

Revision of the aspidoceratids (Ammonitida) of the Internispinosum Zone (Tithonian) of Barda Negra, Vaca Muerta Formation, Argentina

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Abstract. In this paper we revise the aspidoceratid ammonites of the Internispinosum Zone assemblage of the section of Barda Negra in the Picún Leufú Subbasin (Vaca Muerta Formation). The assemblage, which indicates the Fascipartita Subzone, includes the following aspidoceratids: *Hypowaagenia* sp. A, *Aspidoceras quinchaoi* (Zeiss & Leanza), and *Toulisphinctes* cf. *rafaeli* (Oppel); the other ammonites are *Windhausenicerias internispinosum* (Krantz) transient beta and *Zapalia fascipartita* Leanza & Zeiss. The ammonites now assigned to *A. quinchaoi* were formerly described as *Aspidoceras* cf. *euomphalum* Steuer. The composition of the ammonite assemblage shows aspidoceratids dominating in number (71% of the individuals of the sample) and diversity (three genera out of five). The environmental conditions modelled for the area appear as favorable for abundance of aspidoceratids, although do not explain for now the dominance of them in the assemblage which is a unique record in the Neuquén Basin.

Key words. Tithonian, Neuquén Basin, Aspidoceratoidea, *Hypowaagenia*, *Aspidoceras*, *Toulisphinctes*.

Resumen. *Revisión de los aspidocerátidos (Ammonitida) de la Zona Internispinosum (Tithoniano) de Barda Negra, Formación Vaca Muerta, Argentina.* En este trabajo presentamos los resultados de la revisión de los amonites aspidocerátidos de la asociación de la Zona Internispinosum de la sección de Barda Negra en la Subcuenca Picún Leufú. Esta asociación, que indica la Subzona Fascipartita, incluye los siguientes aspidocerátidos: *Hypowaagenia* sp. A, *Aspidoceras quinchaoi* (Zeiss & Leanza), and *Toulisphinctes* cf. *rafaeli* (Oppel); los amonites complementarios de la asociación son *Windhausenicerias internispinosum* (Krantz) transient beta y *Zapalia fascipartita* Leanza & Zeiss. Los amonites ahora asignados a *A. quinchaoi* fueron anteriormente descritos como *Aspidoceras* cf. *euomphalum* Steuer. La composición del conjunto de amonites está dominada por aspidocerátidos en número de individuos (71% de los que componen la muestra) y en diversidad (tres de los cinco géneros). Las condiciones ambientales modeladas para el área de estudio se muestran favorables para la abundancia de aspidocerátidos, sin embargo no explican su dominancia local, lo cual es un registro único para la Cuenca Neuquina.

Palabras clave. Tithoniano, Cuenca Neuquén, Aspidoceratoidea, *Hypowaagenia*, *Aspidoceras*, *Toulisphinctes*.

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INTRODUCTION

Tithonian aspidoceratids are not very abundant in the Neuquén (or Neuquén-Mendoza) Basin, but rather diverse at the genus-level. Five genera have been recorded (Steuer 1897, 1921, Haupt 1907, Behrendsen 1891-1892, Leanza 1945, Leanza 1980, Parent et al. 2007, 2011, 2013, 2015, 2022, and references therein): *Aspidoceras* Zittel, 1868, *Physodoceras* Hyatt, 1900 (including the microconchs as *Sutneria* Zittel, 1884), *Pseudhimalayites* Spath, 1925 (including the microconchs as *Simocosmoceras* Spath, 1925), *Toulisphinctes* Sapunov 1979, and *Hypowaagenia* Schweigert & Schlampp, 2020. Commonly, in a single level a genus is represented by a single species.

Barda Negra is the geographic name generally used to refer to a rather flat, wide area located west of the large basaltic Meseta Barda Negra, about 20 km south of the

Zapala City, in the southern part of the Neuquén (or Neuquén-Mendoza) Basin (Fig. 1). This area belongs to the Geological Sheet 36c (Cerro Lotena, Neuquén Province), which was described by Suero (1951). Almost the whole area is covered by Recent sands and other modern materials, so that outcrops of Upper Jurassic (Vaca Muerta Formation) and Lower Cretaceous marine rocks are rather small and scattered. A short section of the Los Catutos Member of the Vaca Muerta Fm was exposed in a small excavation. This section corresponds to the Internispinosum Zone, and was described along with its ammonites by Parent et al. (2007); all the ammonites come from the level BN-3. The lithology there is similar to the equivalent horizons in Cerro Lotena (see Leanza 1980, Parent & Garrido 2021) but with a higher content of fine sand. The fauna includes bivalves, gastropods and ammonites. The ammonites are generally well-preserved, some microconchs preserve the adult

peristome with the lappets, and few associated aptychi occur.

This ammonite assemblage of the level BN-3 of Barda Negra is largely dominated by aspidoceratids, what is recorded for first time in this basin and, furthermore, they belong to three genera. The high diversity of aspidoceratids is only comparable with records from the nearby locality Cerro Lotena and from Arroyo Cieneguita (see discussion below). This fact and the progress in the knowledge about aspidoceratids of the last years motivated the revision of this assemblage. New specimens and further preparation of those already described in Parent et al. (2007) have shown that the former classification requires revision. On the other hand, the recent study of the ammonite assemblages of the close localities Cerro Lotena and Cerro Granito (Parent & Garrido 2021) allows to refine the dating of the studied level BN-3.

The aim of this paper is to present the results of the revision of the aspidoceratids and the age of the whole faunal association of the level BN-3 of the section of Barda Negra. We take the opportunity to list the taxa of the ancillary molluscan assemblage of this level.

COMPOSITION AND AGE OF THE AMMONITE ASSEMBLAGE

The stratigraphy of the area and the section were already described in Parent et al. (2007). The only ammonites known in the locality were collected from level BN-3 (Fig. 1). This fauna is composed of *Windhausenicerias internispinosum* (Krantz, 1926), *Zapalia fascipartita* Leanza & Zeiss, 1990 (fragmentary large macroconchs), and an assemblage of aspidoceratids, which were in our former paper collectively assigned to *Aspidoceras* cf. *euomphalum* Steuer, 1897.

However, after additional preparation and addition of some few new specimens this assemblage of aspidoceratids has shown to be composed of four morphotypes assigned to three species:

- (1) a rather compressed aspidoceratid with wide primary ribs that fade in the venter, assigned to *Hypowaagenia* sp. A (Fig. 2A-C),
- (2) several specimens bituberculate from the inner whorls up to the body-chamber, which bears wide ribs, assigned to *Aspidoceras quinchaoi* Zeiss & Leanza, 2010 (Figs. 3-5),
- (3) a morphotype in which the lateral tubercles become less numerous from the end of the adult phragmocone, assigned to a variant morphotype of *A. quinchaoi* (Figs. 6), and
- (4) a large involute specimen, with two rows of spines and strong ribs born in the tubercles and irregularly bifurcated, assigned to *Toulisphinctes* cf. *rafaeli* (Oppel, 1863) (Fig. 7).

The age of the level BN-3 was supposed to be early Internispinosum Zone (Parent et al. 2007). However, the recent revision of the himalayitids of Cerro Lotena and Cerro Granito (Parent & Garrido 2021) indicates that the morphotype of *W. internispinosum* present in the studied assemblage (Fig. 8) belongs to the transient beta of this species, typical of the lower part of the Fascipartita Subzone (Internispinosum Zone). *Z. fascipartita* is one of the guide species of this subzone; thus, the new fragmentary

specimens from the level BN-3 make an assemblage typifying the subzone.

In conclusion, the level BN-3 can be assigned to the Fascipartita Subzone of the Internispinosum Zone, uppermost Lower Tithonian (referring to a bipartite subdivision of this stage), as indicated by the association of *W. internispinosum* transient beta and *Z. fascipartita* (Fig. 9).

THE ANCILLARY MOLLUSCAN FAUNA OF THE LEVEL BN-3

Several other molluscs occur in association with the ammonites, and serpulids are abundant mostly adhered to the bivalves and less commonly to the ammonites (Fig. 2C₂). It is worth to report the list of this ancillary fauna because the well-dated horizon provides an accurate stratigraphic position of species which are much cited in the literature, but referred only vaguely to the Tithonian.

- "*Lucina*" cf. *lotenoensis* Weaver, 1931 (1 specimen)
- "*Cucullaea*" cf. *lotenoensis* Weaver, 1931 (1 specimen)
- *Eriphyla lotenoensis* Weaver, 1931 (5 specimens)
- *Damborenella eximia* (Philippi, 1899) (2 juvenile specimens)
- *Tornatellaea mendozana* Gründel, Parent, Cocca & Cocca, 2007 (type material). *T. mendozana* is distinguished from the similar form "*Actaeon*" *andinus* Haupt (1907: pl. 10: 4) by the spiral furrows that become adapically closer in the latter, whereas in the former they are evenly spaced and abruptly crowded in the base (J. Gründel, pers. comm. 05/03/2023).

SYSTEMATIC PALAEONTOLOGY

Conventions and notation. The studied material is housed in the Museo Provincial de Ciencias Naturales "Prof. Dr. Juan A. Olsacher" (MOZ-PI), Zapala. Body-chamber is abbreviated as Bc and phragmocone Ph; macroconch (female shell): [M], microconch (male shell): [m]. Measurements: diameter (*D*), diameter at last septum (*D_{ls}*), diameter at peristome (*D_p*), all given in millimetres (mm). Umbilical wide (*U*), wide of whorl section (*W*), height of whorl section (*H₁*), and ventral or apertural height of whorl section (*H₂*) as dimensionless indexes as ratio to *D*. Length of body-chamber (*L_{bc}*) in degrees [°]. Number of primary (*P*) and ventral (*V*) ribs, and lateral (*T_l*) and umbilical (*T_u*) tubercles, all per half whorl.

All specimens come from the level BN-3 of the section in Fig. 1, described in Parent et al. (2007).

Terminology for sexual dimorphism. Besides the categories macroconch and microconch there is mesoconch. Mesoconch is a term introduced by Chandler (2019), depicting female specimens that became adult in a relatively early ontogenetic stage and thus remained smaller than normal macroconchs. This phenomenon was noticed in aspidoceratids (Parent et al. 2008, Scherzinger et al. 2018) and stephanoceratids (Chandler 2019), but seems wider spread also in other ammonite families. It is especially evident in aspidoceratids (see Parent et al. 2020).

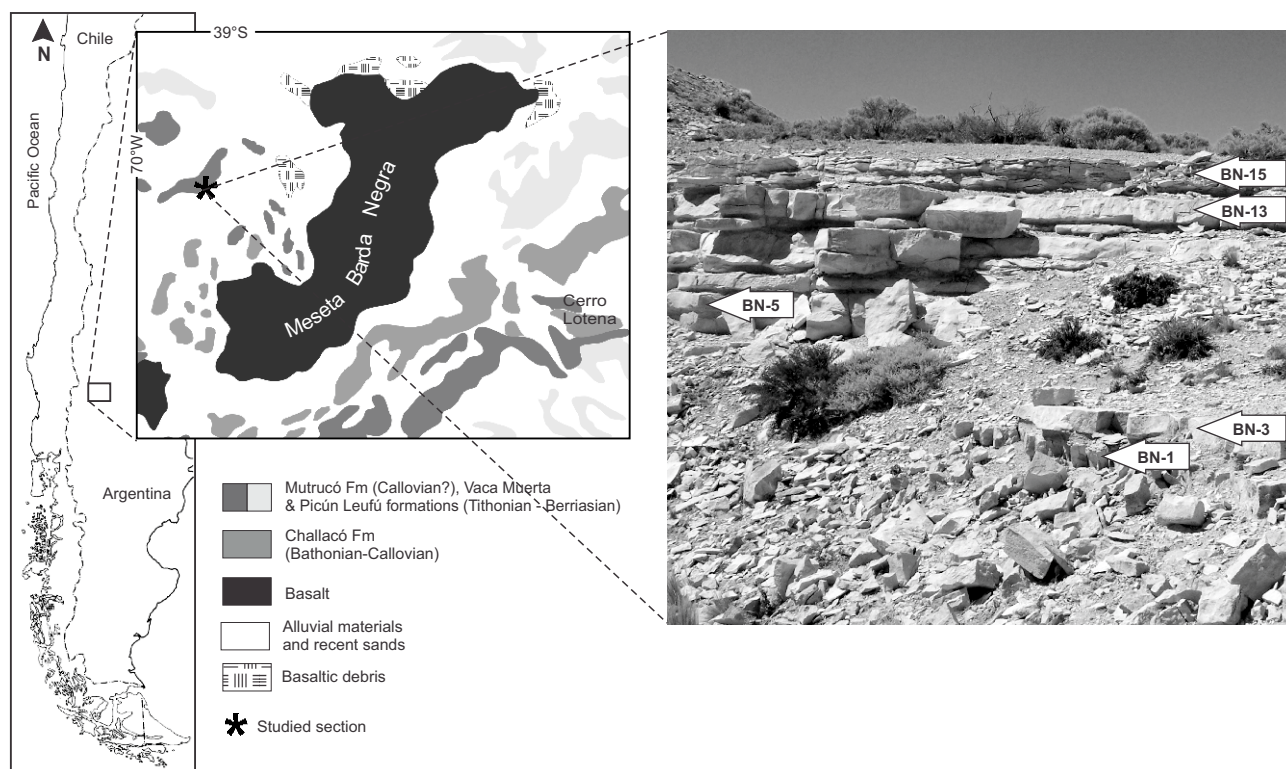


Figure 1. Geologic map of the Barda Negra area and the section where the studied ammonites were collected (modified from Parent et al. 2007).

Order Ammonitida Haeckel, 1866
Suborder Ammonitina Fischer, 1882
Superfamily Aspidoceratoidea Zittel, 1895 emend.
Parent, Schweigert & Scherzinger, 2020
Family Aspidoceratidae Zittel, 1895
Subfamily Hybonoticeratinae Olóriz, 1978

Genus *Hypowaagenia* Schweigert & Schlamp, 2020

Type species. *Hypowaagenia endressi* Schweigert & Schlamp, 2020 (by original designation).

***Hypowaagenia* sp. A**
 Fig. 2A-C

Material. Three incomplete or fragmentary specimens (MOZ-PI-7568/2-4).

Description. The two most complete specimens have maximum $D = 80$ and about 125 mm; moderately inflated ($W/D = 0.4$) and involute ($U/D = 0.3$), with suboval whorl section ($W/H_1 = 1.1$ to 0.9 in the body-chamber).

The phragmocone sculpture consists of wide undivided primary ribs born in the upper umbilical wall. These ribs are somewhat swollen in the lower flank and slightly bent forward towards the venter, where they are blunter and wider. The swellings of the ribs near the umbilical shoulder seem to be the bases of spines.

In the body-chamber the ribs are similar but more closely spaced and not swollen in the lowermost flank, although rare hollow, unfloored ventromarginal spines

occur. These ribs are also well-marked in the internal mould. The test of the body-chamber is relatively thin.

Remarks. This peculiar ammonite combines aspidoceratid features like a stout shell-shape, gross ribs, and typical septal suture line. Among Tithonian aspidoceratids, the sporadic ventrolateral tubercles and dense ribbing from the umbilical shoulder points clearly to the genus *Hypowaagenia*.

Hypowaagenia? bodenbenderi (Behrendsen, 1892) from the Alternans Zone (Parent et al. 2022) differs by the more evolute coiling and rounded whorl section. Our scarce material and the unique specimen known of *H.? bodenbenderi* do not allow for a significant comparison because the intraspecific variability which could eventually relate them cannot be assessed.

The species more similar to *Hypowaagenia* sp. A seems to be *Aspidoceras acanthomphalum* Zittel, 1870 here assigned to *Hypowaagenia*. Zittel (1870: 81) established this species including three syntypes, two from Monte Catria (Apennines of Italy) and a third one from the Klippenkalk of Czorstyn (or Czorsztyn) in Poland. Since no holotype was designated by Zittel (1870), we take the opportunity to designate the specimen illustrated in fig. 4a of his plate 5(29), from beds of originally supposed Tithonian age of the Monte Catria ammonite assemblage as the lectotype of *Aspidoceras acanthomphalum* Zittel, 1870. This lectotype is housed in the Museo di Storia Naturale dell'Università di Pisa and is here refigured in Fig. 2D. Zittel's illustration was obviously based on a plaster cast of this specimen and is still housed in the collection of the

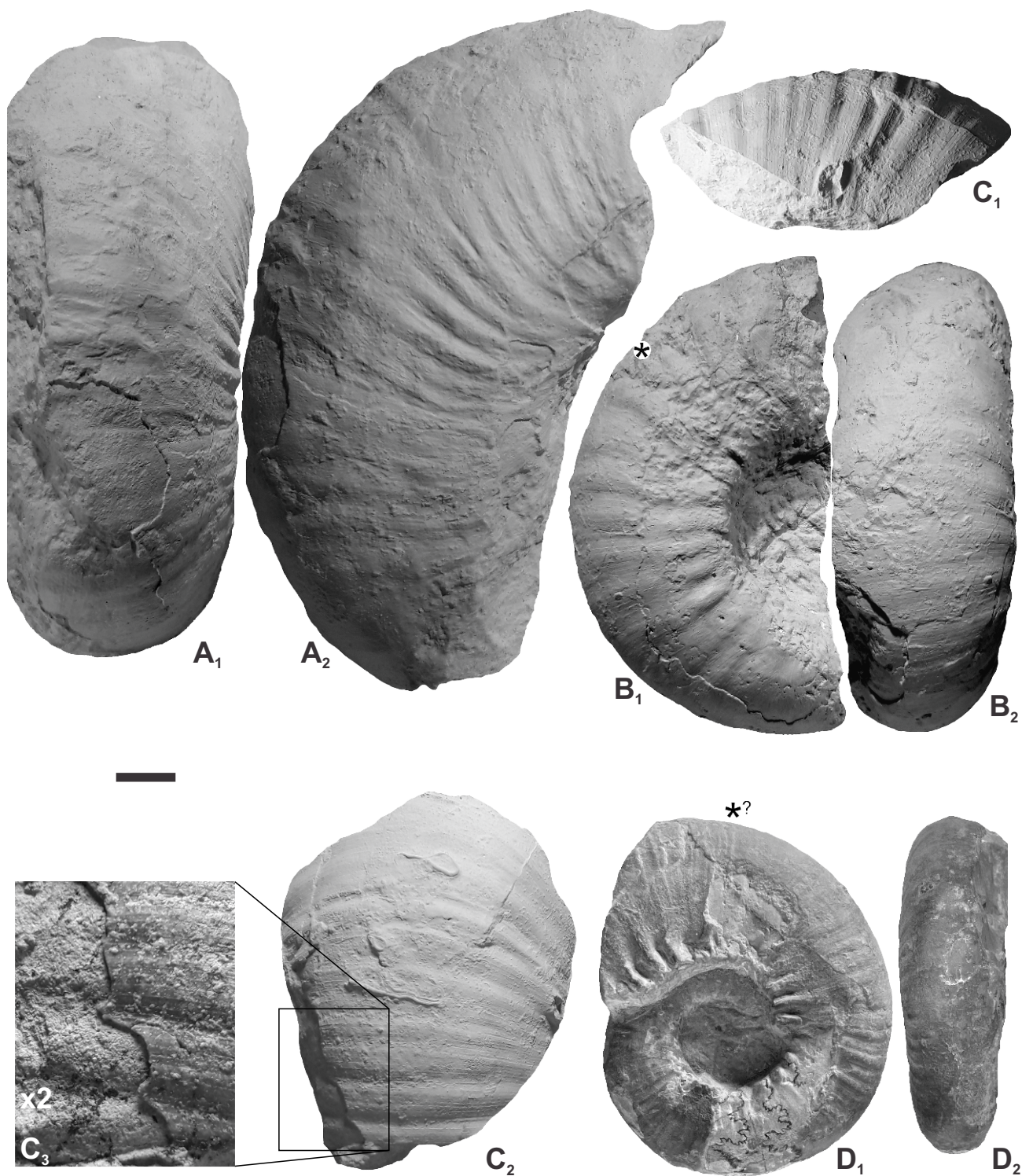


Figure 2. A-C: *Hypowaagenia* sp. A, Barda Negra, level BN-3, Fascipartita Subzone, Internispinosum Zone. A: Adult macroconch body-chamber (MOZ-PI-7568/2). B: Macroconch phragmocone with the beginning of the body-chamber (MOZ-PI-7568/4). C: Portion of macroconch body-chamber (MOZ-PI-7568/3); C₁: lateral view showing a ventrolateral spine; C₂: ventral view; C₃: enlarged view (x2) showing the thin shell with well-marked and -spaced growth lines and the aspect of the internal mould exactly replicating the wide ribs. D: Lectotype (here designated) of *Aspidoceras acanthomphalum* figured by Zittel (1870: pl. 5[29]: 4a), currently in the collections of the Museo di Storia Naturale dell'Università di Pisa (collection number: I-17768). Photographs by courtesy of Chiara Sorbini. – All natural size (x1) except C₃ (x2). The bar indicates 10 mm except for C₃. The asterisks indicate the beginning of the body-chamber.

Bayerische Staatssammlung für Paläontologie und Geologie in Munich, Germany. *H. acanthomphala* from the Beckeri Zone of Lókút Hill in Hungary (Főzy et al. 2022: pl. 56: 6) is a rather complete specimen, its phragmocone very similar to the lectotype but at smaller size, and is more evolute, especially the body-chamber. These differences strongly suggest the Hungarian material represents an earlier transient of the species. This Hungarian specimen preserved with its body-chamber and further specimens described by Čech (1985) show that the present specimens from level BN-3 compose a different ammonite. The morpho-sculptural differences associated with the very different age suggest our Andean specimens could belong to a later species or transient, provisionally named *Hypowaagenia* sp. A, possibly derived from late representatives of *H. acanthomphala* via some yet unknown forms.

Subfamily Aspidoceratinae Zittel, 1895

Genus *Aspidoceras* Zittel, 1868

Type species. *Ammonites rogoznicensis* Zejszner, 1846 (by monotypy)

Aspidoceras quinchaoi Zeiss & Leanza, 2010

Figs. 3-6

Material. Eleven moderately well-preserved (collection numbers in figures), fragmentary or more or less complete macroconchs (including mesoconchs); three aptychi (MOZ-PI-7560/1-3). One large specimen not collected.

Description. Moderately inflate ($W/H_1 = 1.0-1.2$) and involute ($U/D = 0.2-0.3$), with suboval to subcircular whorl section throughout the ontogeny. Innermost whorls with a single row of mid-flank spines preserved as tubercles in the internal mould, and from about $D = 7$ mm a second row in the umbilical shoulder. Ribs connecting the lateral with the umbilical spines occur, but rather irregularly. The two rows of spines persist in most specimens up to the body-chamber, with the umbilical spines being more numerous than the lateral ones in the middle whorls. From about $D = 60$ mm the specimens show more or less strong ventral ribbing. Two specimens are more compressed and the lateral spines are wider spaced from about $D = 80$ mm.

The adult body-chamber is only preserved as fragments. The whorl section is suboval and retains the sculpture of the adult phragmocone, apparently fading towards the peristome. The spines are hollow and unfloored (Fig. 5B). The maximum estimated size at peristome is $D_p = 550-600$ mm.

Mandibles: typical *Laevaptychus*, subspherical triangles with a striated concave side and a punctate convex (external) side (see Parent et al. 2007: fig. 6B-C).

Discussion. These specimens were formerly compared with *A. euomphalum* (lectotype from the Alternans Zone (see Parent et al. 2007, 2011), but differ by the larger size, the development of ribs connecting the tubercles and then covering the ventral area, and importantly by the lower stratigraphic position. It is hard to assess the biological significance of these differences, especially by the incomplete preservation of the lectotype of *A. euomphalum*. They can be interpreted as specific differentiation or merely

as transients within *A. euomphalum*.

Zeiss & Leanza (2010) introduced *Aspidoceras quinchaoi* whose holotype comes from an indeterminate position within the Internispinosum Zone of Cerro Lotena, a locality close to Barda Negra. The holotype is a large phragmocone of 435 mm in diameter. The inner and middle whorls up to where are visible in the holotype match our specimens, as well as the specimen illustrated in Leanza (1980: pl. 8: 1), at comparable diameters. Zeiss & Leanza (2010: 60) assigned our specimens to *A. quinchaoi*. We follow this classification, but only based on the holotype since two of the paratypes are only fragments, and the supposed microconch (specimen in Zeiss & Leanza 2010: pl. 15: 5) is a perfect adult female of *Pseudhimalayites steinmanni* Haupt, 1907 with ventral tubercles, coming from the Rafaeli Subzone of the Internispinosum Zone (see Parent et al. 2013).

The variation of the species described by Zeiss & Leanza (2010) includes specimens which tend to lose the lateral tubercles in the subadult or adult whorls, as our specimen in Fig. 6 which can be considered a large mesoconch.

The specimens from Arroyo Cieneguita described as *A. cf. euomphalum* in Parent et al. (2011: fig. 36A-C) can be also assigned to *A. quinchaoi*.

A. quinchaoi as represented by the present material was already discussed at length, concluding that the two following species could be synonyms (Parent et al. 2007):

(1) *Aspidoceras haupti* Krantz, 1926 from the Internispinosum Zone of Cerro Lotena; its holotype is indistinguishable from our specimens at comparable size (cf. Fig. 3D).

(2) *Aspidoceras neuquensis* Weaver, 1931, from the same locality and stratigraphic position, can be accepted as a synonym by its close resemblance. Unfortunately, the monotypic holotype has been noted missing since 1971 in the Burke Museum of Natural History and Culture, Washington (Liz Nesbitt, pers. comm. 23/03/2022).

Sexual dimorphism. Lappeted microconchs of this species have not been recorded in this study, nor in any other *Aspidoceras* as far as we know. The small specimen with body-chamber in Fig. 3A seems to be a small mesoconch, or could be a juvenile macroconch because it does not show any signs of uncoiling indicating adulthood. Callomon & Cope (1971) and Hantzpergue (1989) assumed that sexual dimorphism within the genus *Aspidoceras* consists of macro- and microconchs differing only by their adult size. However, one would expect that the microconchs bear lateral lappets as in the whole superfamily and its ancestors. We think that the absence of lappeted microconchs in *Aspidoceras* could be explained by the assumption that the males had no shell (Schweigert 1997, 2010), or it was abandoned during sexual maturation.

Genus *Toulisphinctes* Sapunov, 1979

Type species. *Toulisphinctes zieglerei* Sapunov, 1979 (by original designation).

Toulisphinctes cf. rafaeli (Oppel, 1863)

Fig. 7

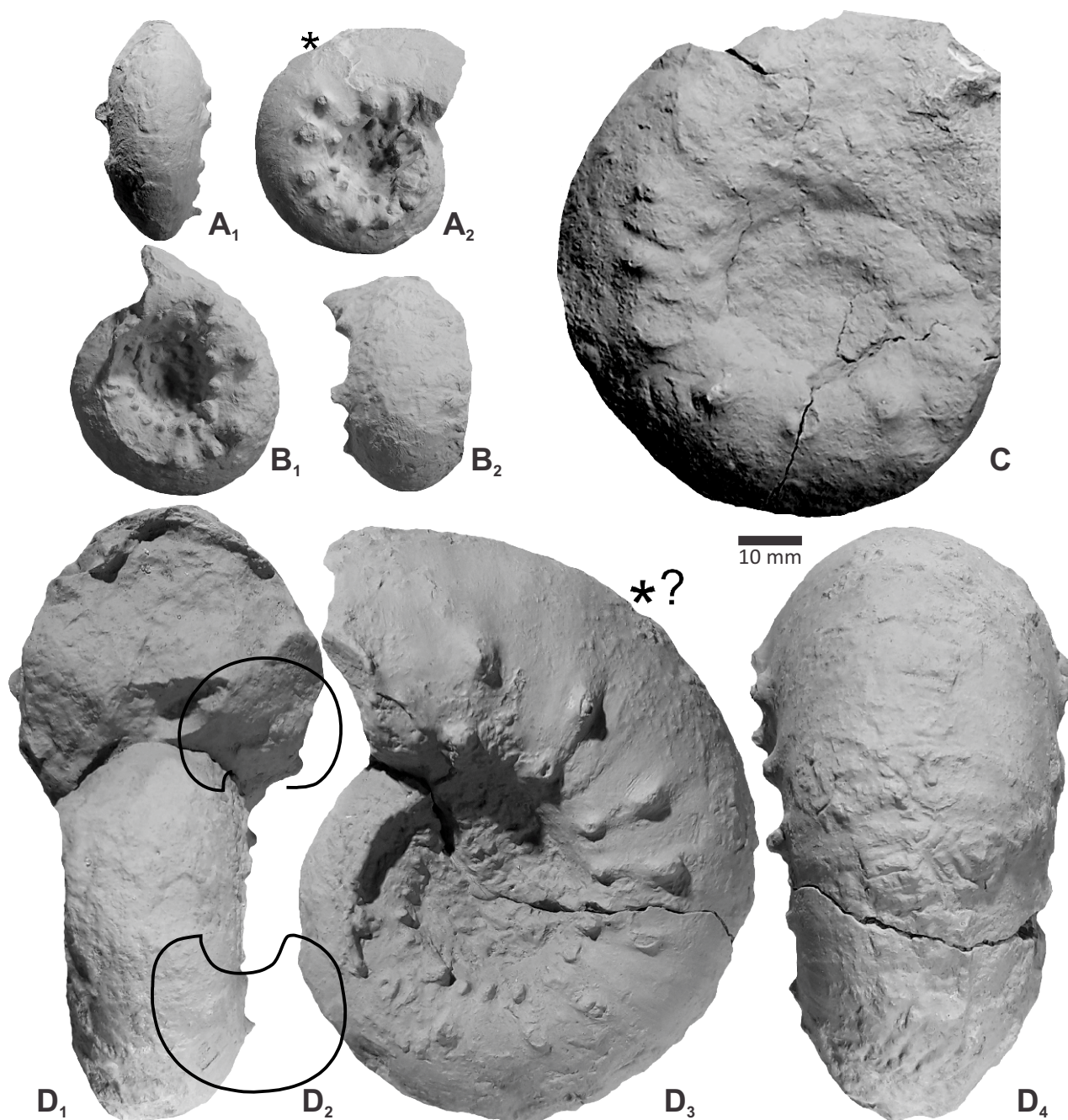


Figure 3. *Aspidoceras quinchaoi* Zeiss & Leanza, 2010, Barda Negra, level BN-3, Internispinosum Zone. A: almost complete small mesoconch or juvenile macroconch female (MOZ-PI-7561/1). B: inner whorls (MOZ-PI-7561/2). C: juvenile macroconch female (MOZ-PI-7564). D: juvenile macroconch female with beginning of the body-chamber (MOZ-PI-7565); D₂: whorl section observed through the fracture seen in D₃ – All natural size (x1). Asterisk at last septum.

Description. One large specimen (MOZ-PI-7566/3) and a fragment (see Parent et al. 2007: fig. 5A). The specimen in Fig. 7 consists of the end of the phragmocone and the beginning of the body-chamber. It is moderately inflated and involute, with periumbilical and lateral spines from which two ribs arise; some ribs born in the umbilical border are unrelated to the spines. All ribs organize to cross the venter evenly spaced. The diameter of this specimen is 380 mm, and unfortunately it is too incomplete for stating if it was mature.

Remarks and comparison. The ornamentation of the present specimens is typical of *Toulisphinctes* and well comparable to that of the holotype of *Toulisphinctes rafaelli* (see Schlegelmilch 1994: pl. 69: 3), and especially to the two topotypic specimens figured by Schneid (1915: pl. 5: 5 and pl. 12: 5). The latter specimens come from the Neuburg Formation in southern Franconia (Germany), Ciliata Zone, rather equivalent to the Fallauxi and lower Ponti zones (Scherzinger & Schweigert 1999), thus to the Proximus-Internispinosum zones. The holotype of *T. rafaelli* seems to

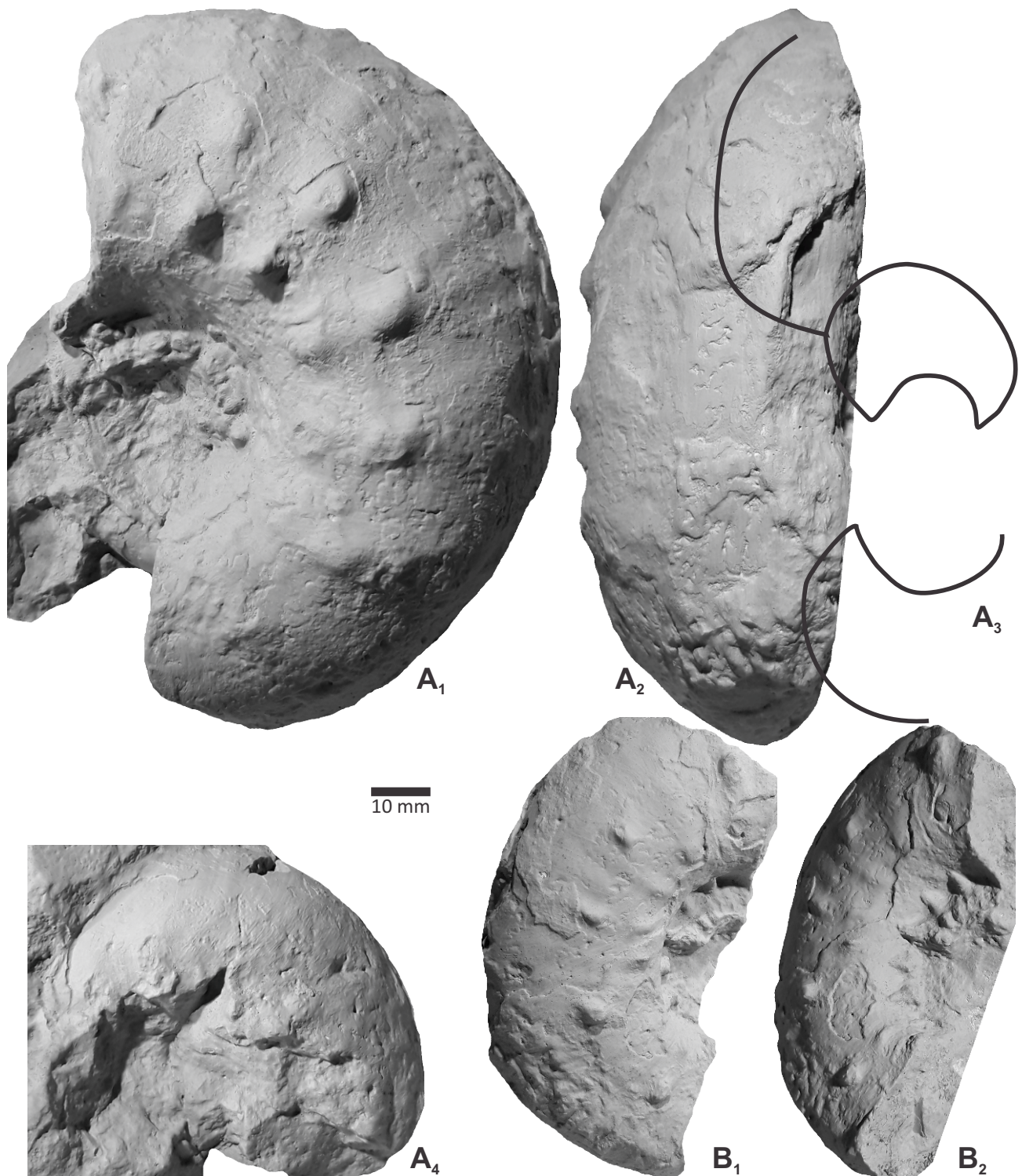


Figure 4. *Aspidoceras quinchaoi* Zeiss & Leanza, 2010, Barda Negra, level BN-3, Internispinosum Zone. A: macroconch female phragmocone (MOZ-PI-7562); A₃: whorl section; A₄: inner whorls. B: macroconch female phragmocone (MOZ-PI-7568/1) showing the spines preserved in the inner whorls – All natural size (x1).

be a body-chamber, but is smaller ($D = 240$ mm) and more compressed than *T. cf. rafaeli* (Fig. 7).

The specimen from the Internispinosum Zone of Pampa Tril (Parent et al. 2015: fig. 81A) is very closely comparable, but somewhat smaller. The specimen from the Proximus Zone of Arroyo Cieneguita (Parent et al. 2011: fig. 36E) is an

adult macroconch, smaller than the present specimen and could be an earlier transient of the same species.

T. cf. rafaeli occurs widely in the Proximus and Internispinosum zones of the Neuquén Basin; it has been recorded in Barda Negra, Cerro Lotena-Cerro Granito (Parent & Garrido 2021), Pampa Tril, and Arroyo

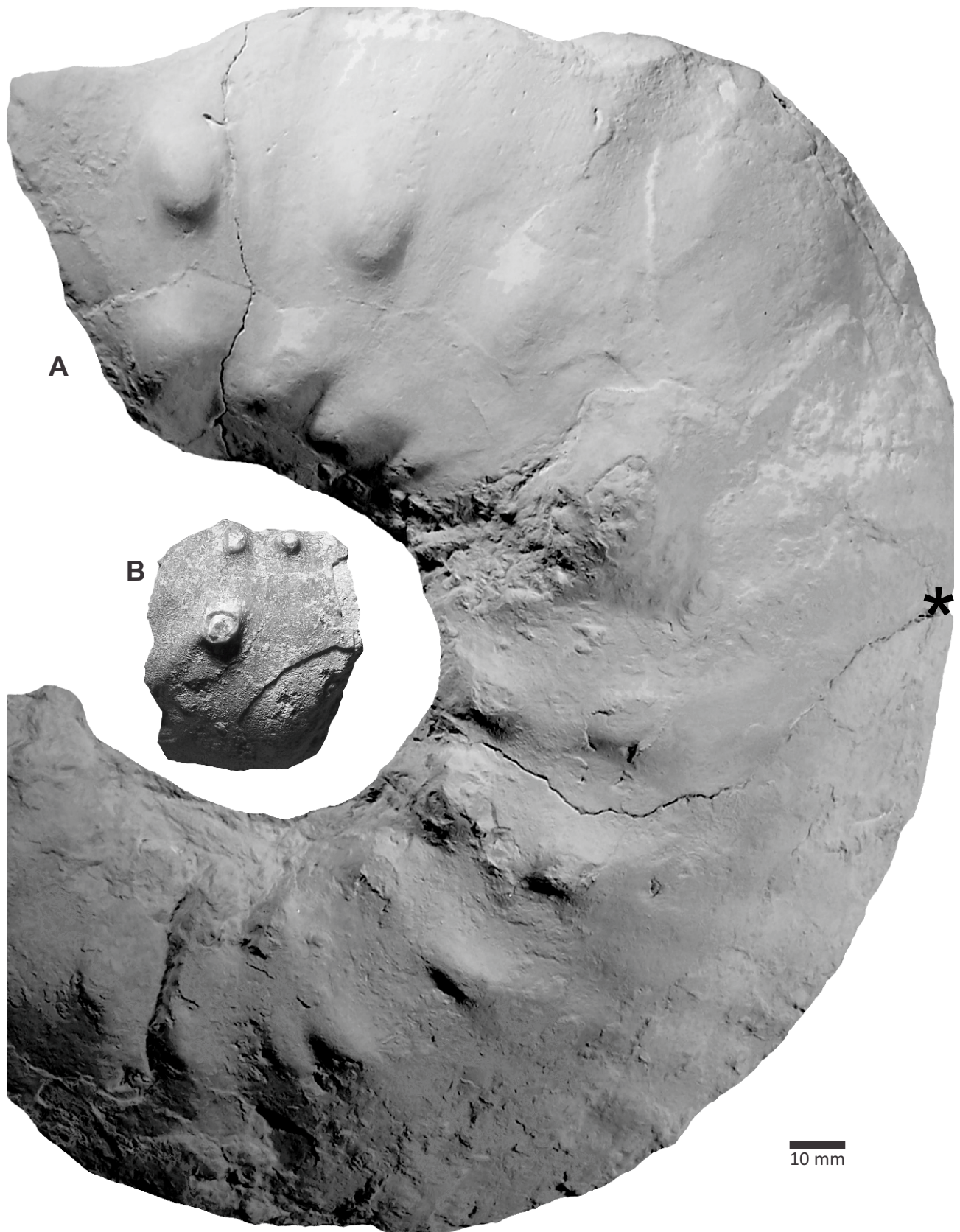


Figure 5. *Aspidoceras quinchaoi* Zeiss & Leanza, 2010, Barda Negra, level BN-3, Internispinosum Zone. **A:** macroconch female end of phragmocone with beginning of the body-chamber (MOZ-PI-7567/1). **B:** portion of macroconch female body-chamber (MOZ-PI-7566/2) showing the hollow unfloored spines. – Natural size (x1). Asterisk at last septum.

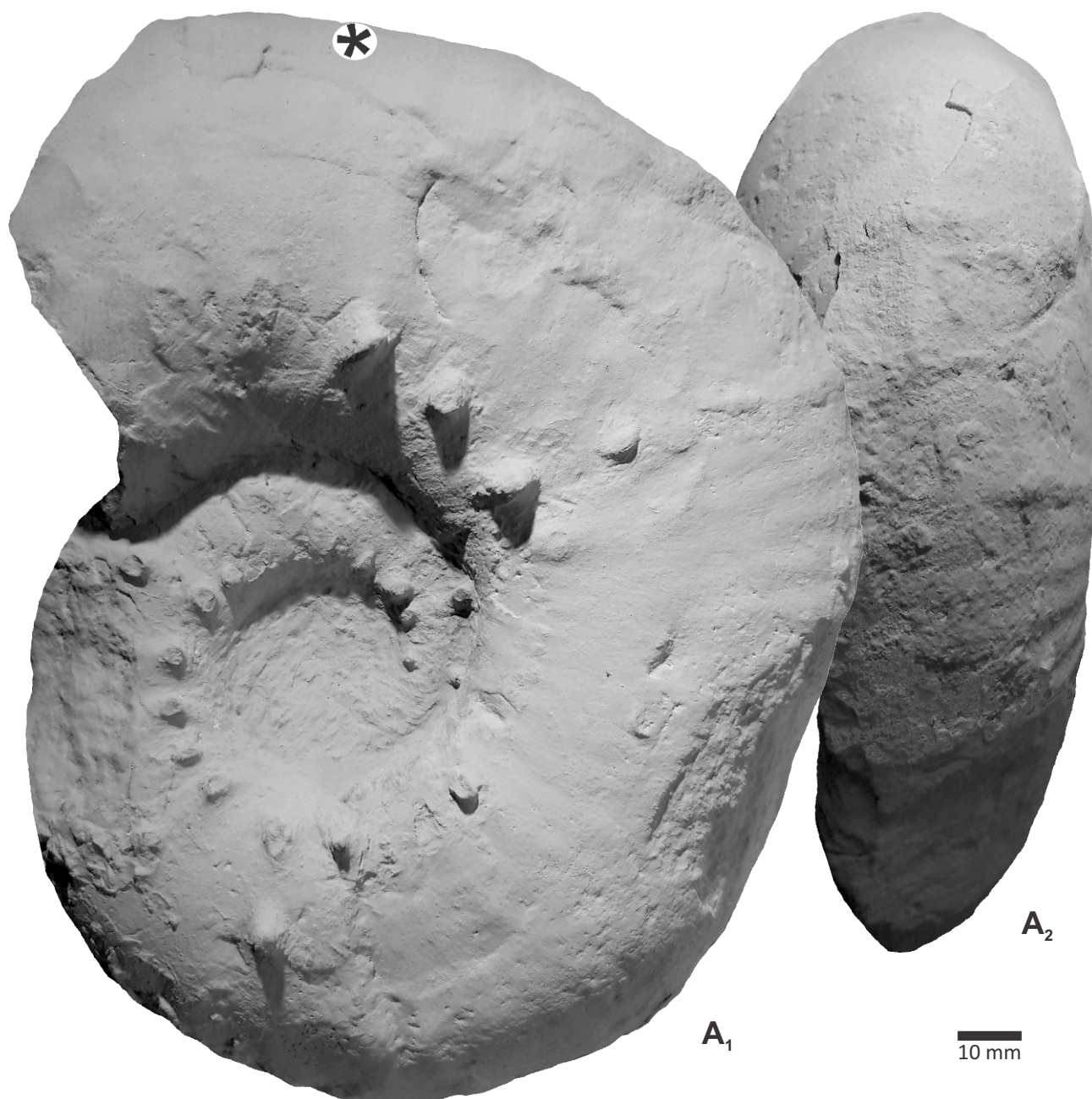


Figure 6. *Aspidoceras quinchaoi* Zeiss & Leanza, 2010, Barda Negra, level BN-3, Internispinosum Zone. Adult mesoconch female with part of the body-chamber (MOZ-PI-7563/1). – Natural size (x1). Asterisk at last septum.

Cieneguita. The oldest known occurrence consists of a very large macroconch phragmocone from level CL-13 of the section in Parent & Garrido (2021), attributable to *T. rafaeli*, indistinguishable from the cited specimens figured by Schneid (1915). The picture which compose these occurrences suggests that *Toulisphinctes* originated in some form that immigrated from the Tethys in times of the Darwini-Semiforme/Malarguensis-Zitteli zones, or even before, and became a well-established component of the Andean ammonite faunas up to the Ponti/Internispinosum Zone.

DISCUSSION AND CONCLUSION

The study of the aspidoceratids of the level BN-3 of the succession of Barda Negra, show the occurrence of three species: *Hypowaagenia* sp. A, *Aspidoceras quinchaoi*, and *Toulisphinctes* cf. *rafaeli*. The age of the assemblage is indicated by the occurrence of *Zapalia fascipartita* and *Windhauseniceratid internispinosum* trans. beta: Fascipartita Subzone of the Internispinosum Zone, latest Late Tithonian (bipartite subdivision) or latest Middle Tithonian (tripartite subdivision).

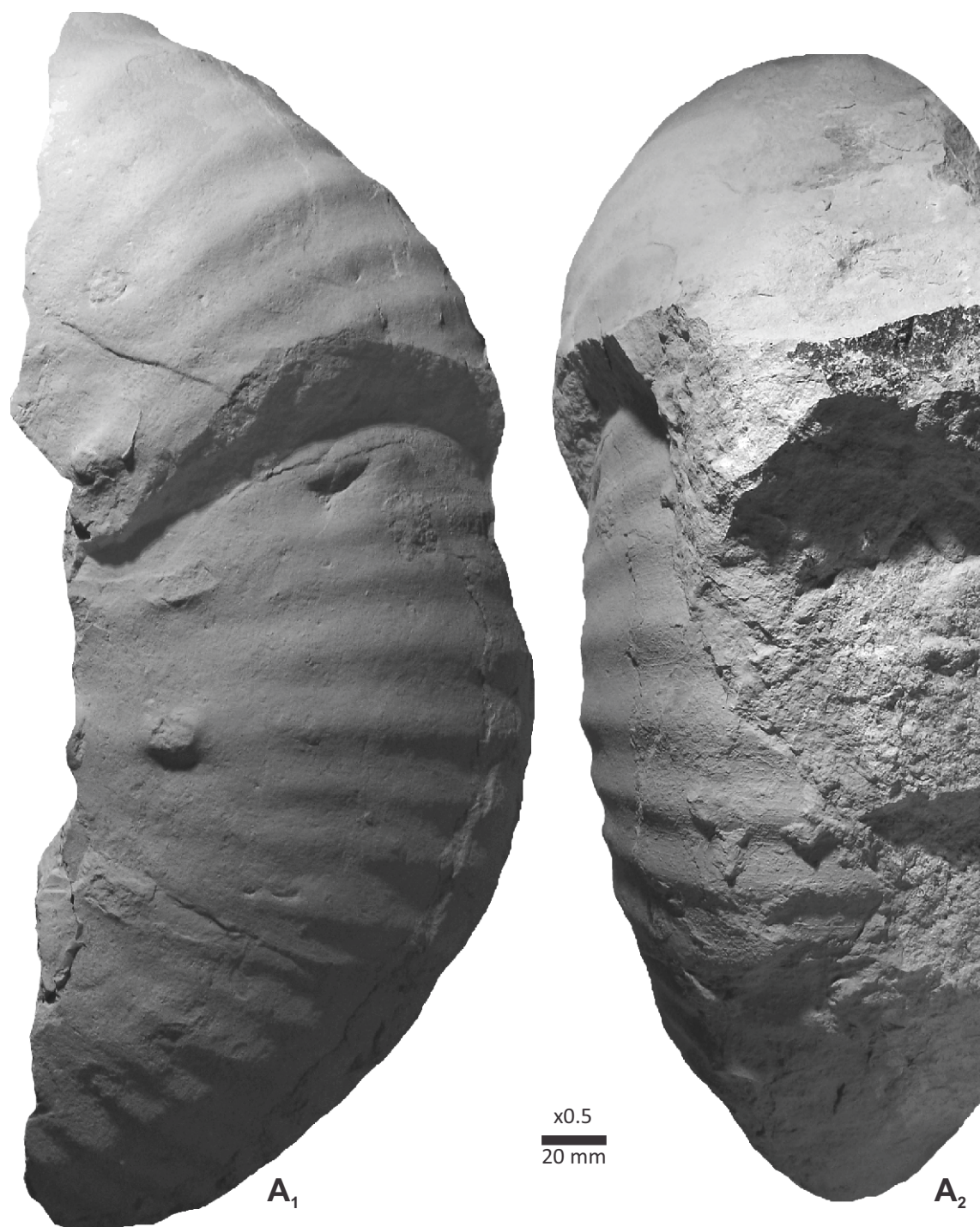


Figure 7. *Toulisphinctes* cf. *rafaeli* (Oppel, 1863), Barda Negra, level BN-3, Internispinosum Zone. Adult macroconch female body-chamber (MOZ-PI-7566/3). – Half size (x0.5).

In the sampled spot of the level BN-3 the totality of ammonites collected, considering every specimen no matter its degree of fragmentation, is distributed as follows:

<i>Hypowaagenia</i> sp. A	3 specimens
<i>A. quinchaoi</i>	12 specimens
<i>T. cf. rafaeli</i>	2 specimens
<i>W. internispinosum</i>	4 specimens
<i>Z. fascipartita</i>	3 specimens

It is well evident the wide dominance of members of the Aspidoceratidae, in abundance and taxonomic diversity: 71% of the specimens belong to this family, and from the five genera (and species) identified, 60% (three genera and three species) belong to the Aspidoceratidae. This high level of aspidoceratid diversity is only comparable, among published data, with the assemblages recorded from the levels CL-43 (top of the Zitteli Zone) and CL-56 (top of the Proximus Zone) of the succession of the nearby locality

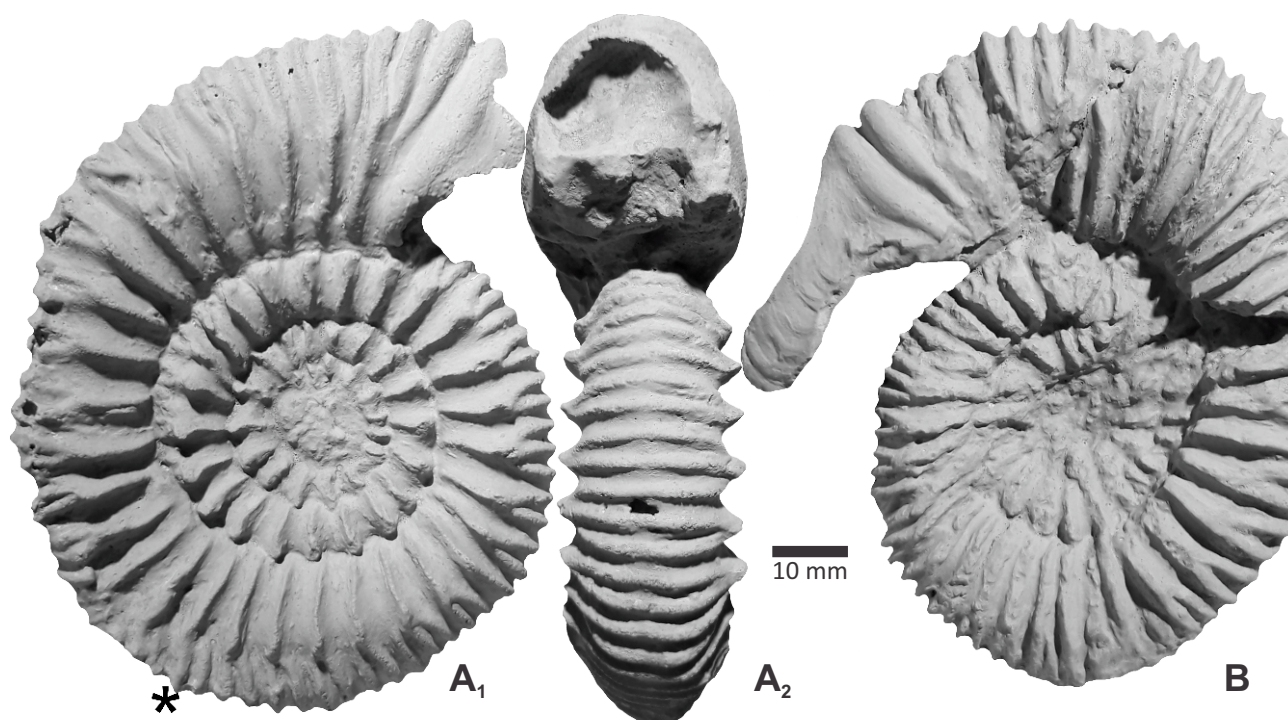


Figure 8. *Windhausenicerias internispinosum* (Krantz, 1926) transient beta, Barda Negra, level BN-3, Internispinosum Zone. **A:** complete adult microconch (MOZ-PI-7558). **B:** complete adult microconch (MOZP-7557). –All natural size (x1). Asterisk at last septum.

Cerro Lotena (Parent & Garrido 2021: 57-58), and from the level AC-7 (Proximus Zone) of Arroyo Cieneguita (Parent et al. 2011). However, aspidoceratids in these assemblages are never dominating in diversity neither in abundance as in level BN-3; thus, it is interesting to briefly explore the potential causes of this abundance.

The succession of the Vaca Muerta Fm in the Picún Leufú Subbasin (southern Neuquén Basin) where the studied section is located, was deposited on a shallow, tidally dominated, mixed carbonate siliciclastic ramp (Spalletti et al. 2000). The study area at Barda Negra has a position very close to the Huincul High, a structure partially emerged in Kimmeridgian and Tithonian times (Hogg 1993, Spalletti 2013) producing a shallow-water area (cf. Spalletti et al. 2000, Veiga & Spalletti 2007), even shallower than the area of Cerro Lotena-Cerro Granito (Parent & Garrido 2021). The lithology of the lower levels of the succession consisting of light-coloured, finely sandy limestones, with no organic matter is typical of marine shallow-water environments. Additionally, the occurrence of the above-mentioned bivalves, gastropods, and serpulids clearly points to such marginal environment. In this context the moderate abundance of fragments of ammonites and bivalves allows to conceive a moderate to high-energetic, shallow and well-oxygenated environment for the study area.

In the section fossils occur only in the level BN-3, the remaining ones being barren (Parent et al. 2007), clearly suggesting that the level BN-3 represents a brief episode during which depth, physiography and environmental conditions allowed ammonites reached this area.

According to our observations from occurrences through Subboreal and Submediterranean areas of the Tethys Ocean (e.g. Western France, Swiss and French Jura Mountains, NW Germany, Holy Cross Mountains in Central Poland), aspidoceratoids have preferred neritic habitats, shallow to moderately shallow environments with carbonate production; the association with perisphinctoids in these environments/facies appears as the norm. This observed pattern agrees with the observations of Ziegler (1967), Checa (1985) and Gygi (1986), and with the more comprehensive models of Westermann (1996). Aspidoceratids were mainly microphagous (Schweigert & Dietl 1999), some must have used their large calcified lower mandibles (*Laevaptychus*) for flushing microfauna from different parts of the water column (Lehmann 1976, Parent et al. 2014, Parent & Westermann 2016, Tanabe et al. 2015). The inferred environment represented by the level BN-3 appears highly favourable for this feeding style what would explain the high relative abundance of aspidoceratids, but not the unique dominance over other ammonites.

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Tethyan Primary Standard		Neuquén Basin		
Stage	Zone	Zone	Subzone	Horizon
TITHONIAN	Upper	Durangites	Koeneni	<i>planulatum</i>
				<i>koeneni</i>
	Upper	Microcanthum	Alternans	<i>striolatus</i>
				<i>azulense</i>
	Lower	Ponti	Internispinosum	<i>bardense</i>
				<i>vetustum</i>
				<i>catutosensis</i>
		Fallauxi	Proximus	<i>internispinosum β</i>
				<i>internispinosum α</i>
				<i>falculatum</i>
	Lower	Semiforme	Zitteli	<i>erinoides</i>
				<i>perlaevis</i>
		Darwini	Malarguensis	<i>malarguensis</i>
				<i>picunleufuense γ</i>
KIMMERIDGIAN	Upper	Beckeri	Picunleufuense	<i>picunleufuense β</i>
				<i>picunleufuense α</i>

Figure 9. Chronostratigraphic assignation of the level BN-3 in the frame of the Andean zonal scale, time-correlated with the Standard Scale of the Tethys (based on Cariou & Hantzpergue 1997, Schweigert 2015 and Parent 2022).

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