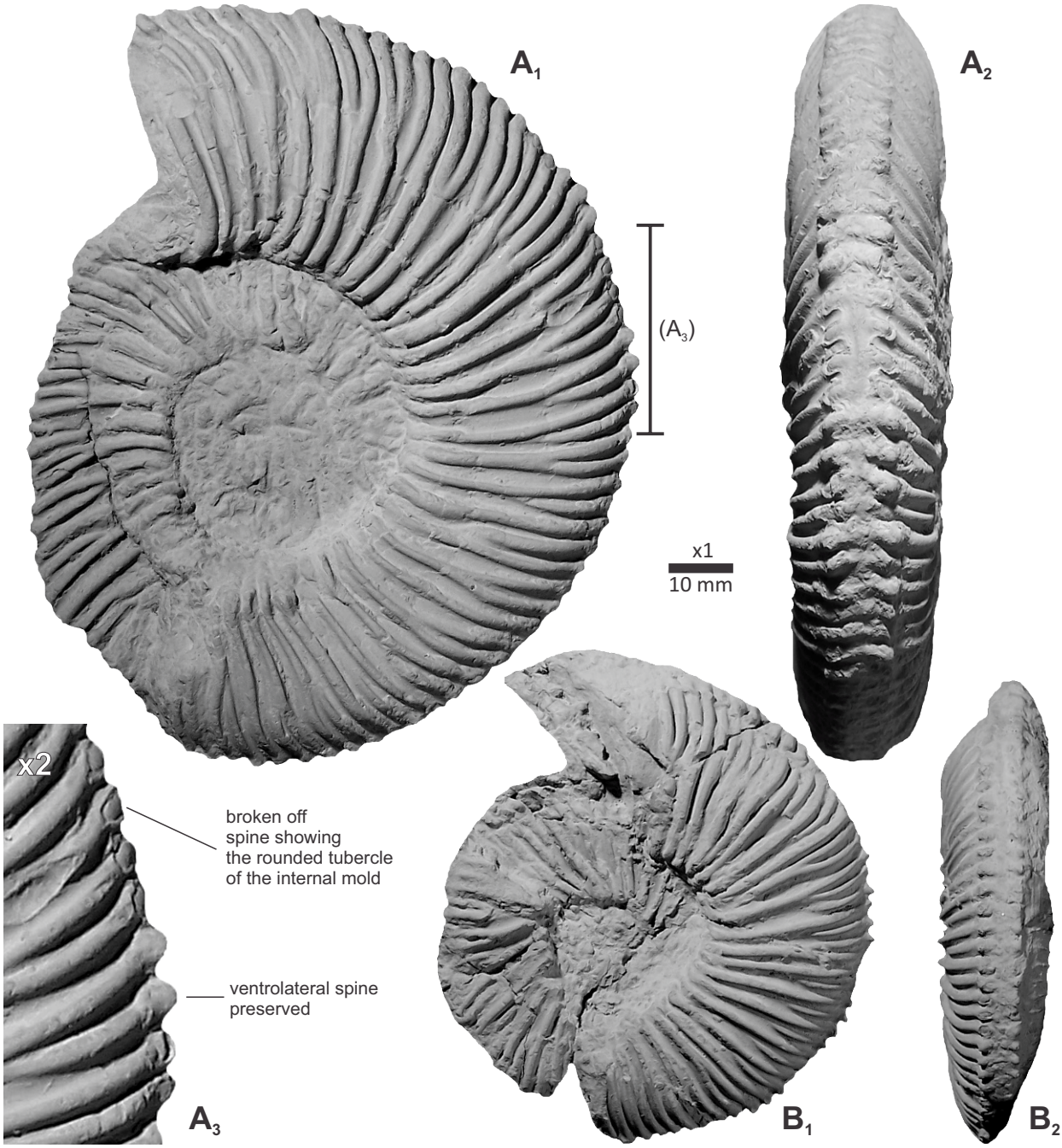

Figure 11. *Quintucoceras denticulatum* n. gen., n. sp., Puerta Quintuco, level PQ-I-38, Wichmanni Zone. **A**: paratype-I, female phragmocone (MOZ-PI-11539); A_1: lateral view (with indication of the detail in A_3); A_2: ventral view showing the narrowing of the smooth ventral band with respect to the inner whorls; A_3: detail (x2) of the denticulate aspect of the ventrolateral spines preserved in test, but preserved as rounded tubercles in the internal mold. **B**: paratype-II, juvenil phragmocone (MOZ-PI-11557/2), note the short early stage of polyschizotomy from mild umbilcal bullae. All natural size (x1), except A_3 (x2).

Derivation of the name: After the denticulate aspect of the ventrolateral spines. Latin *dens*, *dent*: tooth.

Type locality and horizon: Puerta Quintuco. Quintuco Fm, level PQ-I-40, lower Valanginian Wichmanni Zone.

Material: More than 20 specimens from levels PQ-I-38-45. Holotype (level PQ-I-40): complete adult female phragmocone with the beginning of the bodychamber (MOZ-PI-11538). Paratype I (level PQ-I-38): subadult female phragmocone (MOZ-PI-11539). Paratype II (level PQ-I-38): juvenile phragmocone (MOZ-PI-11557/2). Paratype III (level PQ-I-44): female phragmocone (MOZ-PI-11529). Paratype IV (level PQ-I-44): adult male (MOZ-PI-11688).

Description: Female. Compressed platyconic shell (W/H_1 = 0.60-0.75) from at least D = 15 mm, whorl section suboval

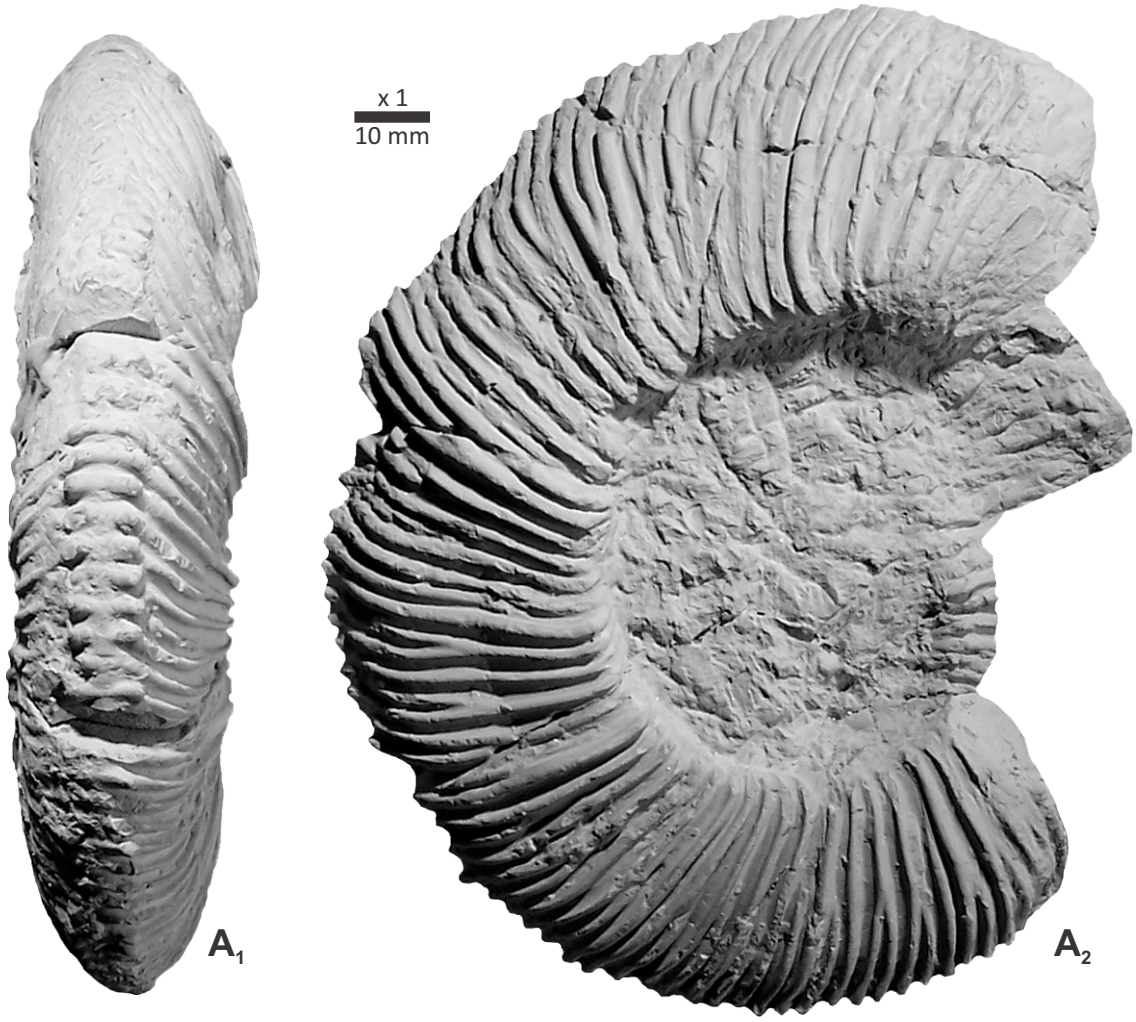

Figure 12. *Quintucoceras denticulatum* n. gen., n. sp., Puerta Quintuco, level PQ-I-38, Wichmanni Zone. Female phragmocone (MOZ-PI-11557/1). Natural size (x1).

with flattish venter in the phragmocone passing to subrectangular in the adult bodychamber; moderately evolute: $U/D = 0.32\text{-}0.45$.

The inner whorls have fine primary ribs (P = 15-20), bifurcated in the middle of the flank. In the ventrolateral shoulder all ribs end in a small spine, and the venter is smooth.

The primary ribs in the middle whorls (P = 25-35) are almost straight, prosocline, or slightly curved forward; most of them bifurcate, just above mid-flank, in secondaries curved forward. Some remain undivided in an irregular arrangement, producing a ratio $V/P = 1.8\text{-}2.2$. All ribs reach the indistinct ventrolateral shoulder evenly spaced, forming a short spine directed outwards or backwards. All ribs cross the venter becoming weaker towards the bodychamber.

The only specimen with the adult bodychamber preserved (possibly complete) is a female (Fig. 14A) studied in the field but not collected because of disintegration. The bodychamber begins at about D_{is} = 280 mm, stout, with strong and widely spaced primaires; two files of tubercles (bases of spines): one at the umbilical shoulder and other in the uppermost flank, fading towards the peristome. The maximum diameter is 420 mm, with $U/D = 0.4$ and $P = 5$.

Male. A relatively small specimen (Fig. 15A), adult as indicated by uncoiling of the bodychamber, preserving only the dorsal curvature of the peristome which indicates a not preserved lappet. It is identical to the female at comparable diameter. The adult bodychamber is one-half whorl long and begins at D_{is} = 45 mm. The diameter at the peristome is $D_p = 60$ mm.

Remarks and comparison: This new species differs from *Quintucoceras pseudowichmanni* n. gen., n. sp. by the extension throughout the adult phragmocone of the forwardly-curved bifurcate ribs, and by the larger and stout, bispinose bodychamber.

The specimens from the lower Valanginian of Pampa Tril described by Parent et al. (2015: fig. 69A-E) as *Lissonia* cf. *riveroi* (Lisson, 1907) are merely inner whorls of this species.

Age and distribution: the species has been recorded from

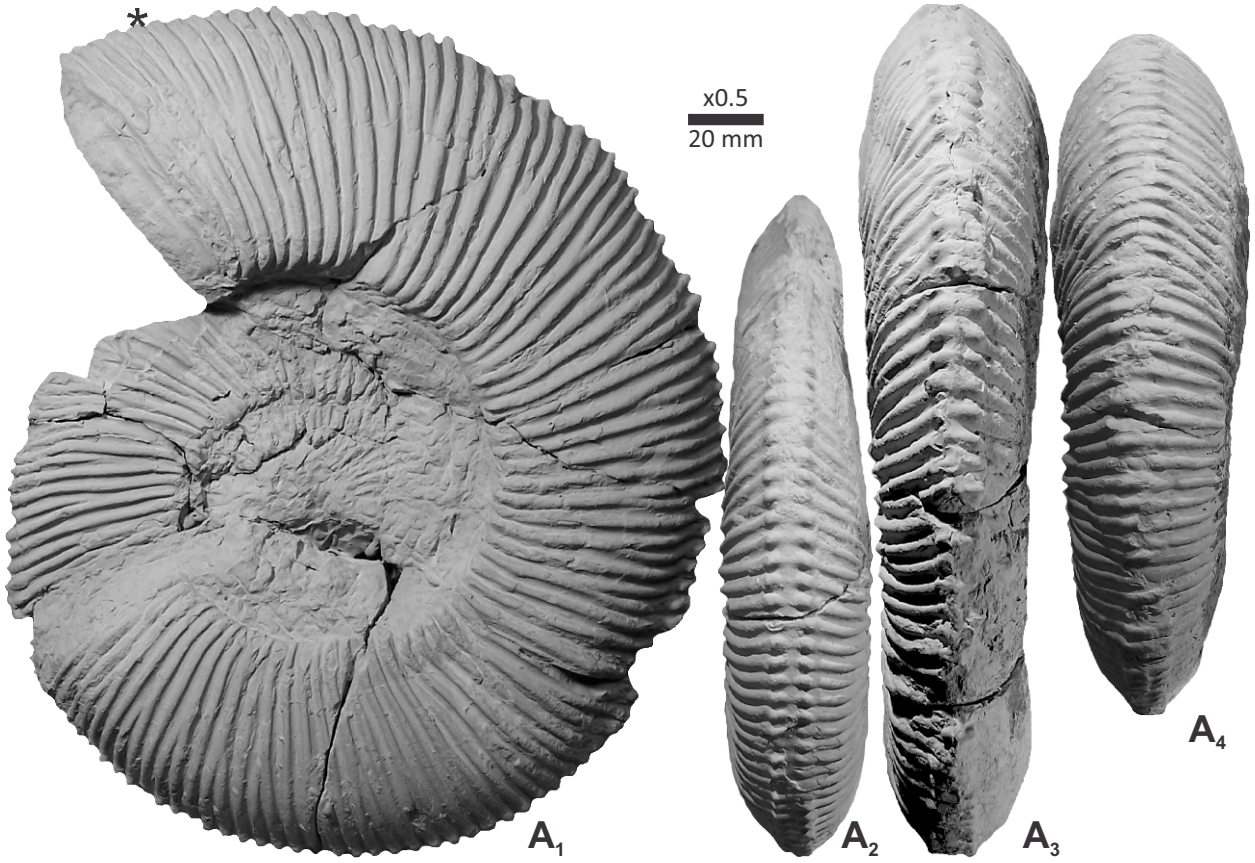

Figure 13. *Quintucoceras denticulatum* n. gen., n. sp., Puerta Quintuco, level PQ-I-40, Wichmanni Zone. Holotype (MOZ-PI-11538), adult female phragmocone with beginning of bodychamber. A_1: lateral view. A_2: ventral view at the beginning of the last whorl. A_3: ventral view in correspondance with the lateral view (A_1). A_4: ventral view of the last portion of the phragmocone and the beginning of the bodychamber. – The asterisk indicates the last septum. All reduced x0.5.

levels currently assigned to the Wichmanni Zone from Puerta Quintuco (this report), and Pampa Tril (Parent et al. 2015).

Quintucoceras macrospinatum n. gen., n. sp.
(Figs. 7, 16-24)

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?1931 *Thurmannia quintucoensis* n. sp. – Weaver: 447, pl. 56: 359 (paratype).
2015 *Lissonia* cf. *riveroi* (Lisson) – Parent et al.: 66, fig. 69F.

Derivation of the name: after the large size of the spines of adult females.

Material: Eighteen specimens from levels PQ-I-45-57. Holotype (level PQ-I-49): complete adult female (MOZ-PI-12249/1). Paratype-I (level PQ-I-49): complete adult female (MOZ-PI-12251). Paratype II (level PQ-I-50): nearly complete adult female (MOZ-PI-12248). Paratype III (level PQ-I-50): female phragmocone (MOZ-PI-11570). Paratype IV (PQ-I-50): female phragmocone (MOZ-PI-11569). Paratype V (level PQ-I-45): nearly complete adult female (MOZ-PI-12250/1). Paratype VI (level PQ-I-46): female phragmocone (MOZ-PI-11565). A fragmentary adult female bodychamber (MOZ-PI-11573/2), level PQ-I-57.

Type locality and horizon: Puerta Quintuco. Quintuco Fm, level PQ-I-49, lower Valanginian Wichmanni Zone.

Description: Female. Large adult size. Shell platyconic; inner whorls involute with $U/D = 0.20$, passing to 0.30-0.40 in the outer whorls. Whorl section higher than wide ($W/H_1 =$ 0.60-0.80), subrectangular-suboval, with flattish venter in the phragmocone and rounded in the adult bodychamber.

Inner whorls with fine and dense, flexuous ribbing, bifurcated in the middle of the flank or lower. Middle and outer whorls of phragmocone with coarse-wiry ribs, bifurcated in the upper half of the flank. Every external rib forms a spine in the ventrolateral shoulder (mostly preserved as swelling or tubercle in the internal mold), and cross the flat venter uninterrupted.

The adult bodychamber begins at variable size: $D_{ls} = 284$ to 384 mm. From the last adult septum there are 5 to 7

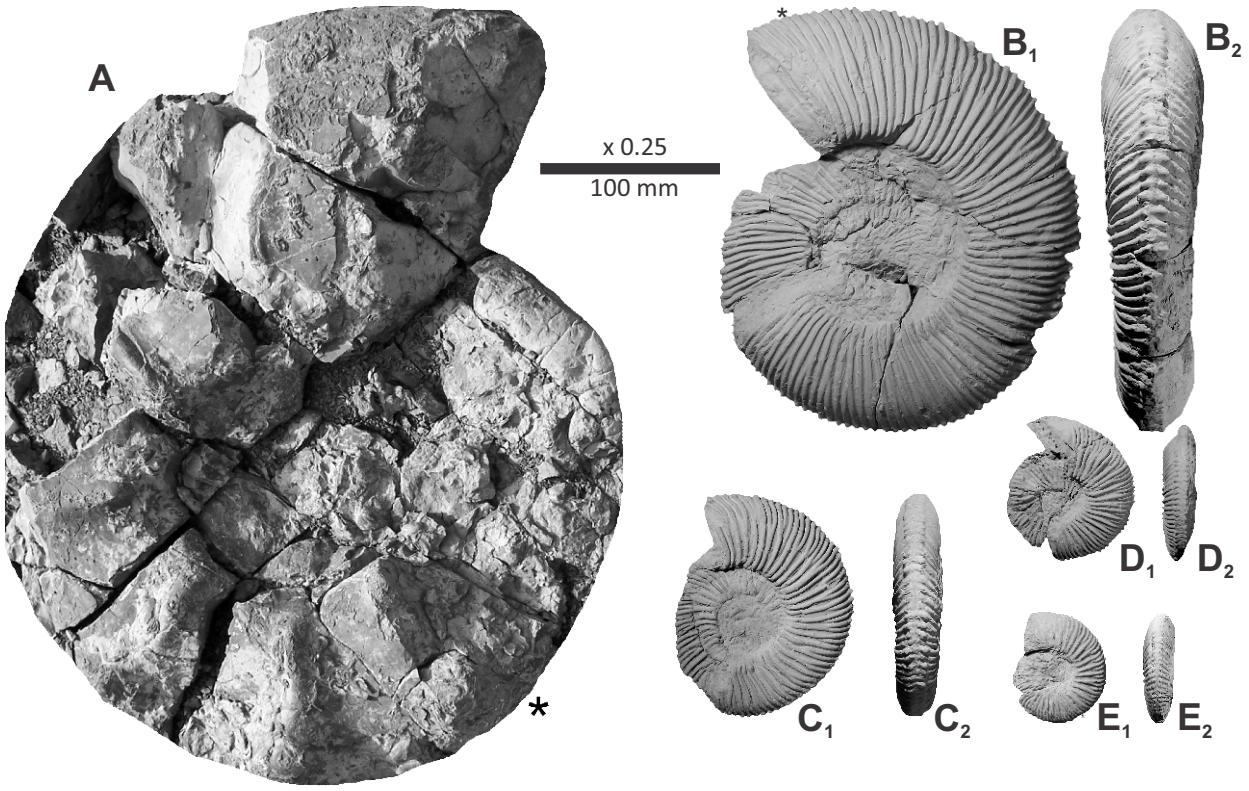

Figure 14. *Quintucoceras denticulatum* n. gen., n. sp., Puerta Quintuco, Wichmanni Zone. Series of specimens showing the ontogeny and sexual dimorphism of the species. **A**: complete adult female (field photograph of a non collected specimen), level PQ-I-43. **B**: holotype, adult female phragmocone, same as in Fig. 13 reduced. **C**: paratype-I, female phragmocone, same as Fig. 11A reduced. **D**: paratype-II, inner whorls, same as Fig. 11B reduced. **E**: paratype-IV, adult male, same as Fig. 15A reduced. – The asterisk indicates the last septum. All reduced x0.25.

strong, undivided primary ribs with a long lateral spine in the upper flank, projected rather parallel to the coiling axis. In the largest specimens the latest spines tend to migrate downwards to the mid-flank. The spines are hollow and unfloored, with rounded closed end.

The adult diameter at peristome of the holotype (Fig. 19) is $D_p = 412$ mm; in the paratype-I is $D_p = 544$ mm.

Remarks and comparison: This species differs from *Quintucoceras denticulatum* n. gen., n. sp. by (1) the unispinate and larger adult female bodychamber (Fig. 7F), (2) the stouter and more involute phragmocone (Fig. 7A, B), with wider ventral area, and (3) in the phragmocone the ribs cross the venter unchanged, rarely weakened.

The paratype of *Thurmannia quintucoensis* Weaver (1931: fig. 359), herein refigured with an additional lateral view (Fig. 8B), is a small nucleus, similar to the inner whorls of *Quintucoceras macrospinatum* n. gen., n. sp., but the shell is more inflate and the smooth ventral band wider.

The female specimen from Pampa Tril (level PT-106) described as *Lissonia* cf. *riveroi* by Parent et al. (2015: fig. 69F) is smaller than the typical of the species, but perfectly matching in sculpture and morphology the adult phragmocone as described above. The uncoiled bodychamber indicates that the specimen is adult, thus it can be considered a mesoconch (early maturing female) of the species. The best resemblance is with the female phragmocone of the early transient of level PQ-I-46 (Fig. 17). As noted above, the specimens from the Pampa Tril levels PT-86-90 can be assigned to *Quintucoceras pseudowichmanni* n. gen., n. sp. and *Quintucoceras denticulatum* n. gen., n. sp. The recognition of the three species out of their type locality shows the same succession of species of *Quintucoceras* n. gen. in two rather distant localities representing different basinal settings. According to these identifications, the Pampa Tril levels PT-86-106 (in Parent et al. 2015) that were formerly assigned to the Riveroi Zone, must be reassigned to the Wichmanni Zone (further discussion below).

Age and distribution: the species has been recorded from levels assigned to the Wichmanni Zone from Puerta Quintuco (this report) and Pampa Tril (Parent et al. 2015).

Quintucoceras aff. *macrospinatum* n. gen., n. sp.
(Figs. 7, 25-26)

Material: Seven specimens from levels PQ-I-51 to 57. An incomplete female phragmocone (MOZ-PI-11566), level PQ-I-51. Three frgmentary phragmocones (MOZ-PI-11527, 11528/1-2), level PQ-I-51. One bodychamber (MOZ-PI-12261/5), level PQ-I-55. One fragmentary phragmocone (MOZ-PI-11573/1), level PQ-I-57. One portion of bodychamber (MOZ-PI-11573/3), level PQ-I-57.

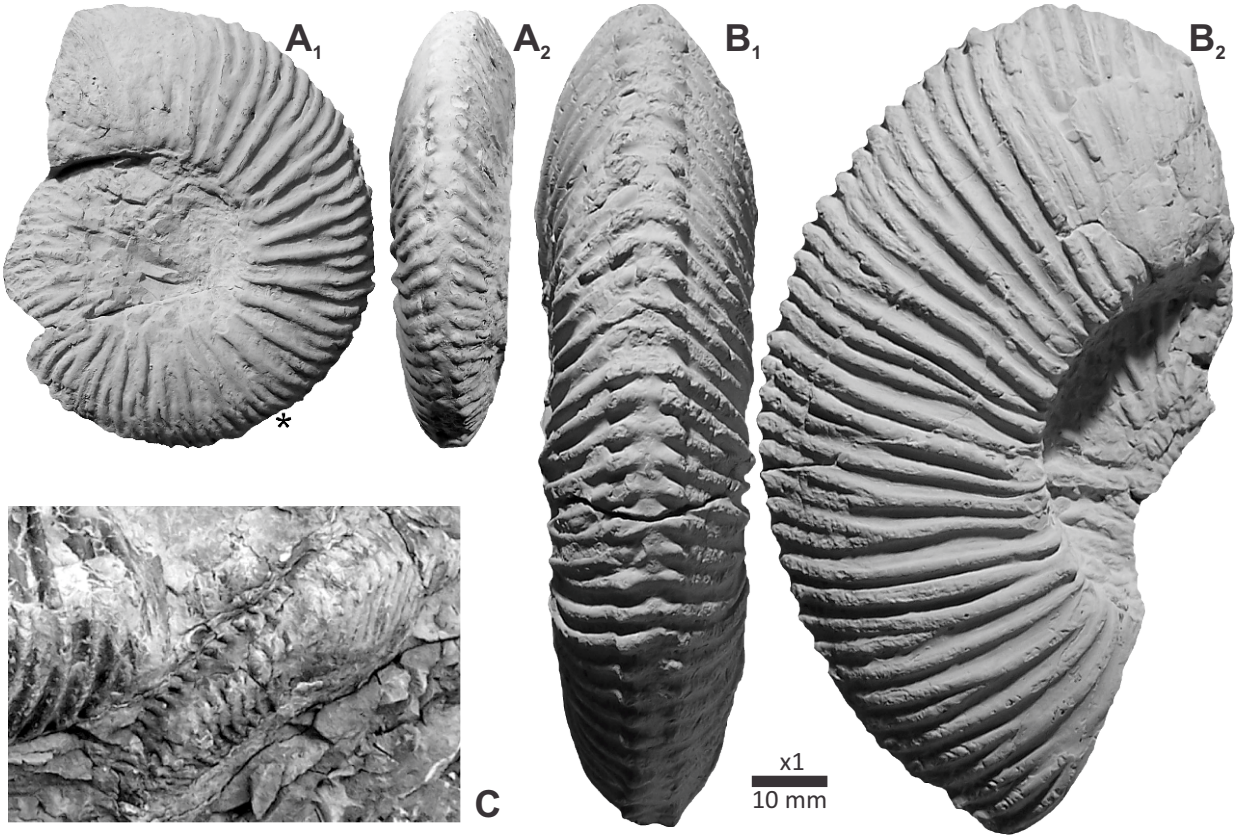

Figure 15. *Quintucoceras denticulatum* n. gen., n. sp., Puerta Quintuco, level PQ-I-44, Wichmanni Zone. **A**: paratype-IV, almost complete adult male (MOZ-PI-11688), L_{BC} = 180°. **B**: paratype-III, adult female phragmocone (MOZ-PI-11529) with a short stage of incipient umbilical spines (B_2); note in B_1 the typical ventrolateral spines directed backwards. **C**: ventral view of the phragmocone of a specimen transitional to *Quintucoceras macrospinatum* n. gen., n. sp. (field photograph of a non collected specimen). – The asterisk indicates the last septum. All natural size (x1).

Description: The phragmocone is compressed and involute. The ribbing consists of strong-wiry ribs divided from the umbilical shoulder or in the upper flank, all forming an indistinct ventrolateral spine and crossing the venter uninterrupted. Some ribs bear umbilical and lateral spines which occur with irregular distribution: in some specimens they are confined to the inner whorls (Fig. 25A, C; 26), in others they can persist up to the end of the adult phragmocone and beginning of the adult female bodychamber (Fig. 25D). The largest fragmentary bodychamber (MOZ-PI-12261/5) suggests an adult female size of not less than 400-460 mm in diameter.

Remarks and comparison: The ammonites included in this species differ from *Quintucoceras macrospinatum* n. gen., n. sp. by (1) bearing umbilical and lateral spines which occur irregularly from the inner whorls and, at least the beginning of the adult female bodychamber, and (2) by the irregular division of the ribs in the umbilical shoulder or in the upper flank. The material is incomplete and fragmentary, hampering the establishment of a definite entity. However, since the stratigraphic range of these specimens (PQ-I-51-57) completely overlap the uppermost part of the range of *Quintucoceras macrospinatum* n. gen., n. sp. they could be merely a spiny morphotype of this species.

Genus *Lissonia* Gerth, 1925

Type species: *Hoplites riveroi* Lisson, 1907; by original designation.

Remarks: In Pampa Tril, in basal beds of the Mulichinco Fm occurs, besides several *L. riveroi*-like specimens, a form of *Lissonia* different from the typical forms attributed to *L. riveroi* of the Riveroi Zone in Argentina (Figs. 27-28). It is more compressed (like the holotype), strongly ribbed in the flanks, and bears small ventrolateral spines in the phragmocone (Fig. 29). In Pampa Tril the basal levels of the Mulichinco Fm are Riveroi-Atherstoni zones in age, indicating that these specimens are somewhat younger than *Lissonia* n. sp. aff. *riveroi* (described below) and *Lissonia riveroi*. The association of this morphotype of *Lissonia* (Fig. 29) with *Olcostephanus atherstoni* (Sharpe, 1856) was described by Leanza (1945) from specimens from Mallín Redondo (Mendoza Province). If these differences correspond to intraspecific variation or evolutionary differentiation from *L. riveroi* cannot be asserted without dedicated collections in these and other localities (work in progress). However, what this material demonstrates is that the genus *Lissonia* includes more than a single species, rather a succession with more or less notorious morpho-sculptural differences.

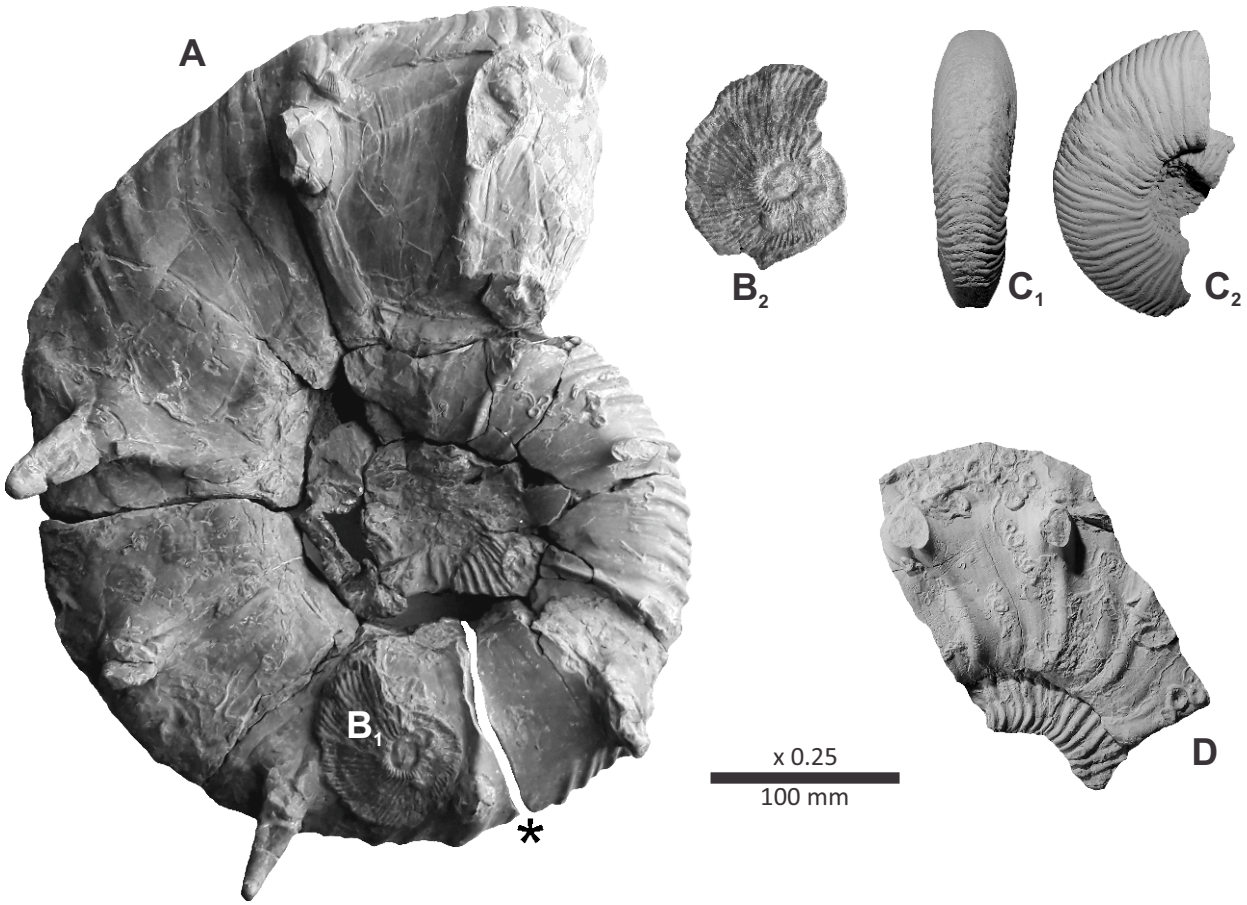

Figure 16. *Quintucoceras macrospinatum* n. gen., n. sp., Puerta Quintuco, Wichmanni Zone. Series of specimens showing the mean ontogeny of an early transient of the species. **A**: paratype-V, almost complete adult female (MOZ-PI-12250/1), level PQ-I-45. **B**: phragmocone (MOZ-PI-12250/2) attached to paratype-V. **C**: paratype-VI, adult female phragmocone (MOZ-PI-11565), same as Fig. 17 reduced, level PQ-I-46. **D**: fragment of adult female bodychamber (MOZ-PI-11564), level PQ-I-46. – The asterisk indicates the last septum. All reduced x0.25.

The genus ranges the middle and upper parts of the lower Valanginian. It is distributed through the eastern border of America, from southern Chile to Colombia (see references in Marin et al. 2023: 8). The genus also occurs in southern USA (as *Perisphinctes aguilerai* Cragin, 1905: pl. 28). We do not know reports from Mexico. In southern Spain the genus would occur as shown by the specimen figured by Hoedemaeker (1982: pl. 2: 6). However, that specimen must represent a homoeomorph since its stratigraphic position in the upper Berriasian is older than the American occurrences, and does not fit the origin of the genus as proposed by Parent et al. (2015), further discussed and improved below.

***Lissonia* n. sp. aff. *riveroi* (Lisson, 1907)**
Fig. 27

Material: Eight specimens. Seven phragmocones poorly preserved (MOZ-PI-12261/3-5, 7-10), level PQ-I-55. One fragmentary bodychamber (MOZ-PI-12261/6), all from level PQ-I-69.

Description: The phragmocone (Fig. 27A-B) is involute and rather compressed; maximum preserved size about *D* = 70 to 90 mm. The ribbing is fine and dense; the primary ribs are flexuous, most of them divided in the middle of the flank. The secondary ribs are projected forward with transverse ventrolateral spines delimiting a narrow ventral groove.

The fragmentary bodychamber (Fig. 27C), belongs to a moderately large individual. It is compressed with subrectangular, higher than wide whorl section. The ribbing is composed of fine, densely spaced, flexuous primary ribs which divide indistinctly in the upper half of the flank. All ribs end forming a ventrolateral swelling which correspond to not preserved spines.

Remarks and comparison: These ammonites differ from the holotype of *L. riveroi* by the more consistent bifurcation of the ribs and the ventrolateral spines in the ending of the ribs. The ammonites usually attributed to *L. riveroi* in Argentina (e.g. Fig. 28B-C; see also Aguirre-Urreta & Rawson 1999: fig. 3G-H; Aguirre-Urreta et al. 2005: fig. 4a-b) are more inflate and the ribs end indistinctly in the venter,

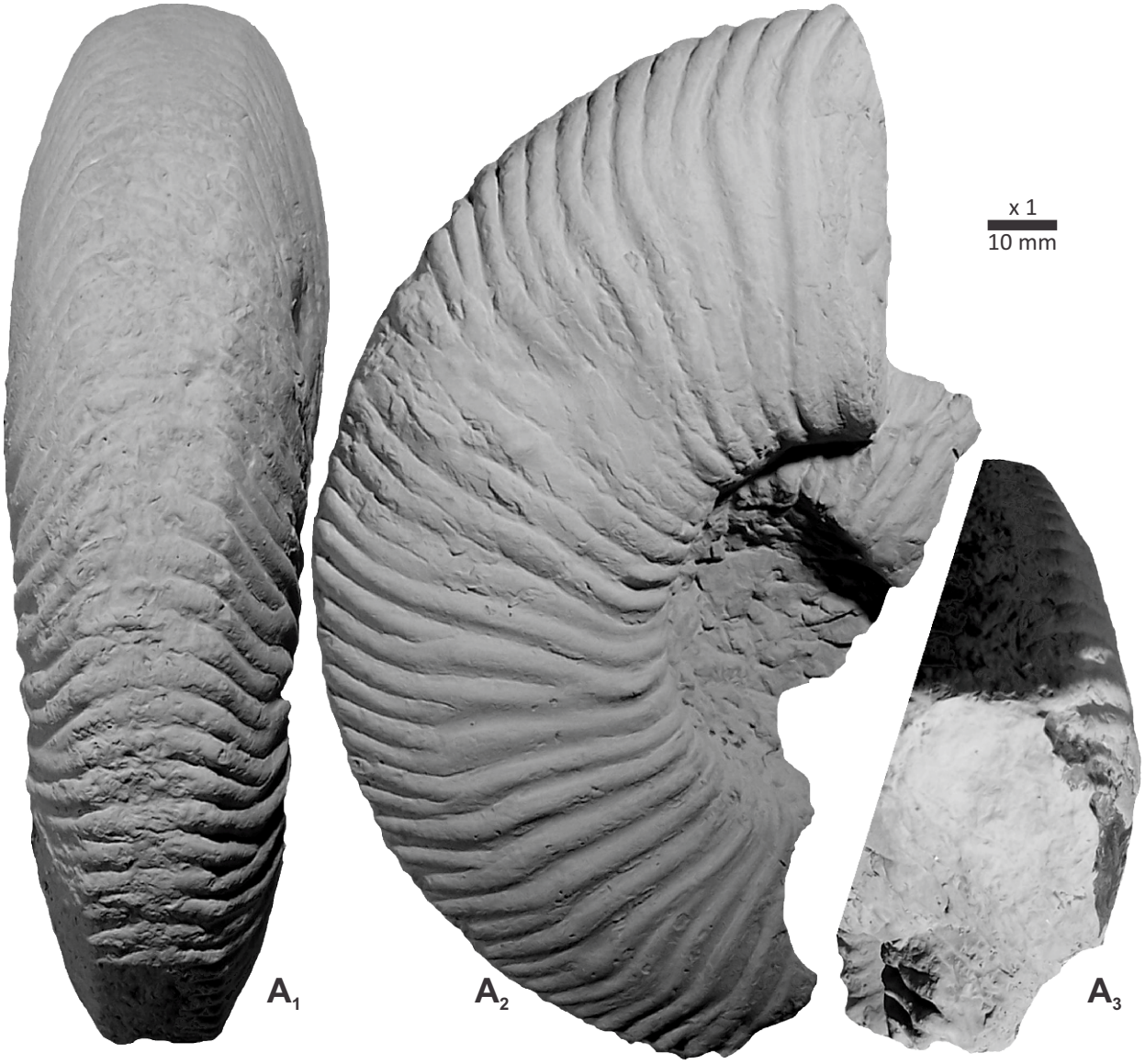

Figure 17. *Quintucoceras macrospinatum* n. gen., n. sp., Puerta Quintuco, Wichmanni Zone. Paratype-VI, adult female phragmocone (MOZ-PI-11565), level PQ-I-46, same as Fig. 16C but natural size (x1).

aside a mid-ventral groove.

One fragmentary specimen (level PQ-I-55, MOZ-PI-12261/10) has no ventrolateral spines and could be assigned to *L. riveroi*.

The present new species is very similar to stratigraphically contiguous specimens of late representatives of *Quintucoceras macrospinatum* n. gen., n. sp. (e.g. Fig. 22B, 23A-B), differing by the finer ribbing with more prominent ventrolateral spines and the ventral groove. Therefore, this species can be considered an intermediate form in shell-shape and sculpture between *Quintucoceras* n. gen. and *Lissonia*. Aguirre-Urreta & Rawson (1999) and Parent et al. (2015) have already suggested similar evolutionary scenarios where *Lissonia* would have evolved from "*Thurmanniceras*" or "*Lissonia* cf. *riveroi*" (= *Quintucoceras macrospinatum* n. gen., n. sp. in Parent et al. 2015).

In the upper part of the Quintuco Fm, above the levels with *L.* n. sp. aff. *riveroi*, occurs *L. riveroi* (Fig. 28B-C) as well as some *Lissonia*-like forms (e.g. Fig. 28A). Unfortunately these specimens from the study area were collected with no stratigraphic control. The specimen in Fig. 28A is coarsely ribbed, resembling later *Quintucoceras macrospinatum* n. gen., n. sp. (e.g. Fig. 22B, 25C), with umbilical spines from which branch two undivided, projected ribs, but only weakened in the venter.

The ventrolateral spines of *L.* n. sp. aff. *riveroi* are hollow (Fig. 27B), and with little transformation they seem to have evolved into the ventrolateral folds which form the end of the ribs in *L. riveroi* (Fig. 28C$_3$; see also Aguirre-Urreta & Rawson 1999: fig. 3H).

The possible evolutionary relationships between *Quintucoceras* n. gen. and *Lissonia* are represented in the phylogenetic model of Fig. 30.

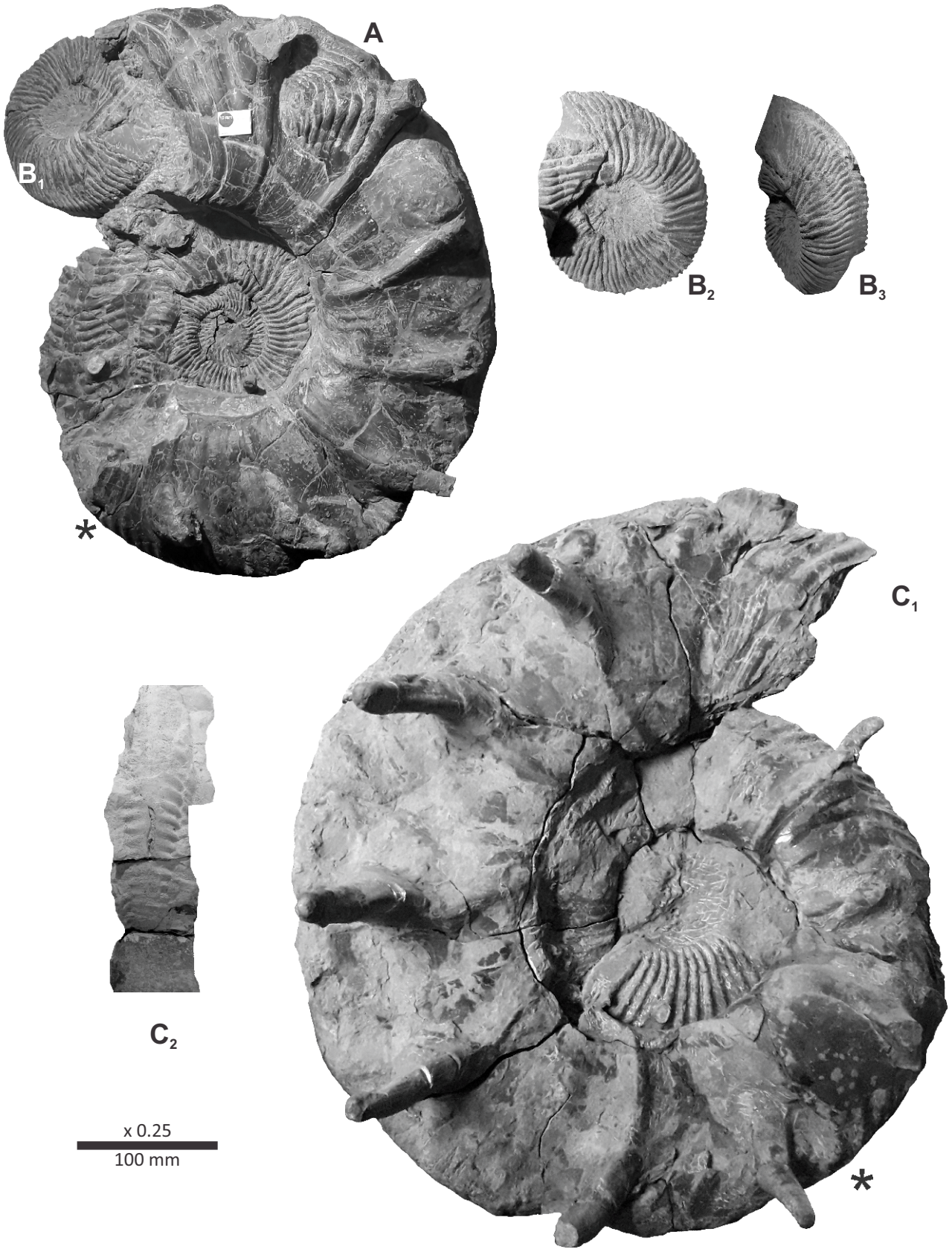

Figure 18. *Quintucoceras macrospinatum* n. gen., n. sp., Puerta Quintuco, level PQ-I-49, Wichmanni Zone. **A**: holotype, complete adult female with peristome (MOZ-PI-12249/1), L_{BC} = 235°, same as Fig. 19 reduced. **B**: female phragmocone attached to the holotype (MOZ-PI-12249/2), L_{BC} = 220°. **C**: paratype-I, complete adult female with peristome (MOZ-PI-12251); C_2: ventral view of the end of the penultimate whorl. – The asterisk indicates the last septum. All reduced x0.25.

Figure 19. *Quintucoceras macrospinatum* n. gen., n. sp., Puerta Quintuco, level PQ-I-49, Wichmanni Zone. Holotype, complete adult female (MOZ-PI-12249/1), L_{BC} = 235°, same as Fig. 18A. – The asterisk indicates the last septum. Reduced x0.5.

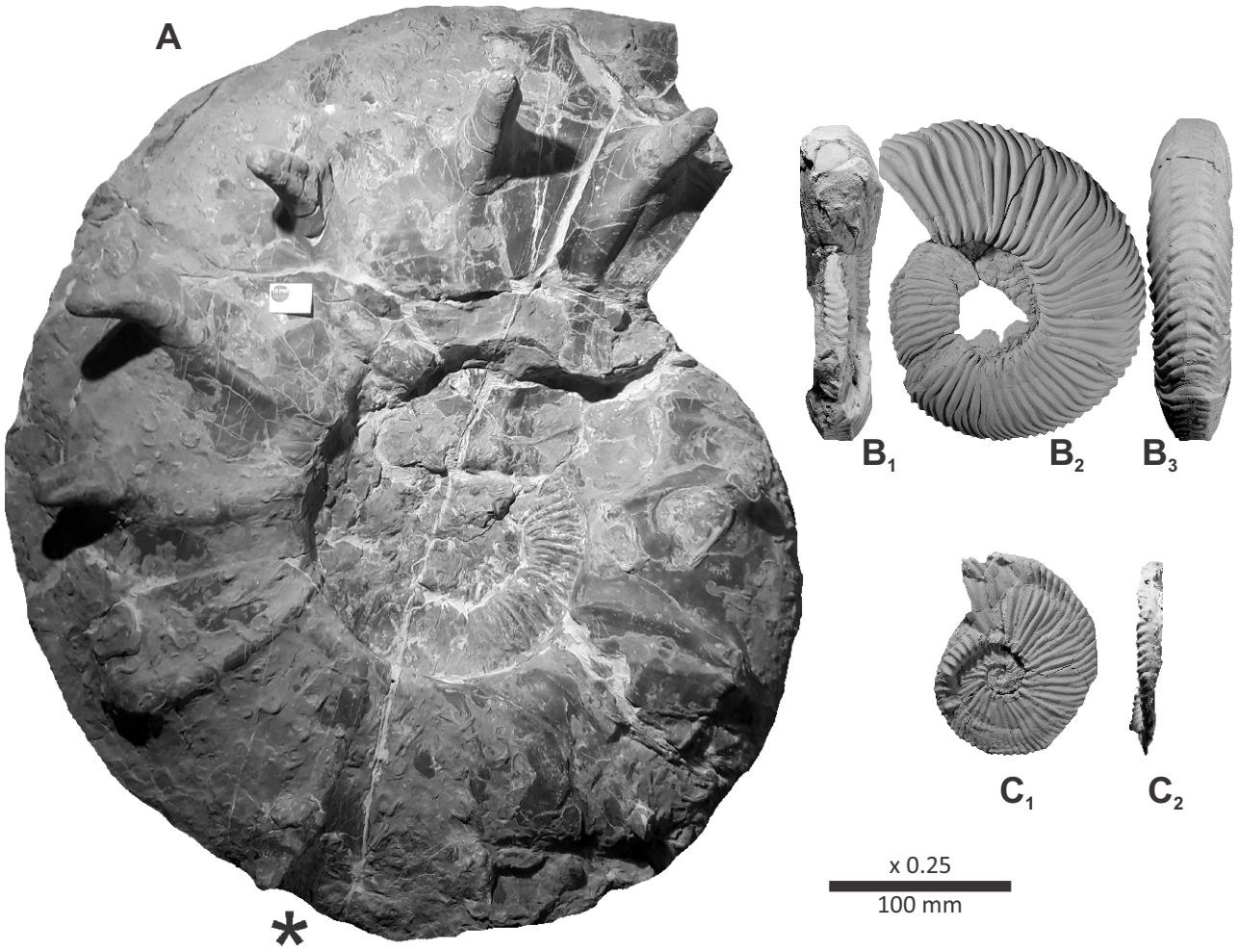

Figure 20. *Quintucoceras macrospinatum* n. gen., n. sp., Puerta Quintuco, level PQ-I-50, Wichmanni Zone. Series of specimens showing the mean ontogeny of the transient of the species in this level. **A**: paratype-II, almost complete adult female (MOZ-PI-12248). **B**: paratype-III, adult female phragmocone (MOZ-PI-11570). **C**: paratype-IV, female phragmocone (MOZ-PI-11569). – The asterisk indicates the last septum. All reduced x0.25.

Genus *Subthurmannia* Spath, 1939

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

***Subthurmannia pacifica* n. sp.**
(Figs. 31-32)

urn:lsid:zoobank.org:act:B8D17CD6-2954-4349-9F48-D33BD4080476

Material: Ten specimens. Holotype: almost complete adult female (MOZ-PI-11544), level PQ-I-32. Paratype-I: phragmocone (MOZ-PI-11555/6), level PQ-I-32. 6 incomplete or fragmentary phragmocones (MOZ-PI-11555/1-3, 7-9), level PQ-I-32. Two phragmocones (MOZ-PI-11703/1-2), level PQ-I-27.

Derivation of the name: After the Pacific (or Palaeopacific) Ocean.

Type locality and horizon: Puerta Quintuco. Quintuco Fm, level PQ-I-32, Wichmanni Zone.

Description: Female. Moderately large, holotype maximum preserved D = 185 mm with only one half of whorl of bodychamber preserved.

Inner whorls involute (U/D c. 0.25-0.30) and compressed (W/H_1 c. 0.50), finely ribbed. The ribs divide from the umbilical shoulder in the innermost whorls, but from mid-flank from about D = 20 mm. The ribs end in a small ventrolateral spine (tubercle); the venter is flattish and smooth.

Middle whorls more evolute (about U/D = 0.45) with compressed suboval whorl section (W/H_1 = 0.70). Ribbing coarse, composed of prosocline, indistinctly divided primary ribs. The ribs end in the venter, forming a swelling or small spine (tubercle) besides a narrow smooth ventral band. The last whorl of the adult phragmocone is rounded and more inflate (W/H_1 = 0.85); the ventral sculpture becomes irregularly divided and mild in the rounded venter.

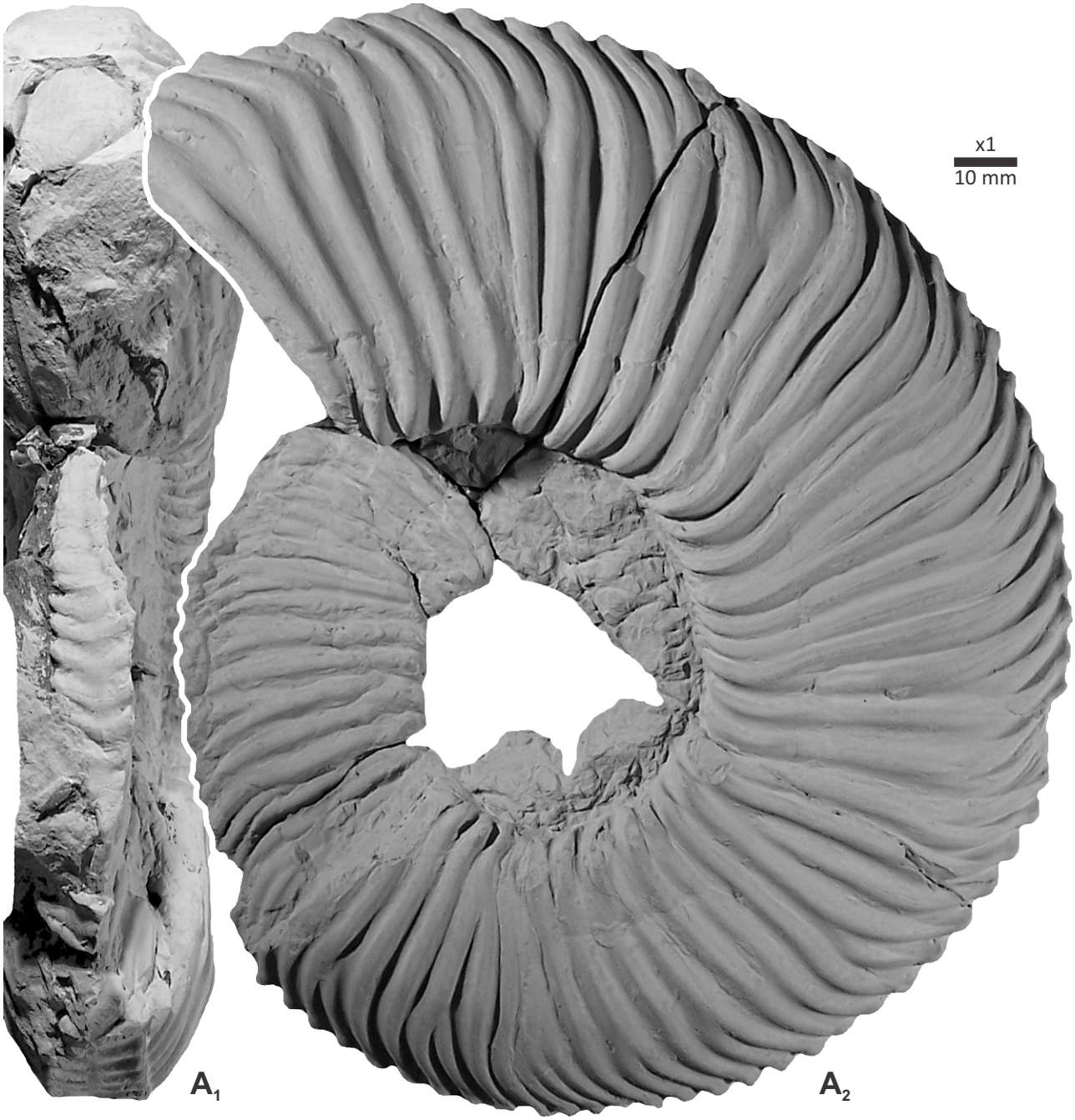

Figure 21. *Quintucoceras macrospinatum* n. gen., n. sp., Puerta Quintuco, level PQ-I-50, Wichmanni Zone. Paratype-III, adult/subadult female phragmocone (MOZ-PI-11570). Same as Fig. 20B. Ventral view in Fig. 22A – All natural size (x1).

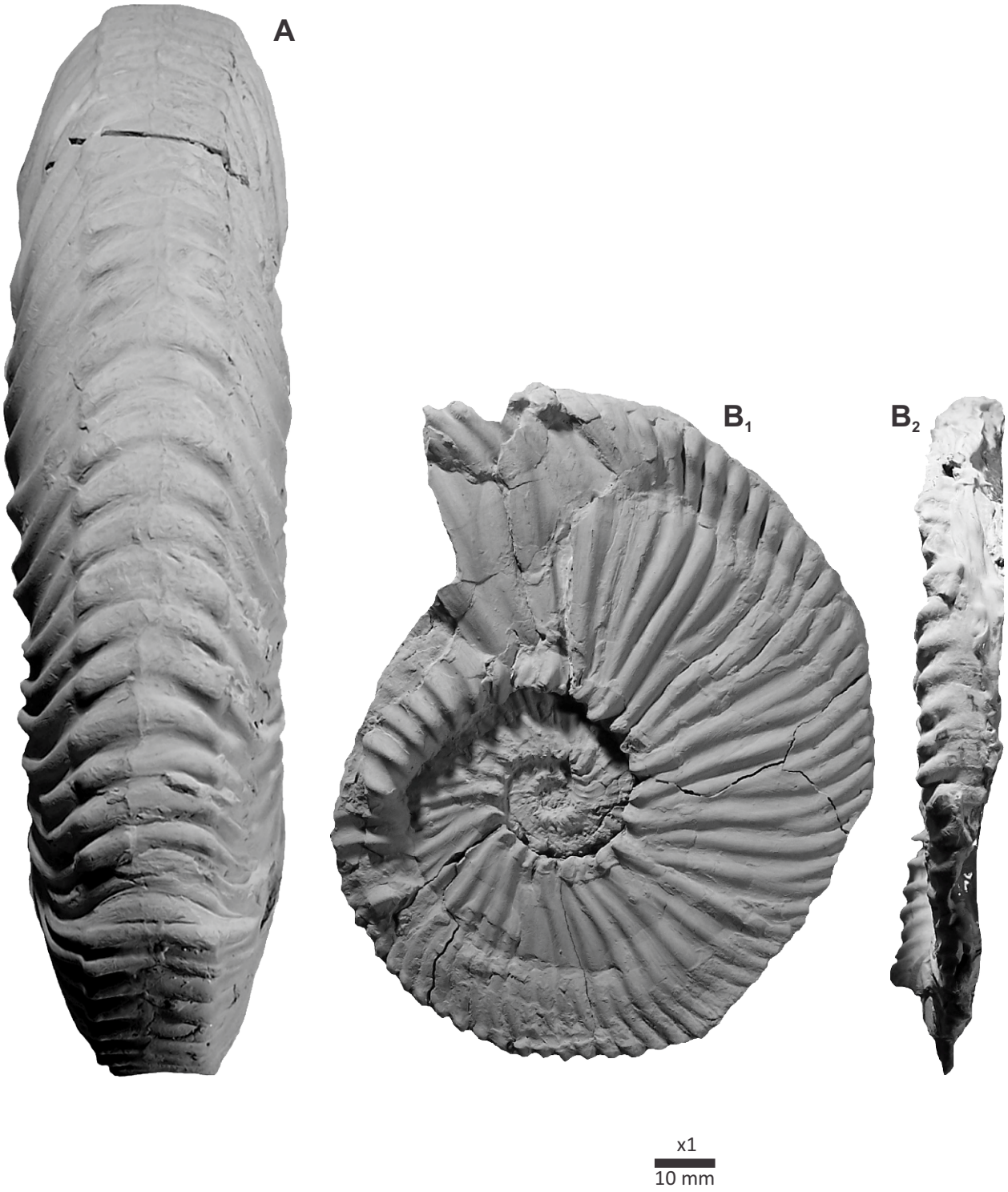

Figure 22. *Quintucoceras macrospinatum* n. gen., n. sp., Puerta Quintuco, level PQ-I-50, Wichmanni Zone. **A**: paratype-III, adult/subadult female phragmocone (MOZ-PI-11570), ventral view (oral and lateral views in Fig. 21). **B**: paratype-IV, female phragmocone (MOZ-PI-11569), same as Fig 20C. Note the short early stage of polyschizotomy from mild umbilcal spines. – All natural size (x1).

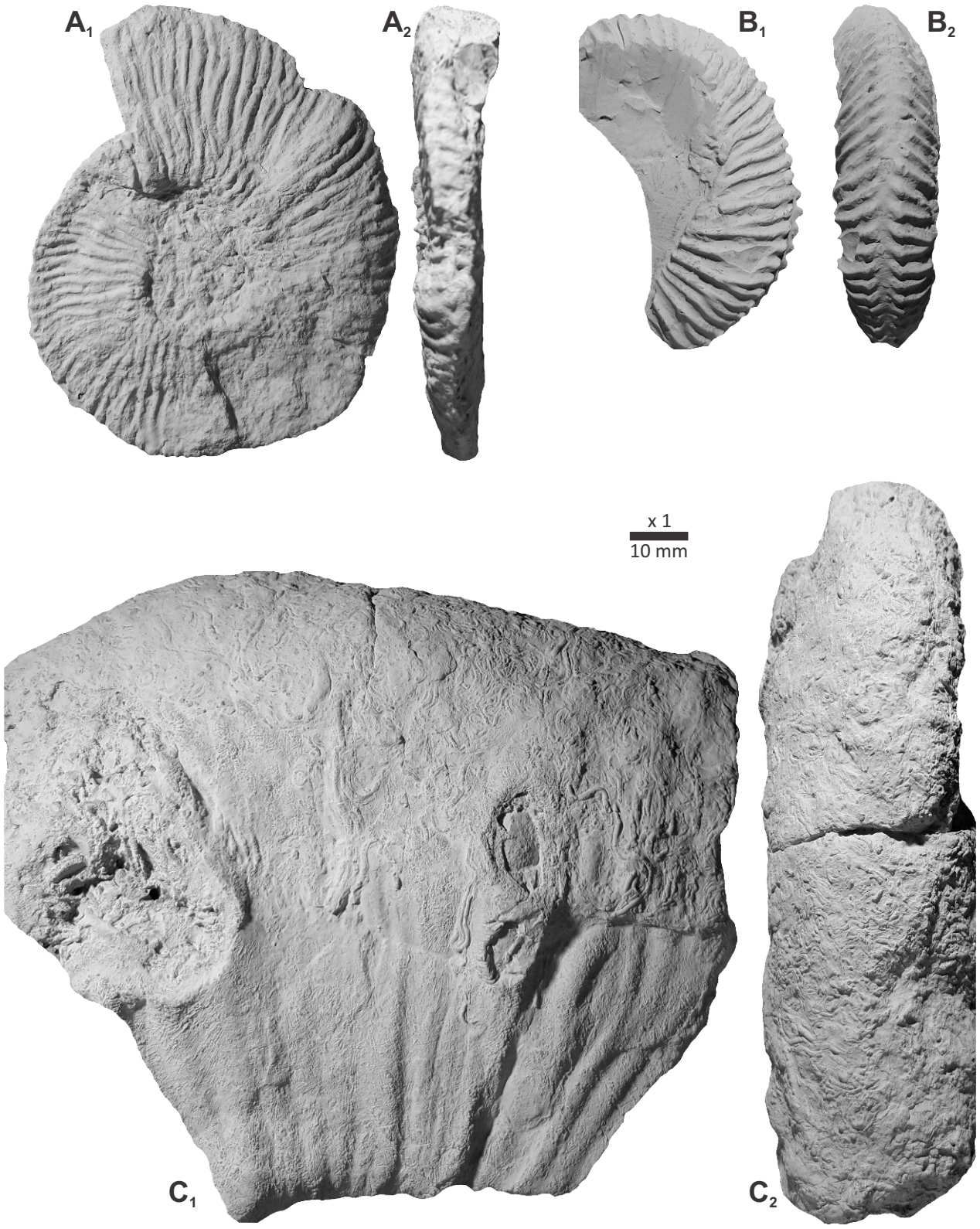

Figure 23. *Quintucoceras macrospinatum* n. gen., n. sp., Puerta Quintuco, level PQ-I-55, Riveroi Zone. **A**: inner whorls/juvenil phragmocone (MOZ-PI-12261/1). **B**: fragmentary phragmocone (MOZ-PI-11575). **C**: fragmentary adult female bodychamber (MOZ-PI-12261/5). – All natural size (x1).

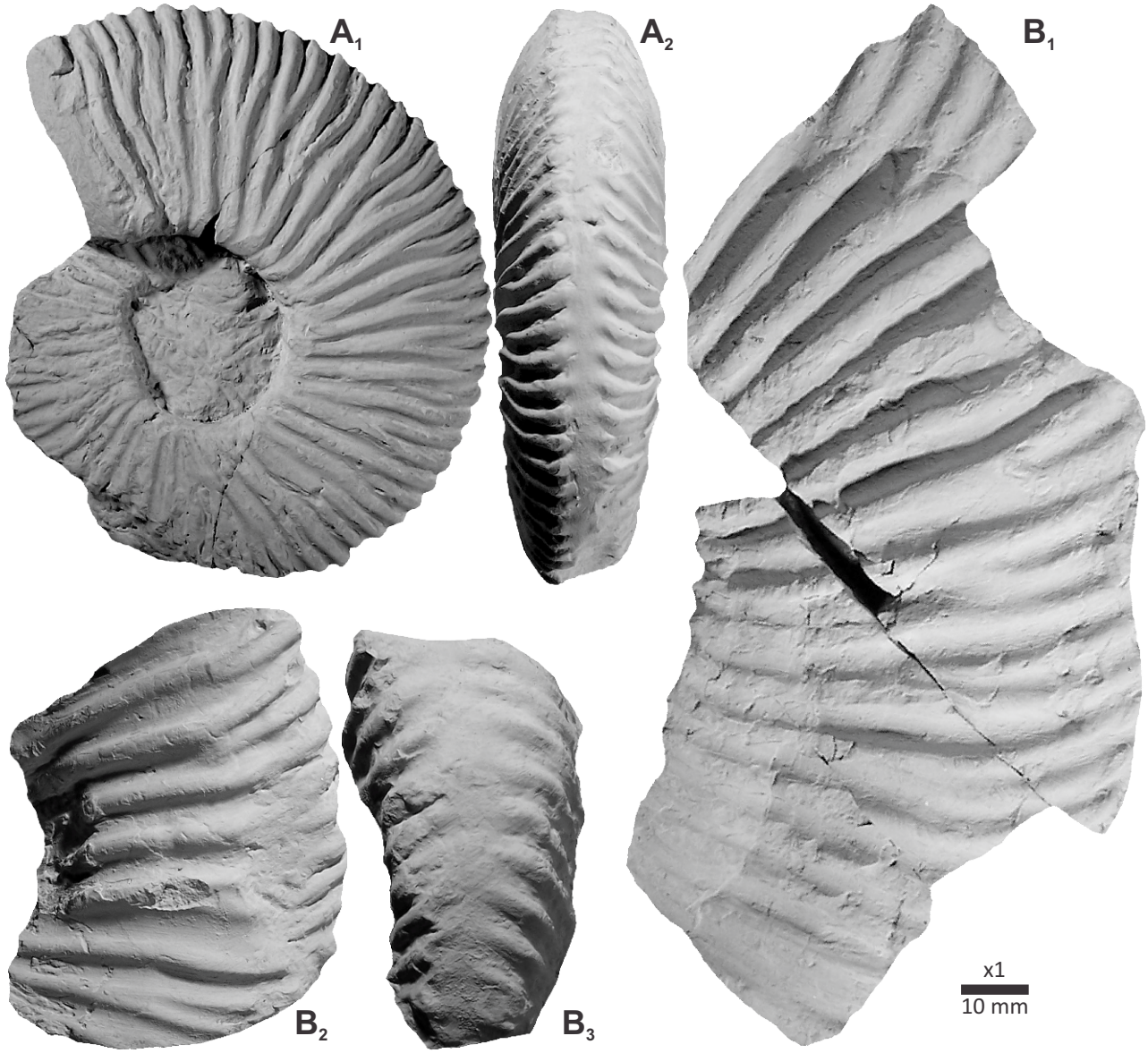

Figure 24. *Quintucoceras macrospinatum* n. gen., n. sp., Puerta Quintuco, level PQ-I-56, Riveroi Zone. **A**: inner whorls/juvenil phragmocone (MOZ-PI-11572). **B**: adult female phragmocone (MOZ-PI-11574/3). – All natural size (x1).

The bodychamber of the holotype (adult) is incomplete (maximum preserved *D* = 185 mm), It begins at about 165 mm in diameter and retains the whorl section of the adult phragmocone. The primary ribs are mostly undivided but some divide in the uppermost flank, fading towards the venter.

Remarks and comparison: The new species differs from *Subthurmannia boissieri* (Pictet, 1867) from the Damesi Zone, by the early lose of the umbilical division of the ribs which, on the other hand, become stronger and markedly interrupted in the venter. Furthermore, the bodychamber is more evolute and with rounded whorl section.

The specimen from the Boissieri Zone of Maroc, figured as *Fauriella latecostata* (Kilian, 1910) by Wippich (2001: pl 14), in our opinion a good *Subthurmannia*, is similar to the females of the present species.

The two specimens from the level PQ-I-27 (Fig. 31A-B) are slightly more compressed and involute (*U/D* c. 0.27), but the sculpture is directly comparable. These specimens seem to represent an early transient of the species.

Age and distribution. Known only in the type locality.

Genus *Sarasinella* Uhlig, 1905

Type species: *Hoplites ambiguus* Uhlig, 1902; by subsequent designation by Lemoine (1906).

Sarasinella cf. *varians* Uhlig, 1910
(Fig. 33)

Material: Three specimens. Two fragmentary

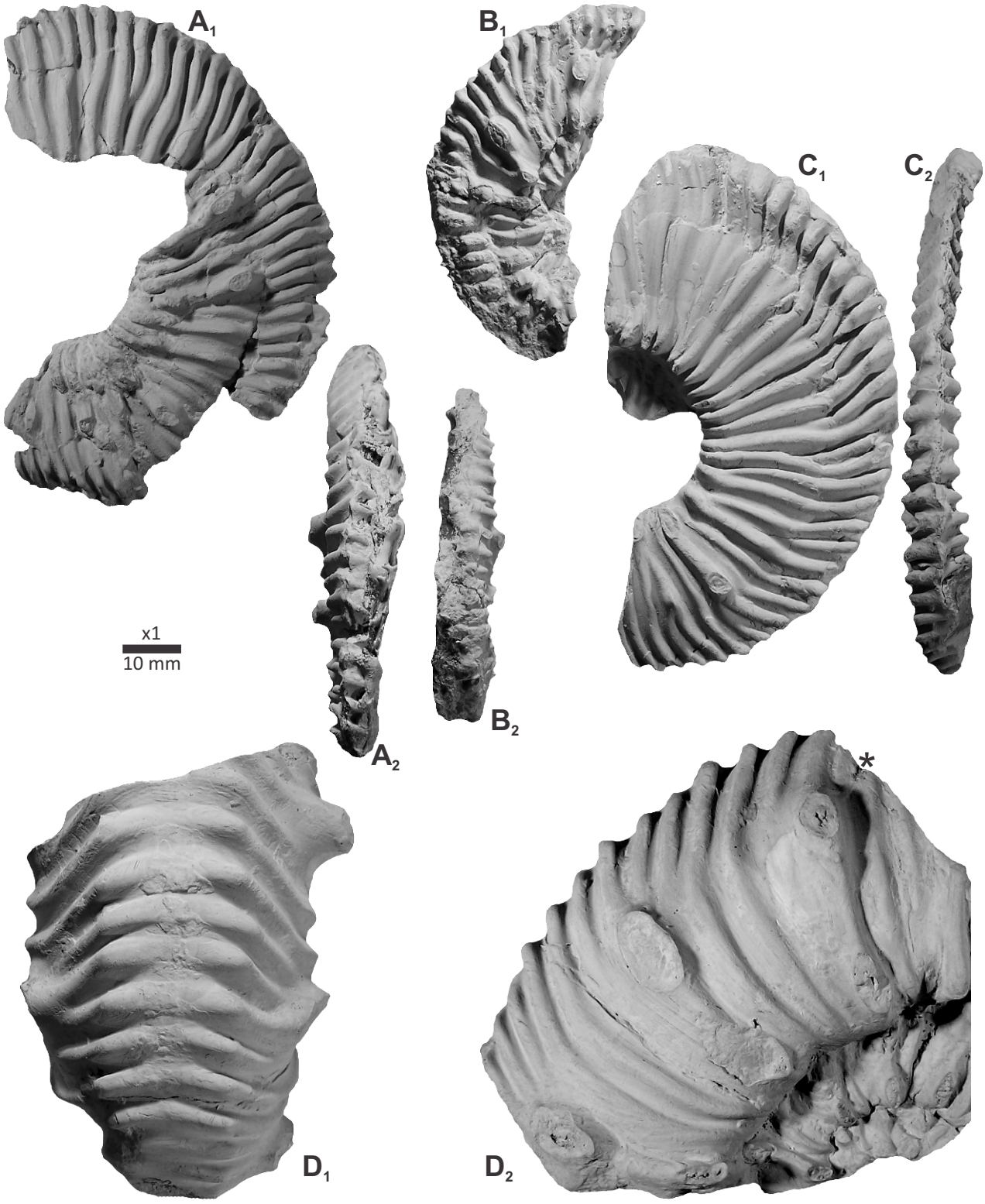

Figure 25. *Quintucoceras* aff. *macrospinatum* n. gen., n. sp., Puerta Quintuco, level PQ-I-51, Wichmanni Zone. **A**: inner whorls/juvenil phragmocone (MOZ-PI-11528/1). **B**: inner whorls/juvenil phragmocone (MOZ-PI-11528/2). **C**: inner whorls/juvenil phragmocone (MOZ-PI-11527). **D**: adult female phragmocone with beginning of bodychamber (MOZ-PI-11566). Note the persistent trituberculation from the inner whorls. – The asterisk indicates the last septum. All natural size (x1).

Figure 26. *Quintucoceras* aff. *macrospinatum* n. gen., n. sp., Puerta Quintuco, level PQ-I-57, Riveroi Zone. Inner whorls/juvenil phragmocone (MOZ-PI-11573/1). Natural size (x1).

phragmocones (MOZ-PI-11555/4-5) and an incomplete bodychamber (MOZ-PI-11541), level PQ-I-32.

Description: The last whorl of the phragmocone is compressed with subrectangular, higher than wide whorl section and tabulate or slightly rounded venter. The primary ribs are strong, originated from an umbilical tubercle, some joined in twos from the base; in the middle of the flank, or upper, they bifurcate from a tubercle. All ribs end in a small ventrolateral spine (preserved as a small bulla in the inner mold) besides a smooth ventral band.

The bodychamber, possibly adult, begins at about D_{ls} = 100 mm. The whorl section is suboval, higher than wide, with tabulate venter. Most ribs originate in an umbilical spine/tubercle, some in twos, and bifurcate indistinctly in about the mid-flank. The secondary ribs and some intercalatories end in a row of ventrolateral spines evenly spaced, leaving a wide smooth ventral band.

Remarks and comparison: One large specimen, not collected, of which remained almost nothing else than the impression in the rock, showed that our incomplete specimens represent successive growth stages, and that the bodychamber in Fig. 33A is incomplete by a quarter of a whorl or more.

The present specimens compose the morpho-sculptural ontogeny of the genus (confirmed by M. Company, pers. com. 25/10/2025), at nearly the same size of the holotype of *S. varians* (Uhlig 1910: pl. 81: 3). The only difference with the latter seems to be that the Andean specimens are less densely ribbed. The rather complex sculptural style of our specimens perfectly match the holotype but with lower rib density. In spite of this close resemblance, a provisional cf.-determination is preferable because of the isolated occurrence of fragmentary specimens.

Erdenella Nikolov, 1979 is based on *Hoplites paquieri* (Simionescu, 1899) whose holotype is very similar to our specimens although older (late Berriasian, Nikolov 1979) and, notably, could be assigned to *Sarasinella* in our view. However, it is not known if this specimen is complete, adult or juvenile, and if the specimen is incomplete, its next whorls could have been like *Erdenella erdenensis* Nikolov, 1979, bituberculate with strong ribs connecting the tubercles, thus making a generic differentiation possible.

Genus *Kilianella* Uhlig, 1905

Type species: *Hoplites pexiptychus* Uhlig, 1882; by subsequent designation by Roman (1938).

Kilianella? sp. A

Description and remarks: A single fragmentary specimen (MOZ-PI-11681) was collected from level PQ-I-14. It consists of an incomplete whorl of an evolute ammonite with subrectangular whorl section, strong ribs with small umbilical spines, a few divided in the upper half of the flank from other small spine. The dorsal side shows that the venter of the previous, unpreserved whorl had ventrolateral spines at the end of the ribs, and a smooth ventral band. This poor material is only important for documenting the possible occurrence of the genus in the Neuquén Basin.

Subfamily Endemoceratinae Schindewolf, 1966
Genus *Karakaschiceras* Thieuloy, 1971

Type species: *Hoplites biassalensis* Karakasch, 1889; by original designation.

Karakaschiceras? sp. A
Fig. 34

Description and remarks: A single specimen (MOZ-PI-12261/2) from level PQ-I-55. It is a poorly preserved phragmocone of 70 mm maximum preserved diameter. Platyconic, rather compressed and involute with flattish flanks and venter. Coarse ribs originate in an umbilical bulla (possibly base of spine), some in twos, and dividing again in the mid-flank. The ventral ribbing is interrupted besides a smooth ventral band.

Our specimen closely resembles, in shell-shape and sculpture, the inner whorls of some *Karaschiceras* in the literature. For example: (1) specimens from the lower Valanginian of Poland figured by Ploch (2018: fig. 16) as *Karakaschiceras heteroptychum* (Pavlow, 1892), (2) *Karakaschiceras* sp. 1 from Spain (Company 1987: pl. 12: 9), and (3) the French specimens of *Karakaschiceras quadristrangulatum* (Sayn, 1907) described by Reboulet (1996: pl. 1: 11-12). Other comparable ammonites are in the

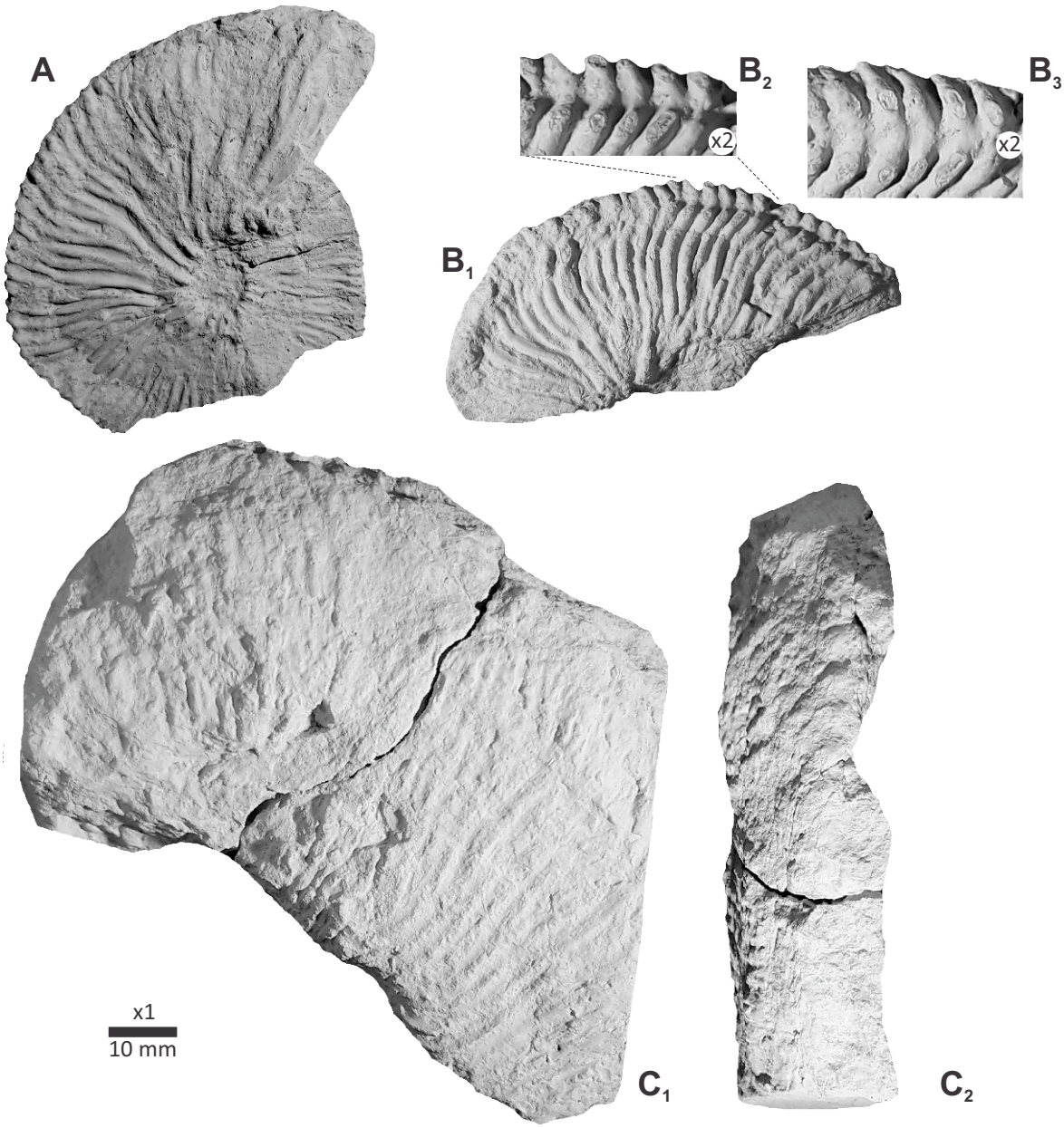

Figure 27. *Lissonia* n. sp. aff. *riveroi* (Lisson, 1907), Puerta Quintuco, level PQ-I-55, Riveroi Zone. **A**: phragmocone (MOZ-PI-12261/3). **B**: phragmocone (MOZ-PI-12261/4). Note the hollow spines (B_2, B_3). **C**: fragment of bodychamber (MOZ-PI-12261/6). Natural size (x1).

genus *Busnardoites* Nikolov, 1966. The most similar seems to be *Busnardoites subcampylotoxus* Nikolov, 1977, differing by its somewhat wider smooth ventral band. However, the holotype of the type species of *Busnardoites* (*Ammonites desori* Pictet & Campiche, 1860; refigured in Nikolov 1977: pl. 6: 2) is tuberculated in the inner whorls, whereas *B. subcampylotoxus* is tuberculated in the bodychamber.

Several specimens from the Neuquén Basin have been described as *Karakaschiceras* by Aguirre-Urreta (1998) and currently assigned to the upper Atherstoni Zone (Aguirre-Urreta et al. 2007). Our specimen comes from a somewhat lower stratigraphic position, in the lower Riveroi Zone of our provisional local zonation.

ORIGIN AND EVOLUTION OF THE NEW GENUS *QUINTUCOCERAS*

The close equivalence (time-correlation) between the Andean Damesi Zone and the Tethyan Boissieri Zone was firmly concluded in Parent et al. (2015, 2017) based on the comparison of ammonite assemblages. In the Damesi Zone of Arroyo del Yeso (Leanza 1945), Pampa Tril (Parent et al. 2015), and Cajón de Almanza (Parent & Garrido 2026) *Subthurmannia boissieri* is well represented in a range of intergrading morphotypes. In Arroyo del Yeso the specimens described by Leanza (1945: pl. 10: 8-10) as *Thurmannites duraznensis* (Gerth, 1921) clearly belong to *S. boissieri*. Gerth (1925) did not designate holotype and we do not know about a lectotype designation, therefore we

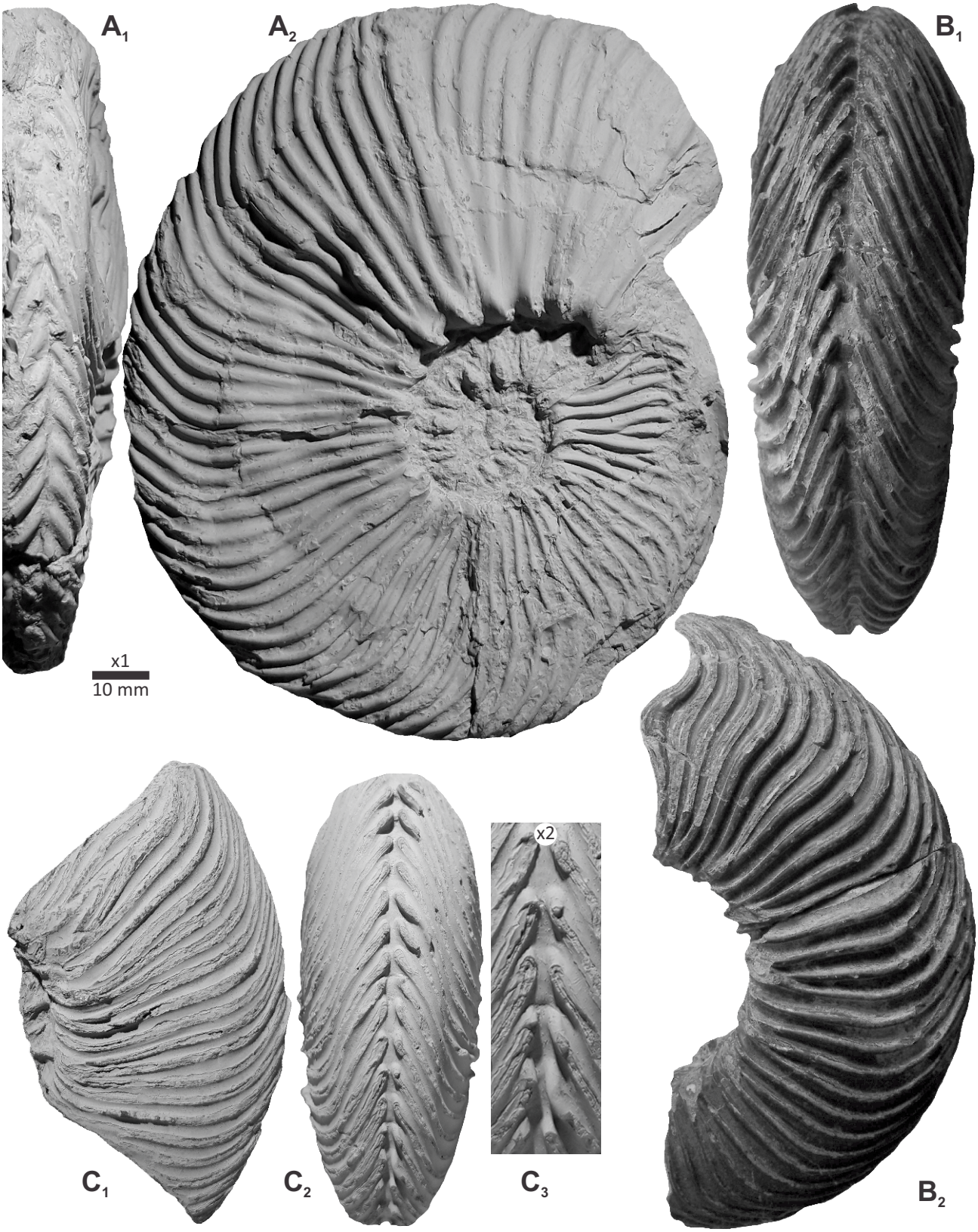

Figure 28. **A**: *Lissonia* aff. *riveroi* (Lisson, 1907), Puerta Quintuco, upper Quintuco Fm, Riveroi Zone. Adult female phragmocone, possibly with beginning of bodychamber (MOZ-PI-11862/2). **B**: *Lissonia riveroi* (Lisson, 1907), Puerta Quintuco, upper Quintuco Fm, Riveroi Zone. Adult male bodychamber with lappet and rostrum (MOZ-PI-6185). **C**: *Lissonia riveroi* (Lisson, 1907), Puerta Quintuco, upper Quintuco Fm, Riveroi Zone. Adult female bodychamber with remains of phragmocone showing strong and distant primary ribs (MOZ-PI-11862/1). Note the ventrolateral ending of the ribs formed by foldings of shell (C_3). – All natural size (x1), except C_3 (x2).

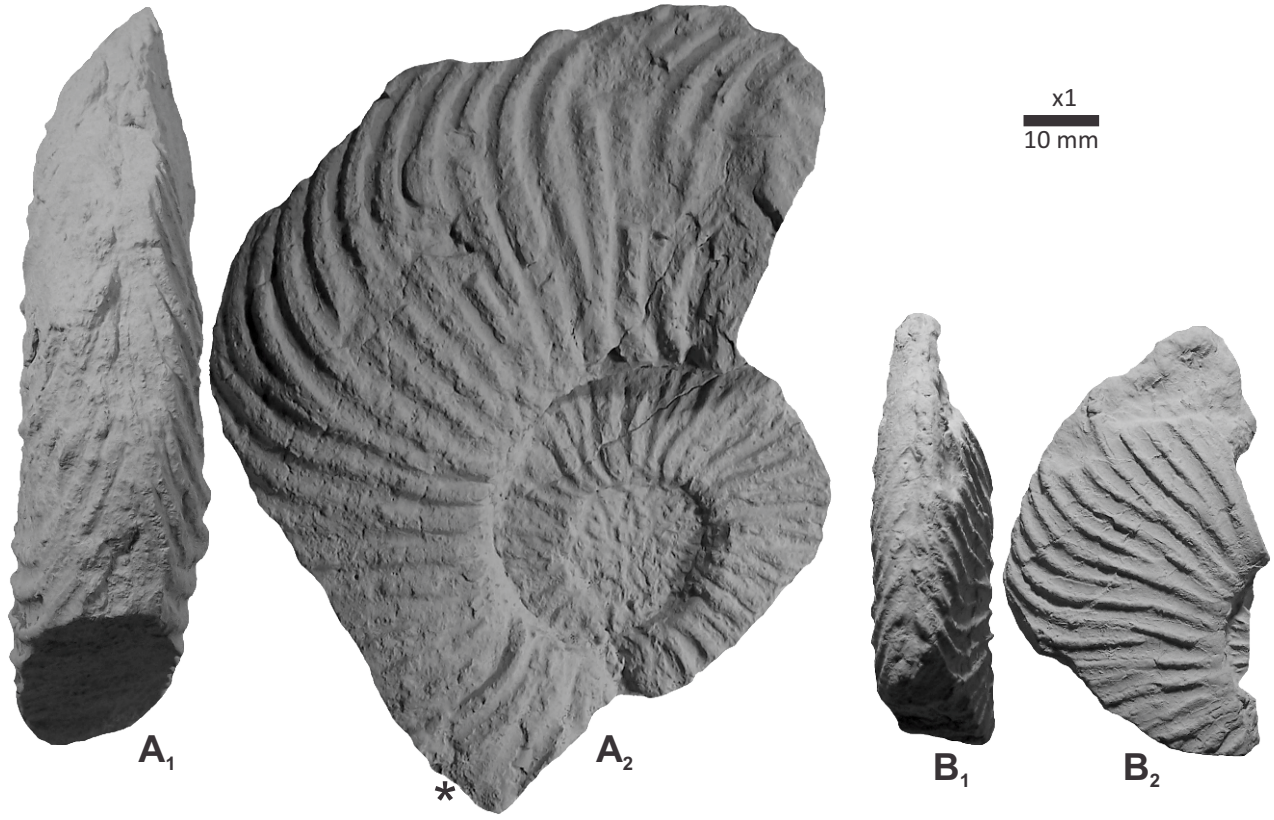

Figure 29. *Lissonia* cf. *riveroi* (Lisson, 1907). Pampa Tril, basal Mulichinco Fm, Riveroi Zone. **A**: adult? female specimen (MOZ-PI-10368/1). **B**: phragmocone (MOZ-PI-10368/6). Note the small ventrolateral tubercles, bases of spines. – The asterisk indicates the last septum. All natural size (x1).

designate lectotype of *Thurmannia duranznensis* the specimen figured by Gerth (1925: pl. 4: 1), refigured herein (Fig. 35). This specimen is very different from the specimens figured by Leanza and does not seem to belong to *Subthurmannia*. Its sculpture composed of fine straight ribs bifurcated only in the middle or upper third of the flank, with some undivided, and all ending in a small bulla besides a narrow smooth ventral band, lacking any sign of swellings or tubercles at the umbilical shoulder.

The mentioned specimens of *S. boissieri* from Arroyo del Yeso are virtually identical to the specimens of Pampa Tril figured in Parent et al. (2017: fig. 8A-D), and occur in the next underlying level of the type horizon of *Quintucoceras wichmanni* n. gen., suggesting, as discussed above, a Pertransiens Zone age for the latter. The morpho-sculptural resemblance between the mentioned specimens of *S. boissieri* and *Quintucoceras wichmanni* n. gen. is very close, they compare well in whorl section and sculpture at similar sizes. However, there are significant differences: *Quintucoceras wichmanni* n. gen. is more involute and the ventral ribs end in a spine besides a smooth ventral band in the phragmocone. This latter structure is present in *S. boissieri*, but only incipiently in the innermost whorls of some specimens (e.g. Parent et al. 2017: fig. $8C_1$), as intraspecific variation. Thus, according to the stratigraphic succession and the close similarity with some intermediate variants, we suggest that *Quintucoceras wichmanni* n. gen. evolved from late Damesi Zone populations of *S. boissieri*. This latter is a Perigondwanian-Tethyan species (see Parent & Garrido 2026 for details), populations of which have settled in the Neuquén Basin at least from the late Noduliferum Zone or earliest Damesi Zone.

In the studied section, above the occurrence of *Quintucoceras wichmanni* n. gen. there is an interval (levels PQ-I-1 to PQ-I-35 in Fig. 4) with a gap in the record of the lineage of *Quintucoceras* n. gen. The next occurrence of a representative is in the level PQ-I-36, in the form of *Quintucoceras pseudowichmanni* n. gen., n. sp. This gap seems to be represented in Pampa Tril by the ammonites from the levels PT-72 to PT-86 (in Parent et al. 2015: figs. 2, 5, 66A-B, and 68A-C), consisting of a series of specimens which can be assigned to the new genus, very close or conespecific with the latter species. These ammonites were described under provisional names (*Thurmanniceras* sp. B and *Pseudoblanfordia* cf. *australis*; see synonymy). To this group also belongs "*Thurmanniceras*" sp. a in Aguirre-Urreta & Rawson (1999: fig. 3I-J). On the other hand, the specimens described as *Lissonia* cf. *riveroi* in Parent et al. (2015: fig. 69A-F) are reassigned with confidence to *Quintococeras denticulatum* n. gen., n. sp. and *Quintucoceras macrospinatum* n. gen., n. sp. (see synonymy and discussion above). The first representatives of *Lissonia* in Puerta Quintuco occur somewhat higher (*Lissonia* n. sp. aff. *riveroi* in level PQ-I-55), but are not

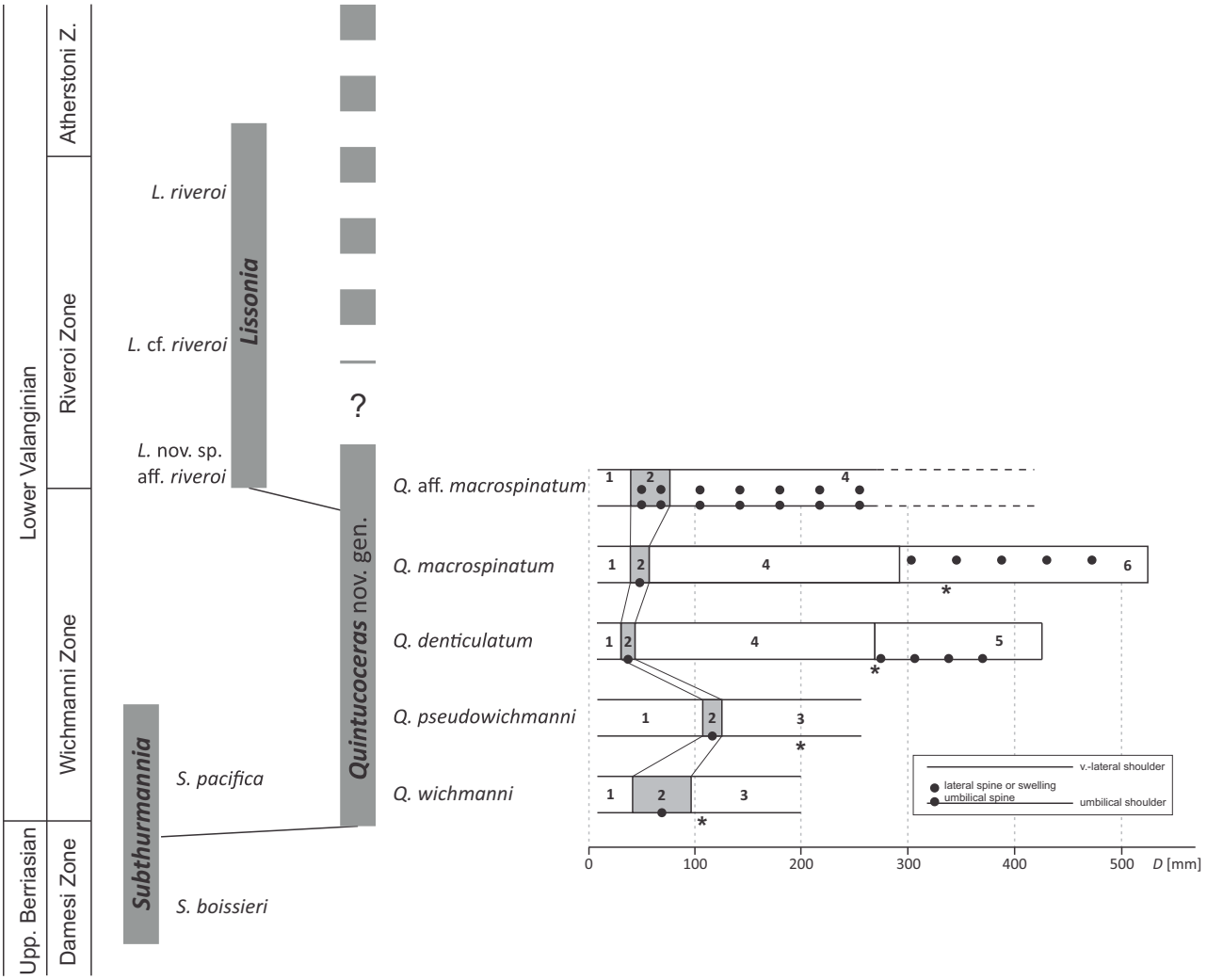

Figure 30. Phylogenetic model for the origin and evolution of *Quintucoceras* n. gen. and *Lissonia* as discussed in text. The evolution of the ontogeny of the females of the species of *Quintucoceras* n. gen. is summarized at right. The sculpture stages are as follows: (1) fine, flexuous ribs; (2) *Neocomites*-like: multiple flexuous ribs from an umbilical spine, divided in the flank, ending in a small ventrolateral spine (present in the the phragmocone of the five species with different positions and durations); (3) dense fine ribbing of mostly undivided primary ribs crossing the venter; (4) strong-wiry, closely spaced, prosocline, mostly bifurcated ribs ending in a ventrolateral spine; (5) gross lateral ribs from an umbilical spine ending in a ventrolateral spine; (6) lateral ribs from the umbilical shoulder with a long lateral or upper flank spine. Occurrence of spines other than the ventrolateral ones is indicated with black dots. The asterisk indicates the mean diameter of beginning of the adult bodychamber. Below 10-20 mm in diameter, and for adult bodychamber in some cases, there are no enough data for characterization.

(yet?) recorded in Pampa Tril. This succession was envisaged in Parent et al. (2015: 67), and seems definitely supported by the new material described here.

The evolution of the lineage *Quintucoceras* n. gen. is represented in the phylogenetic model of Fig. 30. The most remarkable morpho-sculptural trends observed in the succession of species are:

(1) the contraction of the *Neocomites*-like ontogenetic stage (i.e., umbilical spines with bundles of ribs and wide smooth ventral band with ventrolateral spines) which is well developed by *Quintucoceras wichmanni* n. gen. at the origin of the lineage, but later only incipiently and gradually modified (Fig. 30),

(2) the gradual coarsening of the ribbing associated with a decrease of its density in the phragmocone (Fig. 7C-D),

(3) the increase of involution of the phragmocone (Fig. 7A),

(4) the increase of the adult female size (Fig. 7F), and

(5) the change in the sculpture of the adult female bodychamber, from densely ribbed to very coarsely ribbed with long spines.

BIOSTRATIGRAPHY AND TIME-CORRELATION

The chronostratigraphic framing of the studied section is based on the biostratigraphic analysis of the succession of species detailed in Fig. 4. We adopt the ammonite zonal

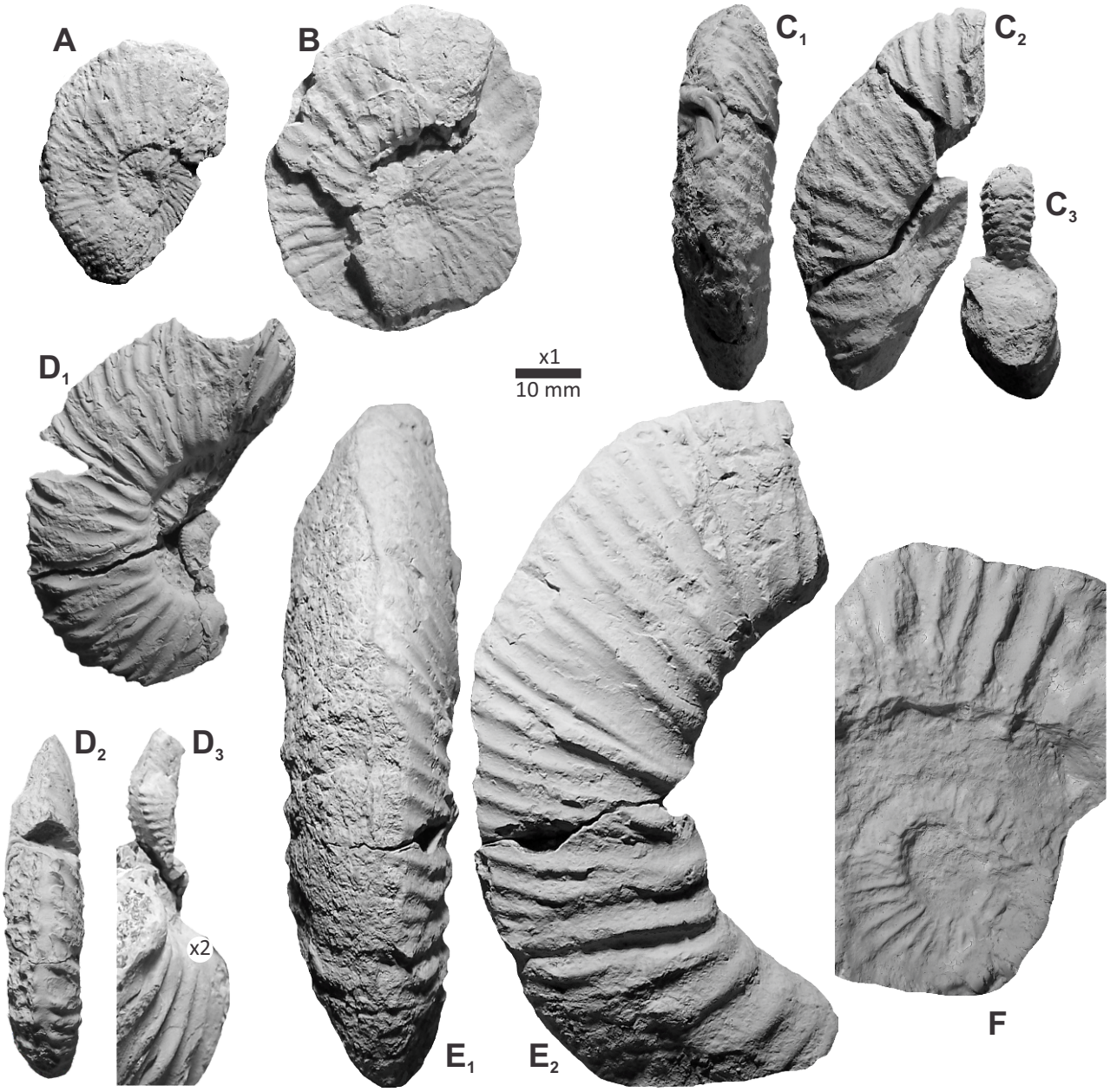

Figure 31. *Subthurmannia pacifica* n. sp., Puerta Quintuco, Wichmanni Zone. **A**: phragmocone (MOZ-PI-11703/1), level PQ-I-27. **B**: phragmocone (MOZ-PI-11703/2), level PQ-I-27. **C**: phragmocone (MOZ-PI-11555/7), level PQ-I-32. **D**: phragmocone (MOZ-PI-11555/6), level PQ-I-32. **E**: fragmentary adult phragmocone (MOZ-PI-11555/3), level PQ-I-32. **F**: plaster cast of the inner whorls of the holotype (MOZ-PI-11544) in Fig. 32, level PQ-I-32. – All natural size (x1), except D_3 (x2).

chronostratigraphic subdivision for the Andean lower Valanginian proposed by Leanza (1945) and expanded by Aguirre-Urreta & Rawson (1999) with the introduction of the Riveroi Zone. This zonation consists of a subdivision in three units: Wichmanni Zone, Riveroi Zone, and the lower part of the Atherstoni Zone.

Our observations included the exposed upppermost part of the thick Vaca Muerta Fm and the whole Quintuco Fm. up to the base of the Mulichinco Fm (Figs. 2-3). In the topmost 15 m of the Vaca Muerta Fm occurs *Quintucoceras wichmanni* n. gen. Below this level, from about 300 m of shales, we have collected loose specimens of the following species:

"*Thurmanniceras*? cf. *neogaeus*" (Leanza, 1945) – The holotype is only know by its lateral view, without information about the presence of bodychamber or the aspect of the ventral area and the inner whorls, and there have not been new collections in the type locality. Under these conditions we use the name in pure morphologic sense: a platyconic ammonite with slightly flexous ribs divided in the mid-flank, each one ending in a ventrolateral swelling; our specimen shows the venter tabulate and smooth.

Spiticeras damesi (Steuer, 1897) – Two incomplete phragmocones of the type morphotype of the species, that is

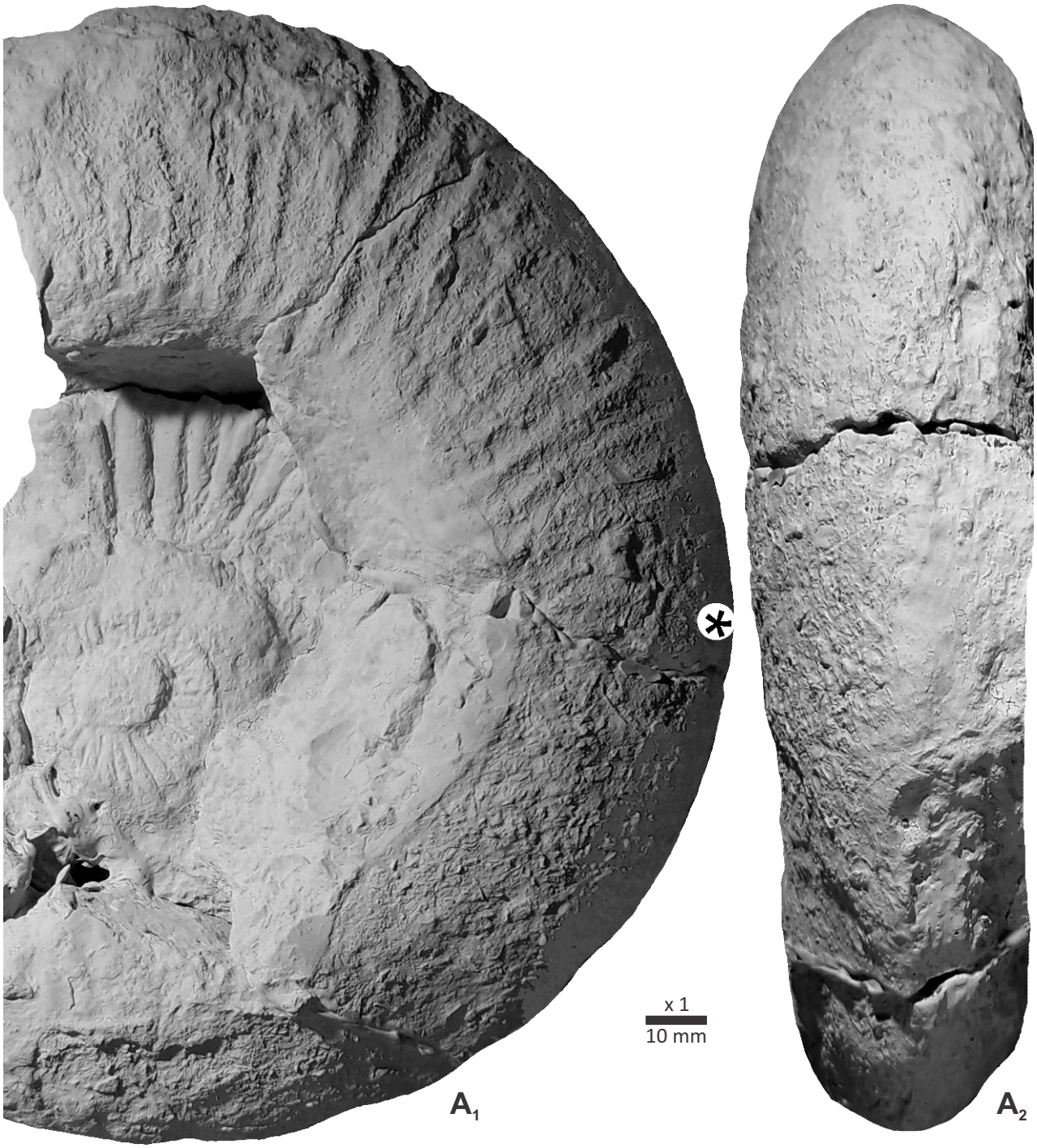

Figure 32. *Subthurmannia pacifica* n. sp., Puerta Quintuco, level PQ-I-32, Wichmanni Zone. Holotype (MOZ-PI-11544), almost complete adult female. Plaster cast of inner whorls in Fig. 31F. – The asterisk indicates the last septum. Natural size (x1).

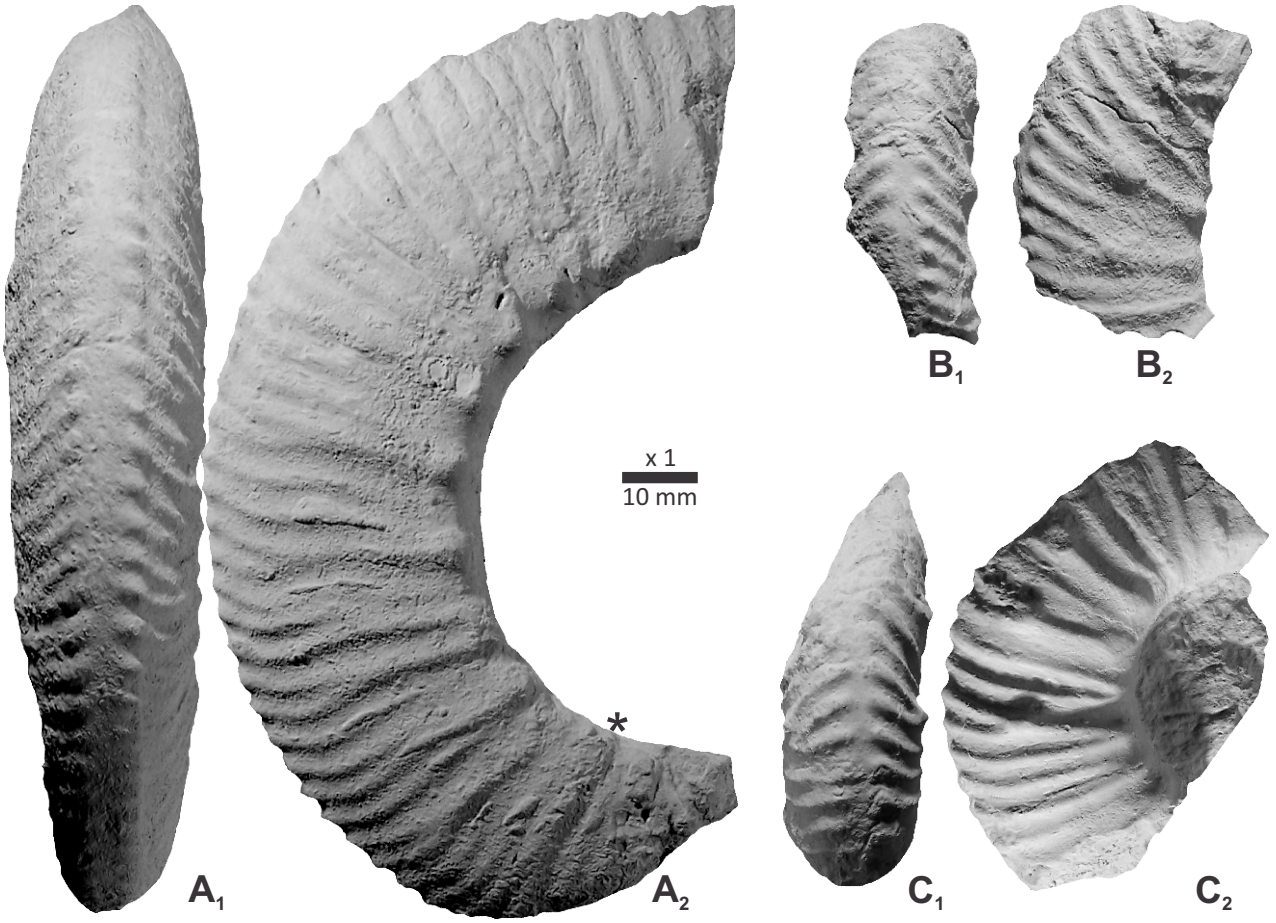

Figure 33. *Sarasinella* cf. *varians* Uhlig, 1910, Puerta Quintuco, level PQ-I-32, Wichmanni Zone. **A**: incomplete bodychamber (MOZ-PI-11541). **B**: fragmentary phragmocone (MOZ-PI-11555/4). **C**: fragmentary phragmocone (MOZ-PI-11555/5). – The asterisk indicates the last septum. Natural size (x1).

perfectly matching the holotype (see Parent 2022: fig. 28H) at comparable diameter. The holotype comes from an unknown horizon of the Berriasian of Arroyo Alberjillo (Steuer 1897: 98). However, the stratigraphic position in the upper Berriasian seems to be well established by Leanza (1945: 89) who described several specimens, closely comparable with the holotype, from the level m (Damesi Zone) of the section of Arroyo del Yeso.

Cuyaniceras cf. *transgrediens* (Steuer, 1897) – Several incomplete phragmocones, one very similar to the specimen figured by Leanza (1945: pl. 12: 4) as *Cuyaniceras argentinum* Leanza, 1945.

These ammonites, except "*T.*? cf. *neogaeus*", are typical of the Andean upper Berriasian Damesi Zone. The same association was described by Leanza (1945) from Mallín Redondo, including also *Spiticeras andium* Leanza, 1945 and *Spiticeras mammatum* Leanza, 1945, and dated as Damesi Zone. "*T.*? cf. *neogaeus*" is almost indistinguishable from the specimen of *Thurmaniceras thurmanni* (Pictet & Campiche, 1860) figured by Sayn (1907: pl. 5: 1 and 14) from the lowermost Valanginian. Thus, it is possible that the Damesi Zone ranges into the early Pertransiens Zone, but more complete assemblages are necessary to establish a more confident time-correltion between the Andean and Tethyan zonations.

The occurrence of *Quintucoceras wichmanni* n. gen. in the top levels of the Vaca Muerta Fm indicates it most likely belongs to the Wichmanni Zone. The first occurrence of *Lissonia* (possibly including *L. riveroi*) is recorded in the level PQ-I-55, thus it could be assigned provisionally as the local base of the the Riveroi Zone.

The base of the Riveroi Zone was stated by Aguirre-Urreta & Rawson (1999) by the first appearance of *L. riveroi*. However, the first and last occurrences of any species are, for any sampling season at any place and in every section, of different ages, determined by a mix of biological, taphonomical, and sampling factors. Thus, they mark nothing but a contingent record with few chronostratigraphic value for fine time-correlation, because of their intrinsic instability. The biostratigraphic unit biohorizon (sensu Gabilly 1971, Callomon 1985, Page 1995, Parent 2022) could be advantageously used, not only for defining the base of the zones but also for fine time-correlation. The biohorizon, a biostratigraphic (observable)

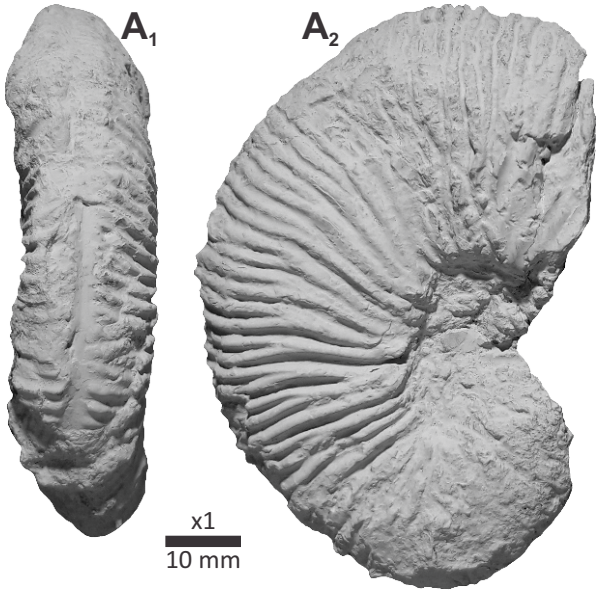

Figure 34. *Karakaschiceras*? sp. A, Puerta Quintuco, level PQ-I-55, Riveroi Zone. Phragmocone (MOZ-PI-12261/2). – Natural size (x1).

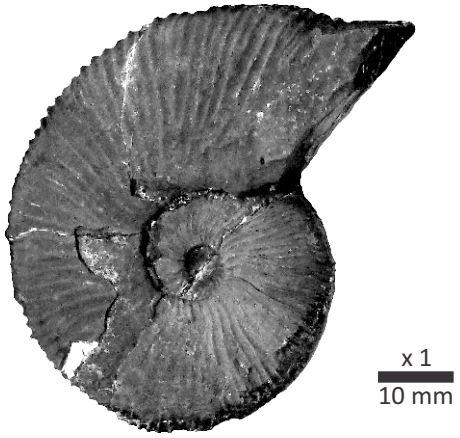

Figure 35. Lectotype (here designated, see text) of *Thurmannia duraznensis* Gerth (1925: pl. 4: 1). Photographic refiguration of the specimen Gerth-21-P1080317. Arroyo Durazno (Mendoza Province), Upper Tithonian. – Natural size (x1).

unit, is the closest possible approximation to a time-plane that can be obtained from the stratigraphic record, thus it is the material link between biostratigraphic observation and chronostratigraphic classification and datation. It can be said that the biohorizon is a perfect representation of the time-rock duality.

Although our material includes a succession with many complete adult specimens we have refrained for defining biohorizons waiting for new records of *Quintucoceras* n. gen. in other localities, associated with ammonites of other genera.

According to the results and discussion above, we have worked out a time-correlation chart (Fig. 36) between our section and those two which have provided the best data for comparison: Pampa Tril (Parent et al. 2015, 2017), and Cerrito de la Ventana (Aguirre-Urreta & Rawson 1999).

In the lower part of the studied section (levels PQ-I-14-32) occur other species new for the basin: *Kilianella*? sp. A, *Subthurmannia pacifica* n. sp., and *Sarasinella* cf. *varians*. This assemblage is assigned to the Wichmanni Zone according to the classification adopted.

CONCLUSION

We have described a new fauna of early Valanginian ammonoids from material collected from recently discovered outcrops east of the Cerro Quintuco, in the locality known as Puerta Quintuco. The fauna includes a succession of ammonites which conform to a lineage which is herein described as the new genus *Quintucoceras*. Five species are included in this new genus: the older, *Quintucoceras wichmanni* n. gen. (most likely derived from Andean populations of *Subthurmannia boissieri*); *Quintucoceras pseudowichmanni* n. gen., n. sp.; *Quintucoceras denticulatum* n. gen., n. sp.; *Quintucoceras macrospinatum* n. gen., n. sp. (the type species), and *Quintucoceras* aff. *macrospinatum* n. gen., n. sp. The lineage evolves throughout the Wichmanni Zone and, at least, the base of the Riveroi Zone (early Valanginian), but could have extension into to the Atherstoni Zone.

This phylogeny was already envisaged from the succession of Pampa Tril (Parent et al. 2015: 67). The early members of the lineage have been described in the literature as Thurmanniceras or *Neocomites*. The morpho-sculptural similarities between these genera are in some cases notable. However, the present study based on complete and almost complete adult females has shown that the resemblance is confined to short parts of the ontogeny.

The specimens described as *Lissonia* n. sp. aff. *riveroi* are considered the origin of the genus *Lissonia*, branched from *Quintucoceras* n. gen. The occurrence of this species is taken as the provisional marker of the base of the non-standard Riveroi Zone. In these levels also occurs a specimen of *Karakaschiceras*? sp. A.

In the lower part of the studied section, assigned to the Wichmanni Zone, occurs a distinct assemblage with three species: *Kilianella*? sp. A, *Subthurmannia pacifica* n. sp., and *Sarasinella* cf. *varians*.

Acknowledgements. For discussion, information and literature: Miguel Company (Universidad de Granada, Granada), Héctor A. Leanza (Museo Argentino de Ciencias Naturales, Buenos Aires), Peter F. Rawson (University of Hull, England), Stéphane Reboulet (Université Lyon, Villeurbanne), Zdeněk Vašíček (Czech Academy of Sciences, Ostrava-Poruba), Armin Scherzinger (Immendingen-Hattingen), Günter Schweigert (Staatliches Museum für Naturkunde, Stuttgart). Mary Sears (Museum of Comparative Zoology Harvard University, Harvard) and Ann H. Crawford (Boulder) for their help with literature. For photographs of original specimens at their care: Ron Eng and Liz Nesbitt (Burke Museum of Natural History, Seattle), and Georg Heumann (Bonner Institut für Organismische Biologie, Bonn). For important help in the field: Dania Pascua (Servicio Geológico, Dirección Provincial de Minería de la Provincia del Neuquén, Zapala) and Segio Cocca (Zapala). Belén Boilini (Museo Provincial de Ciencias Naturales "Prof. Dr. Juan A. Olsacher, Zapala) for her continuous efforts and guidance in the collections of the

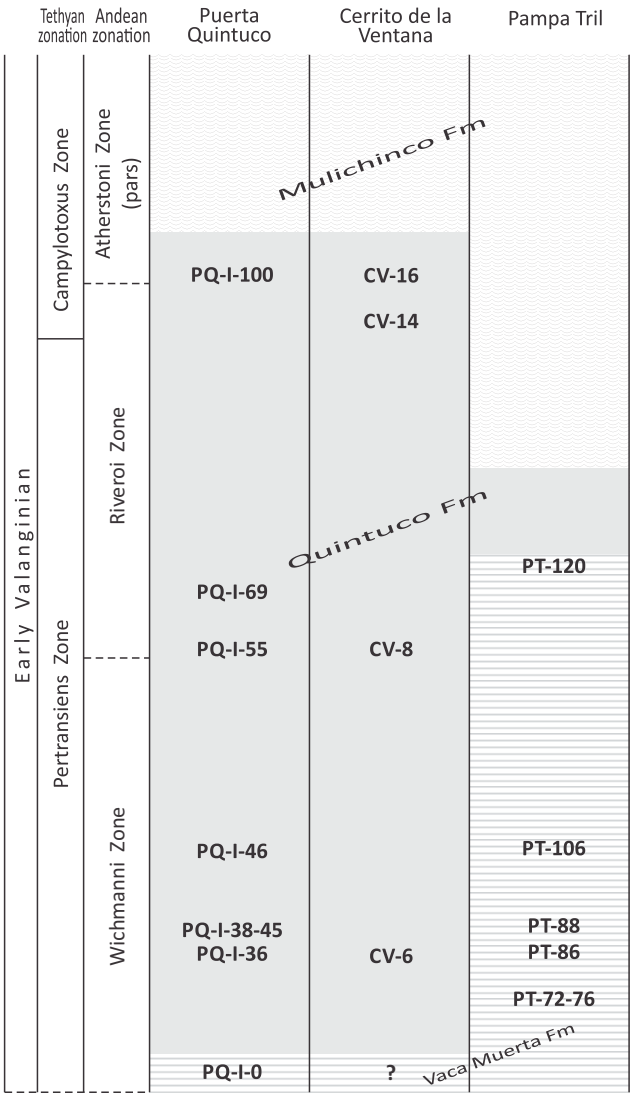

Figure 36. Time-correlation chart between the studied section (PQ), Pampa Tril (PT), and Cerrito de la Ventana (CV), based on levels of reference mostly with comparable ammonites as discussed in text. Data: Pampa Tril from Parent et al. (2015), Cerrito de la Ventana from Aguirre-Urreta & Rawson (1999). Andean zonation (based on Leanza 1945 and Aguirre-Urreta & Rawson 1999) tentatively time-correlated with the Tethyan zonation from Reboulet et al. (2011). Broken lines at the base of non-standard zones.

MOZ. Jeronimo Andrés Ferrari (Museo Provincial de Ciencias Naturales "Prof. Dr. Juan A. Olsacher, Zapala) prepared special complementary photographs and 3D visualizations. Rosa Torres and Beatriz Rivas (Museo Provincial de Ciencias Naturales "Prof. Dr. Juan A. Olsacher, Zapala) for preparation of plaster casts. The Dirección Provincial de Minería de la Provincia del Neuquén for enabling the development of fieldwork. The very careful refereeing by the reviewers of the journal Vasily Mitta (Russian Academy of Sciences, Moscow) and Miguel Company (Universidad de Granada, Granada), has significantly improved the manuscript. The editor Andrés Greco helped us very much in different ways for the preparation of the final manuscript.

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Boletín del Instituto de Fisiografía y Geología
ISSN 1666-115X

Volumen 94, 2026

Rosario - 2026

Impreso en Argentina