

# The Tithonian ammonite fauna of the transect Cerro Lotena–Cerro Granito, Vaca Muerta Formation, Argentina. III. Family Aspidoceratidae: Genus *Pseudhimalayites* Spath

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**Key words:** ammonites, Late Jurassic, Neuquén Basin, evolution, biostratigraphy, palaeobiogeography.

**Abstract.** The Aspidoceratid genus *Pseudhimalayites* Spath (Oxfordian–Tithonian) consists of stout and depressed females with three rows of spines occurring at different ontogenetic stages; the males are smaller with apertural lappets. An important succession of these ammonites from the Tithonian of the southern Neuquén Basin has been studied and three species are described: *Pseudhimalayites* n. sp. A (lower Zitteli Zone), *Pseudhimalayites andinus* (Leanza & Olóriz) with two transients (Zitteli–Proximus zones), and *Pseudhimalayites steinmanni* (Haupt), the type species (top of Proximus Zone and lower Internispinosum Zone). These three species show a rather similar shell shape with little variation; the main differences consist of changes in the female adult size and the sizes of onset and offset of the rows of spines. The males gradually lose their sculpture in the adult body-chamber, becoming smooth in the latter species.

All the American records of the genus are reviewed, it being currently known from Tithonian occurrences only, from Cuba and Mexico besides the Neuquén Basin. The studied succession is considered an Andean lineage branched and differentiated from the Tethyan main lineage in the Darwini Zone.

## INTRODUCTION

This paper is the third one of a series containing the results of our study of the stratigraphy and palaeontology of the Tithonian outcrops of the Neuquén Basin (Fig. 1) along

the transect Cerro Lotena – Cerro Granito, in the Neuquén Province. The Family Himalayitidae Spath, 1925 was the subject of the first paper of this series (Parent, Garrido, 2021), and the Family Simoceratidae Spath, 1924 the second one (Parent *et al.*, 2025).

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## STRATIGRAPHIC FRAMEWORK

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

**TITHONIAN**

**Alternans Zone**

**Internipinosum Zone**

**Proximus Zone**

**Zitteli Zone**

**Malarg. Z.**

**Piculn. Z.**

**References**

- Mudstone
- Sandy shale
- Calcilutite
- Marl
- Calcareous siltstone
- Silty sandstone
- Calcareous sandstone
- Fine-grained sandstone
- Conglomerate
- Ammonites
- Occurrence of *Pseudhimalayites*
- Estimated occurrence of the holotype of *Simoceras adversum andinum*
- Estimated occurrence of the lectotype of *Aspidoceras steinmanni*

0 10 20 m

**Fig. 2. The studied section of Cerro Lotena (after Parent *et al.*, 2025)**

framework of the study area has already been described in Parent, Garrido (2021). The chronostratigraphic scheme of ammonite zonation adopted (Fig. 3) is that used in Parent *et al.* (2025).

A complete list of the ammonite successions of the four sections was given in Parent, Garrido (2021: 56–60). In these successions, there are several associations of morphotypes of different species which can be used to define new biohorizons for refining the zonal chronostratigraphic subdivision of the Andean Tithonian at the highest level of time-resolution. However, this task is something which must be done after the main body of the remaining ammonite fauna has been described, which is still work in progress.

Occurrence of the specimens is denoted by level-numbers with the prefix CL of the corresponding section at Cerro Lotena (Fig. 2).

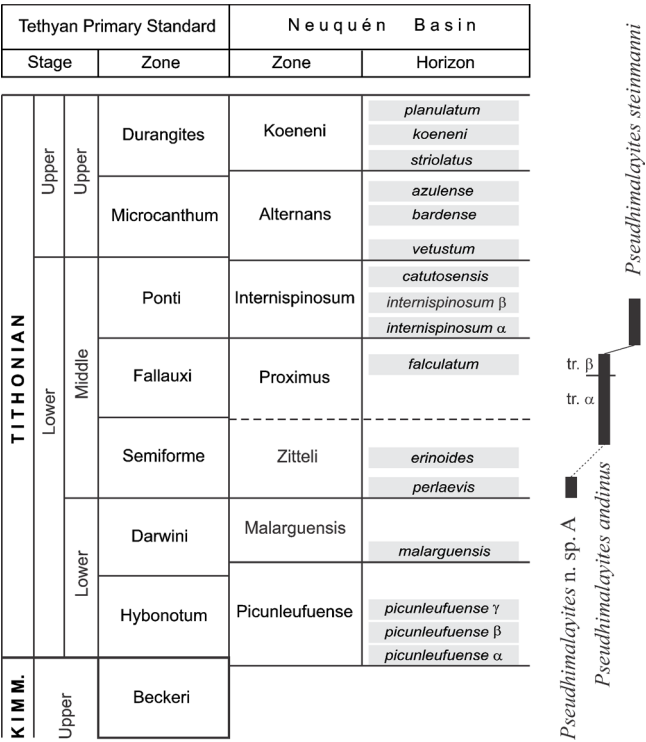


Fig. 3. Stratigraphic ranges of the successive species of *Pseudhimalayites* in Cerro Lotena

The transients *Pseudhimalayites andinus* indicated as tr. α and tr. β. Chronostratigraphic framework from Garrido *et al.* (2018) updated in Parent (2022)

### SYSTEMATIC PALAEONTOLOGY

The ontogeny of the sculpture is taken as the main basis for specific discrimination and characterization. The whorl section and involution are also considered for species deli-

mitation; however, their intraspecific variation may be very wide. It is essential to recognize what kind of specimens are being described (juvenile or adult, complete or incomplete, phragmocone or body-chamber, sex). Thus, we note for every specimen studied its sexual condition, and its growth/developmental stage with the terms: (1) inner whorls or postembryonic, juvenile ontogeny, (2) middle whorls or subadult (not fully adult), and (3) outer whorls or adult portion of the shell (fully grown and developed, sexually mature individual).

**Sexual dimorphism.** 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). The recent studies of the anatomy of the soft-body based on two exceptionally preserved specimens (Klug *et al.*, 2021, 2025) strongly support this correspondence. However, in some ammonite 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) by which the sole adult size does not indicate the sex of every specimen. The local environmental conditions may induce different maturation timing in different groups of a species, leading to variation in the age and size at maturity, and so different adult sizes (see Bucher *et al.*, 1996; Matyja, Wierzbowski, 2000). The adult females of any species may have very different sizes (e.g., Parent *et al.*, 2008a), as is the case for males, but these latter although variable in adult size may be recognized from the presence of apertural modifications, especially the lappets.

Additional terms have been proposed by different authors for labelling intermediate or extreme sizes further than macro- and microconchs, like miniconch, megaconch, or others (e.g., Ivanov, 1971; Mitta 1990; Matyja, 1986). For female specimens that became adult in a relatively early ontogenetic stage and thus remained smaller than normal macroconchiate females (e.g., Parent *et al.*, 2008a; Scherzinger *et al.*, 2018), the term ‘mesoconch’ was introduced (Chandler, 2019).

Since a modern revision of sexual dimorphism in ammonites along with a nomenclature including all these phenomena and variations is pending, we state herein the condition of every specimen combining, if necessary, the use of the terms macro- and microconch, and the supposed sexual condition.

**Biometry and sculpture.** Body-chamber is abbreviated Bc and phragmocone Ph. Measurements (all taken between tubercles or ribs): diameter (*D*), diameter at last septum (*D*<sub>ls</sub>) and diameter at adult peristome (*D*<sub>p</sub>), umbilical width (*U*), whorl width (*W*), whorl height (*H*<sub>1</sub>), and whorl ventral (or apertural) height (*H*<sub>2</sub>); all given in millimetres [mm]. Report

of biometric features is given in the form of dimensionless numbers or “indexes”, mainly ratios to their corresponding value of  $D$ , allowing plain comparisons of shell shape in a range of size. Length of body-chamber ( $L_{BC}$ ) in degrees [ $^{\circ}$ ]. Number of umbilical ( $T_U$ ), lateral ( $T_L$ ), and ventral ( $T_V$ ) tubercles per half-whorl; measurements per-half-whorl are more sensitive to the ontogenetic changes in density than per-whorl (see also Tajika, Klug, 2020), and allow the consideration of incomplete whorls.

The tubercles in the studied specimens (and in almost all Aspidoceratidae) represent the base which formed in the internal mould of spines, which are rarely preserved. The ventral tubercles in the genus *Pseudhimalayites* are elongated radially, transversal to the ventral area so that they can be considered bullae.

**Repositories.** The material described is housed at the Museo Provincial de Ciencias Naturales “Prof. Dr. Juan A. Olsacher”, Zapala (MOZ-PI).

## Order Ammonitida Haeckel, 1866

### Superfamily Aspidoceratoidea Zittel, 1895 emend. Parent, Schweigert, Scherzinger, 2020

Family Aspidoceratidae Zittel, 1895

Subfamily Aspidoceratinae Zittel, 1895

#### Genus *Pseudhimalayites* Spath, 1925

**Type species.** *Aspidoceras steinmanni* Haupt, 1907, by original designation.

**Diagnosis.** See Schweigert (1997, p. 6). Énay, Howarth (2019, p. 88) provided a definition that requires an emendation. The ventral bullae gradually merge forming ribs which weaken towards the adult peristome, even fading off; but there is no groove. The lappets at the aperture of males are long and straight in the known specimens. The stratigraphic range of the genus is Oxfordian–Tithonian (see Schweigert, 1997). The type locality of *A. steinmanni* was clearly indicated as Cerro Lotena by Haupt (1907), and the exact type horizon is herein recognized (discussion below).

**Remarks.** *Pseudhimalayites* is a long-lived lineage mainly developed in the Southern Tethys, ranging at least from the Early Oxfordian up to the latest Early Tithonian (Schweigert, 1997; Parent *et al.*, 2023). The microconchs of the genus have been formerly assigned to the morphogenus *Simocoscocerat* Spath, 1925 (type species: *Ammonites adversus* Oppel, 1865) as demonstrated by Schweigert (1997; see also Fözy, Scherzinger, 2013).

Andean representatives of the genus *Pseudhimalayites* have been invariably described or cited as *Pseudhimalayites steinmanni* (e.g., Haupt, 1907; Gerth, 1925; Krantz, 1928;

Weaver, 1931; Leanza, Olóriz, 1987; Vennari, 2016), as *Pseudhimalayites subpretiosus* (Uhlig, 1878) by Parent (2001), Parent *et al.* (2011b, 2015), Garrido *et al.* (2018), Parent, Garrido (2021), or even as *Simocoscocerat adversus* (Oppel, 1865) *andinum* Leanza, Olóriz, 1987. The new material from Cerro Lotena described below, including representatives from various levels of the Zitteli-Internispinosum zonal interval, shows that at least three species can be differentiated (Fig. 3). This succession includes *Simocoscocerat adversus andinum*, whose holotype is considered a male of the species *Pseudhimalayites andinus* (Leanza, Olóriz, 1987) [M and m].

*P. steinmanni* was considered junior synonym of the Semiforme Zone species *Pseudhimalayites subpretiosus* by Schweigert (1997), followed by Parent (2001). The similarity between the inner whorls of some Proximus Zone Andean representatives and the holotype of *P. subpretiosus* has been demonstrated (Parent *et al.*, 2011b). However, there persisted some doubts because the adult whorls of the holotype of *P. subpretiosus*, a nucleus, are unknown. On the other hand, it has been found that *P. steinmanni* is a stratigraphically later species, confined into the Internispinosum Zone, roughly equivalent of the Ponti Zone (Parent, Garrido, 2021 and this report). The inner whorls of the Andean form of comparable stratigraphic age and at a comparable diameter with the holotype of *P. subpretiosus* are quite different as described below. Consequently, we abandon the use of *P. subpretiosus* for the Andean representatives.

The genus is rather rare in the Neuquén Basin, as everywhere, and the occurrences consist of a few specimens in scattered levels. The representation in the studied section of Cerro Lotena (Fig. 2) has produced the best and most complete record of the basin. The succession of species recorded and described below is (Fig. 3):

- *Pseudhimalayites* n. sp. A [*perlaevis* Hz., base of the Zitteli Zone]: Figs. 4, 5;
- *Pseudhimalayites andinus* (Leanza, Olóriz, 1987) transient  $\alpha$  [upper Zitteli Zone]: Figs. 5, 6, 7A, B;
- *Pseudhimalayites andinus* (Leanza, Olóriz, 1987) transient  $\beta$  [upper Proximus Zone]: Fig. 7C;
- *Pseudhimalayites steinmanni* (Haupt, 1907) [lower Internispinosum Zone]: Figs. 8–12.

This reinterpretation of the Andean *Pseudhimalayites* lineage (Fig. 13), based on the new material, leads to the need of a re-description of the successive species, especially for distinguishing *P. andinus* from *P. steinmanni*.

#### *Pseudhimalayites* n. sp. A

Figs. 4, 5; App. 1

?2012. *Pseudhimalayites steinmanni* (Haupt) – Villaseñor *et al.*: pl. 1, figs. 18–20

2021. *Aspidoceras* cf. *casitense* Imlay – Parent, Garrido, p. 57

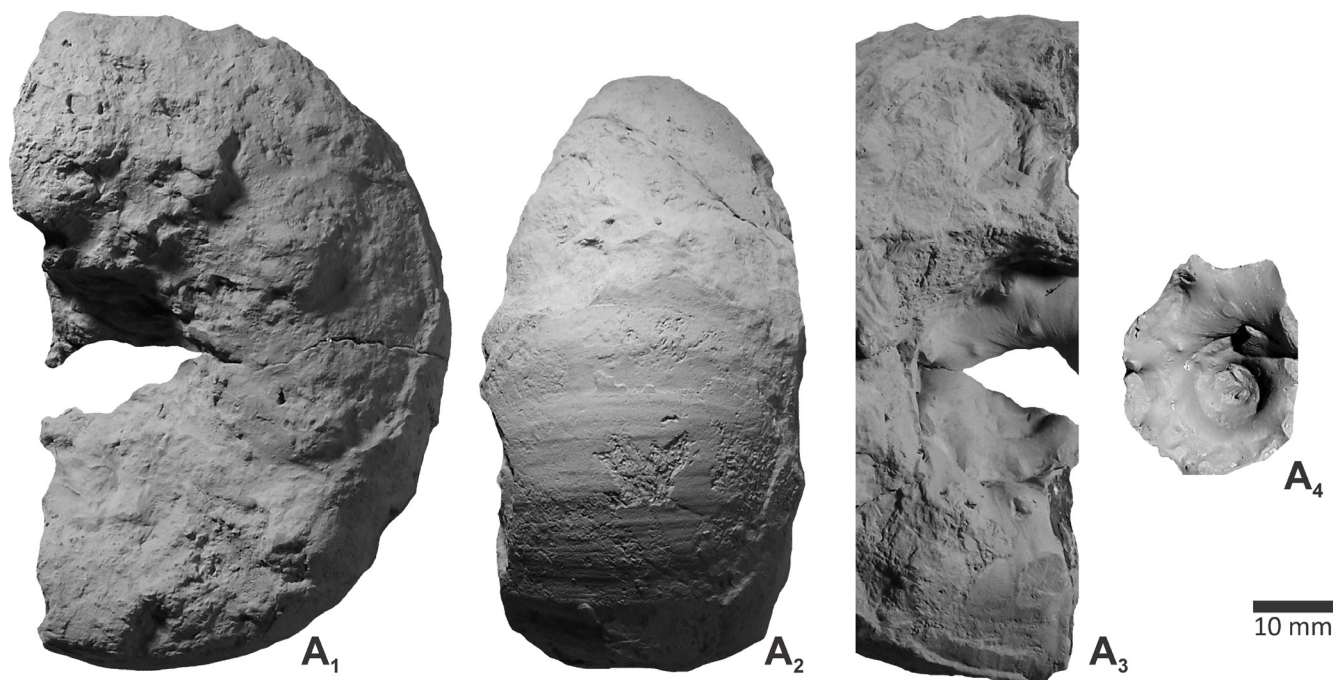


Fig. 4. *Pseudhimalayites* n. sp. A. Adult? female phragmocone (MOZ-PI-7523) from level CL-13, *perlaevis* Hz., base of the Zitteli Zone

A<sub>4</sub> – plaster cast of the inner whorls obtained from the umbilical sediment matrix. Natural size (×1)

**Material.** One specimen, a poorly preserved phragmocone (MOZ-PI-7523) from level CL-13.

**Description.** A female phragmocone (maximum  $D = 85$  mm), apparently adult, with test in the inner whorls and on the venter of the outer whorl.

Inner whorls ( $D = 15\text{--}40$  mm) moderately involute, with suboval whorl section; the umbilical wall pass indistinctly to the rounded flanks. Two rows of widely spaced spines, umbilical and lateral, corresponding one-to-one. The umbilical spines are small; the first at  $D$  c. 25 mm. The lateral spines are strong with oval base, ending spatulate while covered by the umbilical wall of the next whorl; the first from at least,  $D$  c. 10 mm. Venter not discernible.

Outer whorl ( $D = 65\text{--}85$  mm) rather involute with subrectangular whorl section, wider than high ( $W/H_1$  c. 1.2) with widely rounded venter and high, vertical umbilical wall. Two rows of similar umbilical and lateral tubercles, strong, with subcircular base. Venter with wide and weak, rounded ribs and well-marked growth lines.

**Remarks and comparison.** The studied specimen does not differ significantly in whorl section and involution from *P. andinus*. The significant differences are observed in its deeper stratigraphic position and in its sculpture ontogeny (Fig. 5): in *P. andinus* the umbilical tubercles appear at

a smaller size and the ventral tubercles persist much longer, up to the adult phragmocone.

The specimen from Puebla, Mexico, figured as *Pseudhimalayites steinmanni* by Villaseñor *et al.* (2012: pl. 1: 18–20) is a small phragmocone which can be closely compared with the inner whorls of the present species, in the degree of involution, the small umbilical spines, and the prominent lateral spines. The Mexican specimen would come from the Semiforme Zone which could be correlated to include the basal Zitteli Zone level CL-13.

*Aspidoceras casitense* Imlay, 1939 (see also Peña-Muñoz, 1964, pl. 6: 1, 2) from the Tithonian of Mexico looks very similar to *Pseudhimalayites* n. sp. A. However, according to the original description, it bears umbilical and lateral, conical tubercles from the innermost whorls onwards, and its venter is smooth throughout ontogeny, the typical sculpture ontogeny of the genus *Aspidoceras* Zittel, 1868.

**Distribution and age.** The specimen comes from the level CL-13 which yields *Choicensisphinctes erinoides* (Burckhardt, 1903) tr.  $\beta$ , *Toulisphinctes rafaeli* (Oppel, 1863), *Pseudolissoceras zitteli* (Burckhardt, 1903), *Pasottia andina* Parent *et al.*, 2008b, *Cieneguiticeras perlaevis* (Steuer, 1897), and *Semiformiceras?* sp. A. This association is very similar to that of the *perlaevis* Hz. (Parent *et al.*, 2011b, p. 82) which is at the base of the Standard Zitteli Zone.

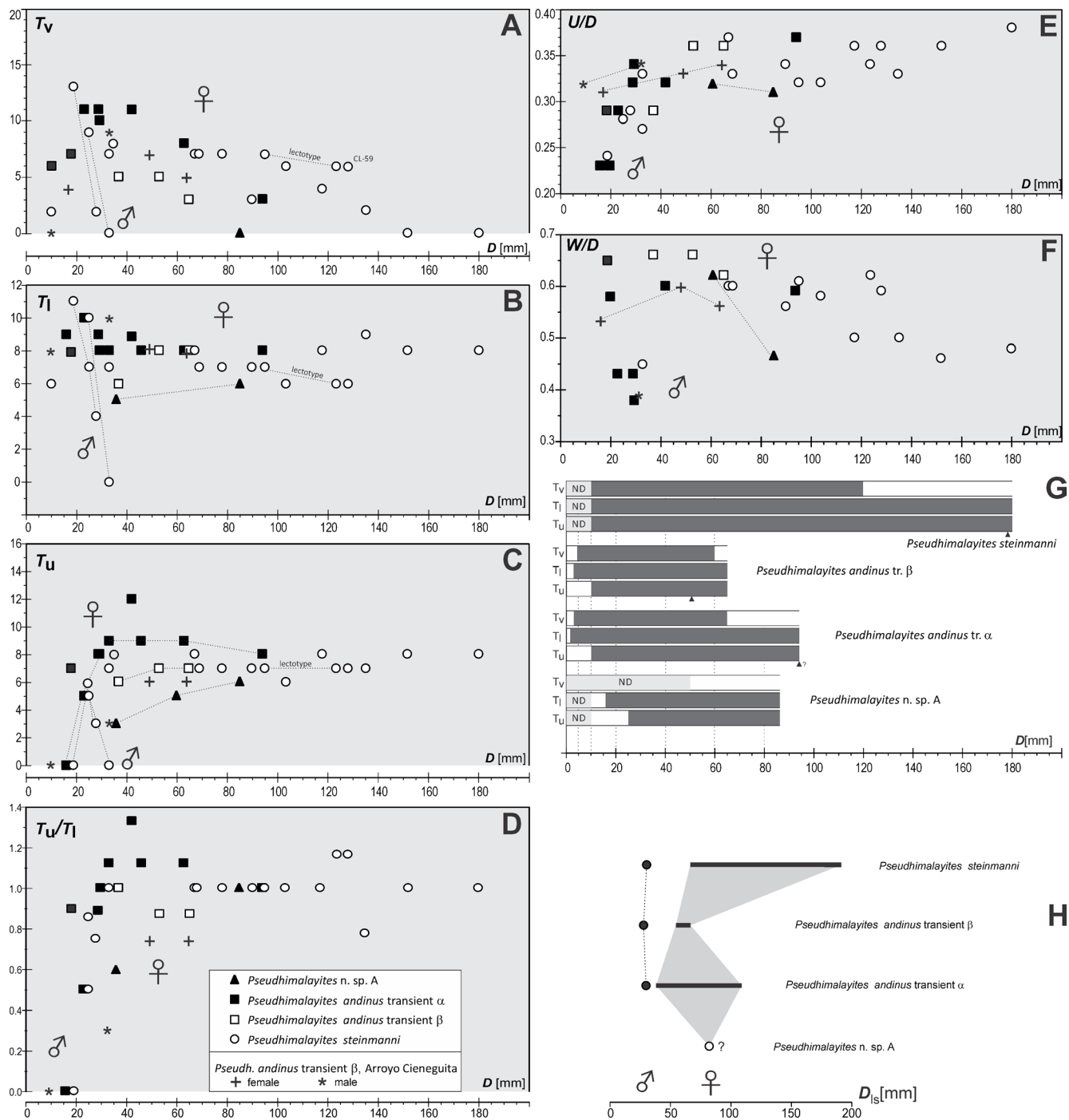


**Fig. 5. Ontogeny of sculpture and morphology, and adult size variation of Andean *Pseudhimalayites* Spath**

**A.** Ventral tuberculation; **B.** Lateral tuberculation; **C.** Umbilical tuberculation; **D.** Ratio of umbilical to lateral numbers of tubercles per half whorl vs. diameter; **E.** Relative umbilical diameter; **F.** Relative width of whorl section; **G.** Diameter of onset and offset of tuberculation: gray for tubercles present, white for no tubercles; ND: no data. For  $D < 5$  mm only partial observations, smooth whorls for  $D < 3$  mm; **H.** Changes of adult size (measured by the  $D_{is}$ ) in the successive species of the genus. It is based on few specimens, not adequate for statistical comparison but illustrative of the pattern

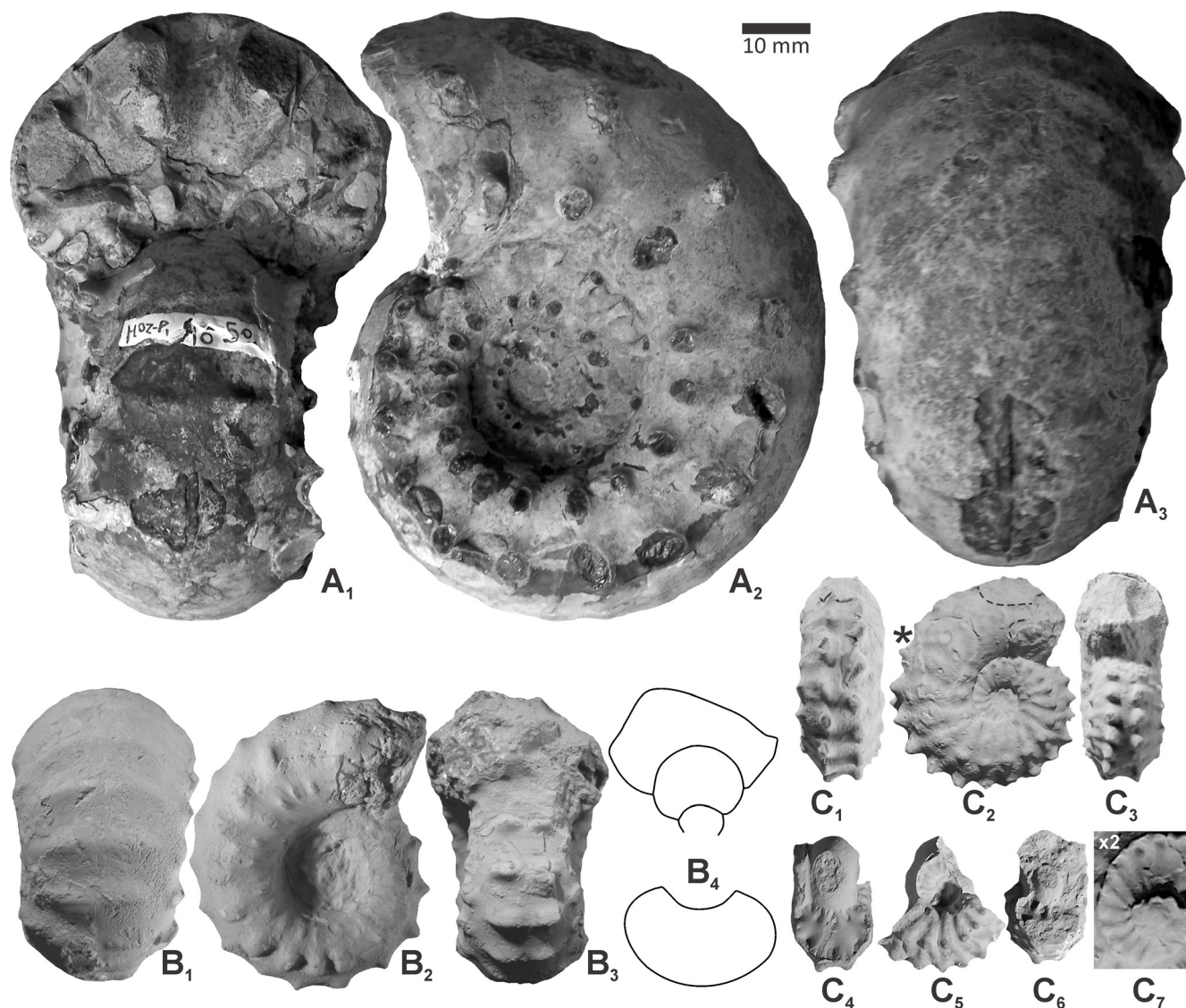


Fig. 6. *Pseudhimalayites andinus* (Leanza, Olóriz, 1987) transient  $\alpha$ , upper Zitteli Zone

**A.** Adult female phragmocone (MOZ-PI-4050) from level CL-33; **B.** Adult female phragmocone (MOZ-PI-7524) from level CL-33; **B<sub>4</sub>**: whorls section; **C.** Complete adult male (MOZ-PI-4903) from level CL-37; **C<sub>4</sub>–C<sub>6</sub>** – inner whorls views after dissection; **C<sub>7</sub>** – inner whorls ( $\times 2$ ) from **C<sub>2</sub>**. All natural size except **C<sub>7</sub>** ( $\times 2$ )

***Pseudhimalayites andinus* (Leanza, Olóriz, 1987)**

Figs. 5–7; App. 1

?1928. *Aspidoceras* (*Pseudhimalayites*) *steinmanni* Haupt – Krantz, p. 47

?1931. *Aspidoceras steinmanni* Haupt – Weaver, p. 434, figs. 339, 340

\*1987. *Simocoscoceratops adversum andinum* n. ssp. – Leanza, Olóriz, p. 204, fig. 2 (holotype)

1989. *Simocoscoceratops pszczolkowskii* n. sp. – Myczyński, p. 94, pl. 8, fig. 4; pl. 10, figs. 4a, 5

1990. *Simocoscoceratops pszczolkowskii* n. sp. – Myczyński, fig. 3, pl. 1: 1a

1992. *Pseudhimalayites steinmanni* (Haupt) – Westermann, pl. 81, fig. 3

2001. *Pseudhimalayites subpretiosus* (Uhlig) – Parent, p. 27, fig. 8I, J

2003. *Simocoscoceratops pszczolkowskii apulcoensis* n. ssp. – Villaseñor *et al.*, p. 51, fig. 4A–D

2011b. *Pseudhimalayites subpretiosus* (Uhlig) – Parent *et al.*, p. 79, fig. 37A–C

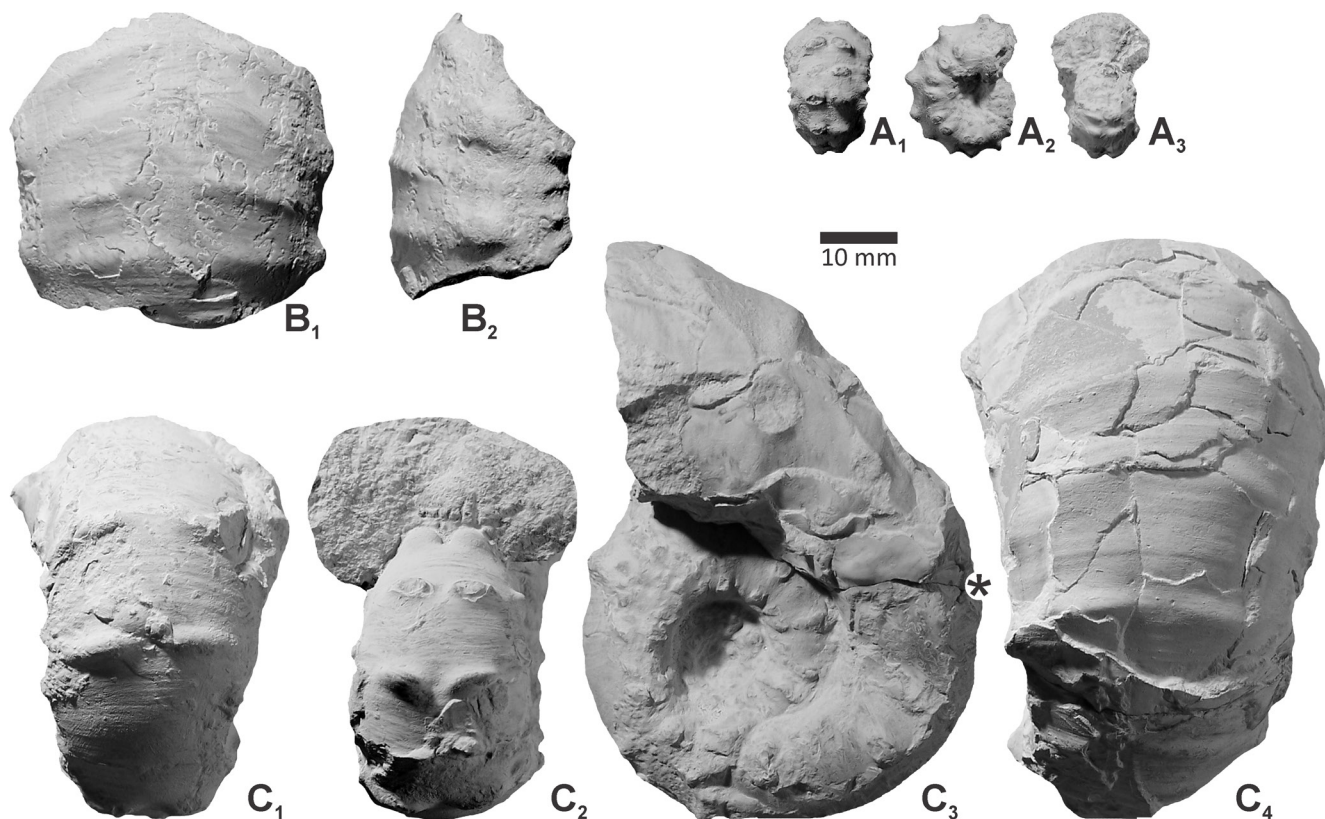


Fig. 7. *Pseudhimalayites andinus* (Leanza, Olóriz, 1987)

**A.** Female inner whorls of transient  $\alpha$  (MOZ-PI-7525) from level CL-41, upper Zitteli Zone; **B.** Fragmentary female phragmocone of transient  $\alpha$  (MOZ-PI-8250/1) from level CL-43, uppermost Zitteli Zone; **C.** Almost complete adult female of transient  $\beta$  (MOZ-PI-7615) from level CL-56, upper Proximus Zone. All natural size ( $\times 1$ ). The asterisk indicates the last septum

2013. *Pseudhimalayites subpretiosus* (Uhlig) – Parent *et al.*, p. 39, fig. 25B

2018. *Pseudhimalayites subpretiosus* (Uhlig) – Garrido *et al.*, p. 16, fig. 14

2021. *Pseudhimalayites cf. subpretiosus* (Uhlig) – Parent, Garrido, p. 57

2021. *Pseudhimalayites subpretiosus* (Uhlig) – Parent, Garrido, p. 58 (level CL-56)

2022. *Pseudhimalayites subpretiosus* (Uhlig) – Parent, p. 29, fig. 21I, J

**Holotype.** The specimen figured by Leanza, Olóriz (1987: fig. 2) is an almost complete male specimen collected at Cerro Lotena, from a level 51 m above the base of the Vaca Muerta Fm. that would correspond to the level CL-46 or CL-47, lower Proximus Zone (Fig. 2). According to these authors it corresponds to the upper part of the Zitteli Zone.

**Material.** Two female phragmocones (MOZ-PI-4050, 7524) from level CL-33. One complete male specimen

(MOZ-PI-4903) from level CL-37. One small female phragmocone (MOZ-PI-7525) from level CL-41. One fragmentary female phragmocone (MOZ-PI-8250/1) from level CL-43. One complete adult female (MOZ-PI-7615) from level CL-56.

**Description.** The shell-shape ontogeny is rather invariable in all female specimens. However, the adult size and the sculpture ontogeny show differences between the older specimens (levels CL-33-43) and those from upper levels (CL-56). They are considered as transients  $\alpha$  (older) and  $\beta$ . The innermost whorls of the transient  $\alpha$  as described below, are known by the dissection of a juvenile female specimen (Fig. 13D) from the Zitteli Zone in Pampa Tril (level PT-12, *erinoides* Hz. in Parent *et al.*, 2015), almost identical to that in Fig. 6B. The male of the transient  $\beta$  as described below, is known only by a complete specimen (Fig. 13F) from the *falculatum* Hz., Proximus Zone of Arroyo Cieneguita (Parent *et al.*, 2011b, fig. 37C).

**Transient  $\alpha$**  (Figs. 5, 6, 7A, B) Female. Maximum preserved diameter  $D = 94$  mm, largest specimen completely

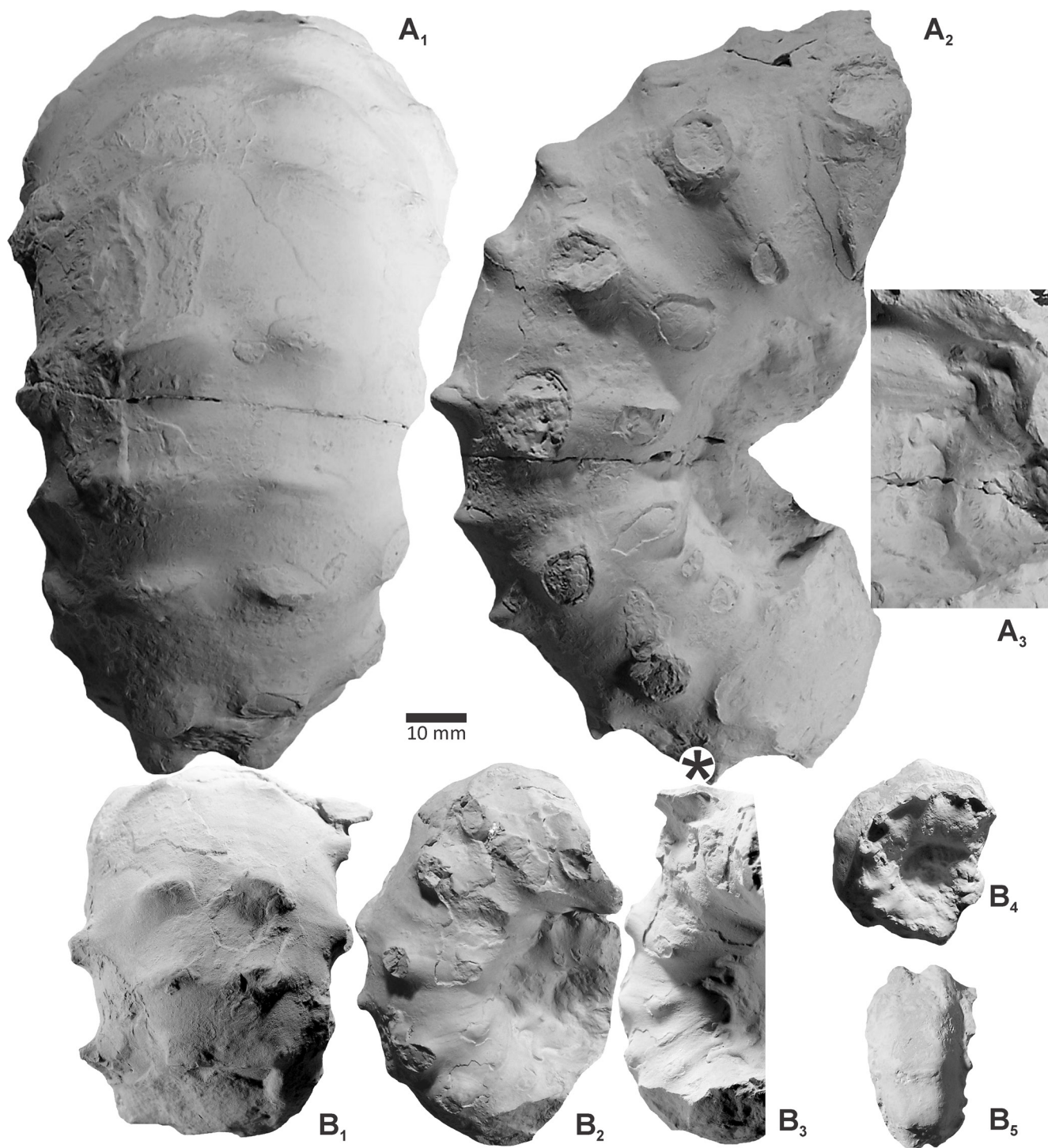


Fig. 8. *Pseudhimalayites steinmanni* (Haupt, 1907)

**A.** Juvenile female body-chamber (MOZ-PI-7279) from level CL-59, uppermost Proximus Zone; **B.** Juvenile female phragmocone (MOZ-PI-7626) from level CL-60, *internispinosum*  $\alpha$  Hz., basal Internispinosum Zone; B<sub>4</sub>–B<sub>5</sub> – inner whorls views after dissection. All natural size ( $\times 1$ ). The asterisk indicates the last septum

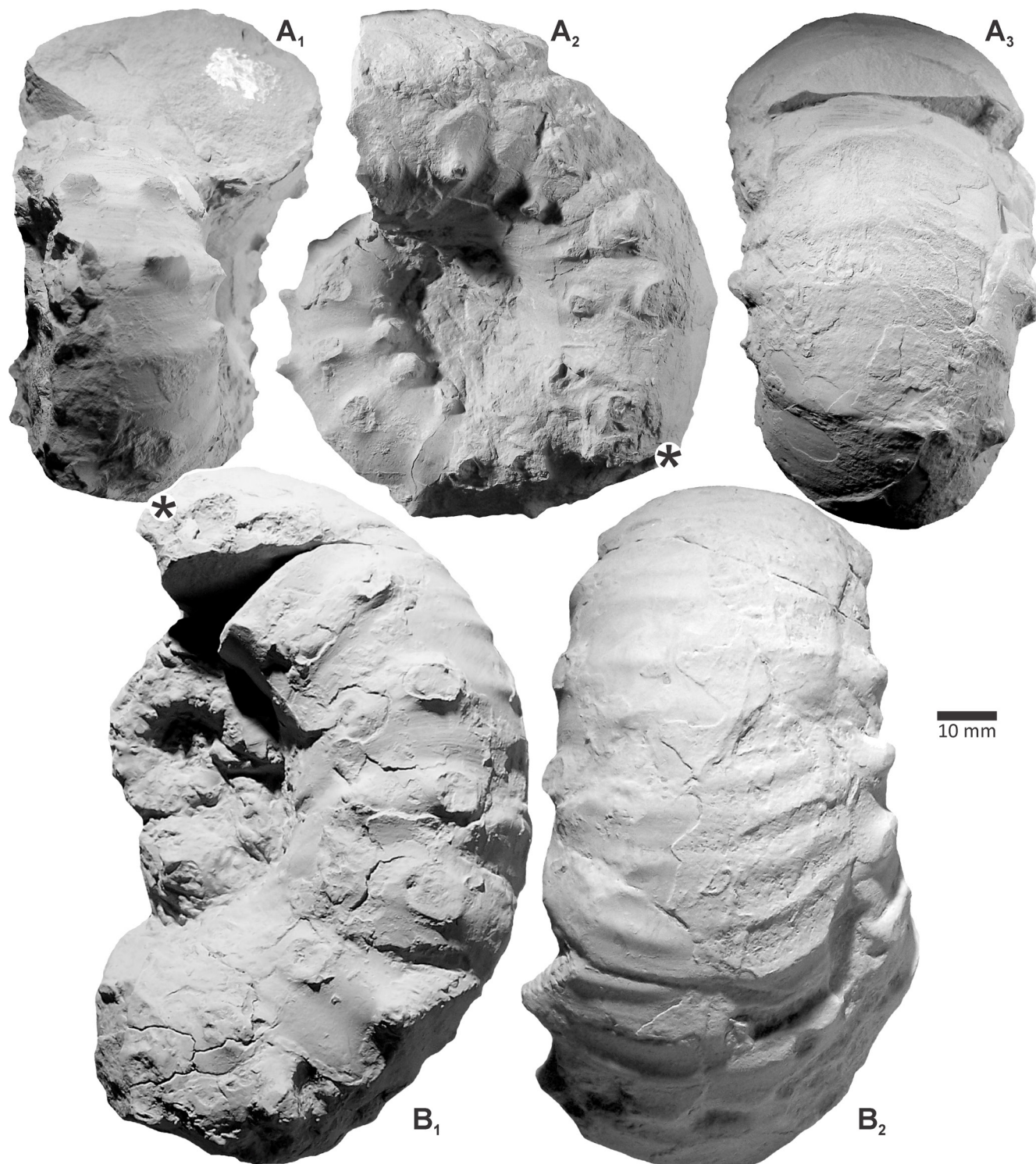


**Fig. 9.** *Pseudhimalayites steinmanni* (Haupt, 1907), level CL-60, *internispinosum*  $\alpha$  Hz., basal Internispinosum Zone

**A.** Almost complete adult female (MOZ-PI-7528); **B.** Almost complete adult female (MOZ-PI-7529/1). All natural size ( $\times 1$ ). The asterisk indicates the last septum

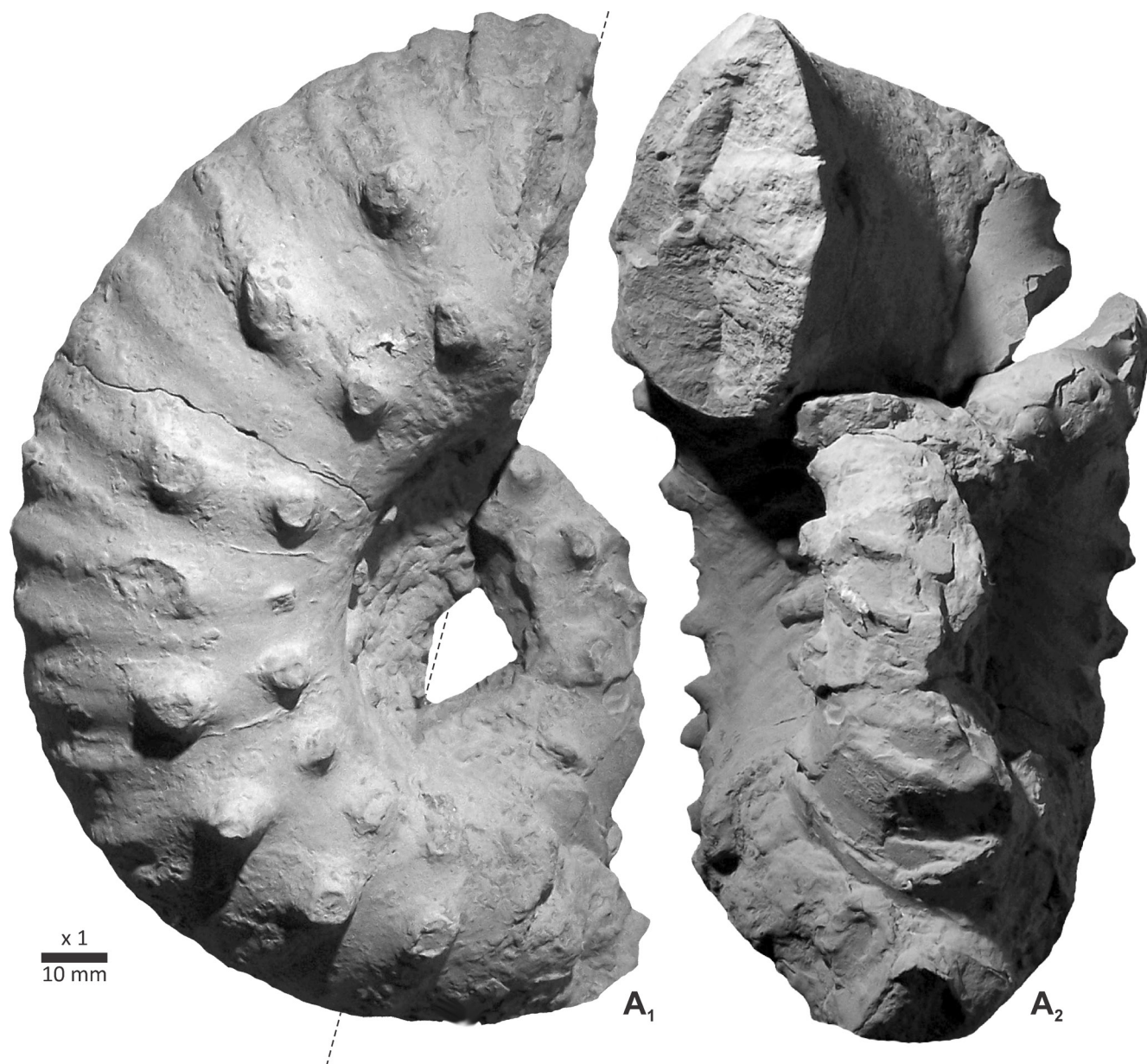


Fig. 10. *Pseudhimalayites steinmanni* (Haupt, 1907), level CL-60, *internispinosum*  $\alpha$  Hz., basal Internispinosum Zone

Adult female phragmocone (MOZ-PI-7530); ventral view and cross-section in Fig. 11A, B. Natural size ( $\times 1$ )

septate. Inner whorls globose, involute with depressed whorls, more evolute in the outer whorls. Body-chamber unknown. The sculpture is composed of three rows of tubercles with weak connecting ribs. All tubercles correspond to hollow spines. Ventral tubercles from  $D = 3.5$  mm to 60–65 mm, in the shape of spatulate bullae. Lateral tubercles from  $D = 2$  mm to the beginning of the body-chamber at least; at first these are bulbous in the test and in the internal mould, but from  $D = 8$ –9 mm onwards they become spiny,

progressively longer, with the ending becoming spatulated, covered by the umbilical wall of the next whorl. Umbilical tubercles from about  $D = 10$  mm to the end of the phragmocone at least; the corresponding spines are small, conical, with a pointed end.

Male. Small and involute. Innermost whorls ( $D < 5$  mm) globose and ventrally smooth. Inner whorls ( $D < 13$ –15 mm) much resembling the corresponding female inner whorls. From about  $D = 10$  mm occur well-marked ribs born in the

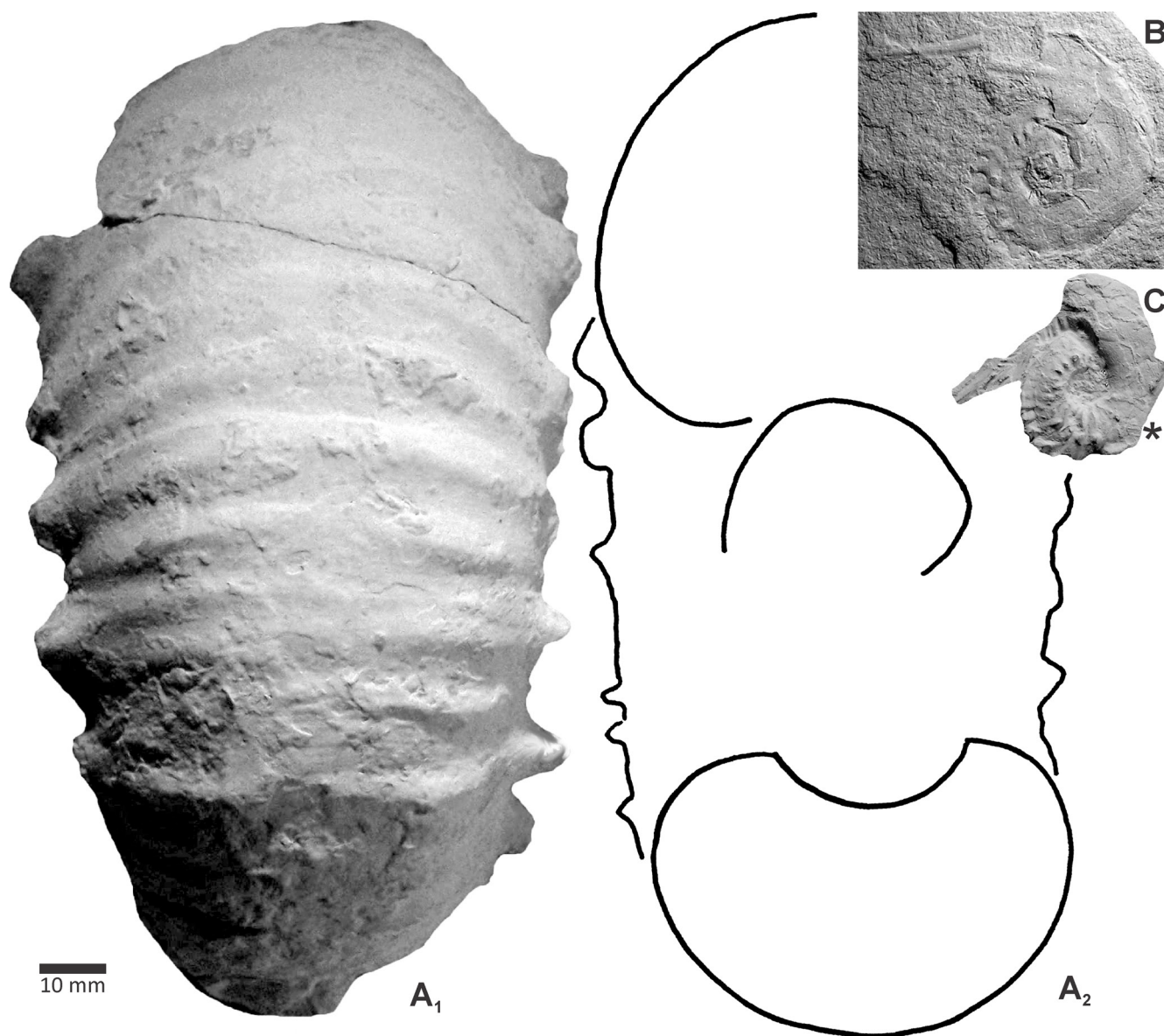


Fig. 11. *Pseudhimalayites steinmanni* (Haupt, 1907)

**A.** Adult female phragmocone (MOZ-PI-7530), level CL-60, *internispinosum*  $\alpha$  Hz., basal Internispinosum Zone; lateral and apertural views in Fig. 10; **A<sub>2</sub>**: cross-section through the broken line in Fig. 10A<sub>1</sub>; **B.** Complete adult male (MOZ-PI-7612) from level CL-62, lowermost Internispinosum Zone; **C.** Complete adult male (MOZ-PI-8349) from level CL-79, middle Internispinosum Zone. All natural size ( $\times 1$ ). The asterisk indicates the last septum

umbilical tubercles; they bifurcate from the lateral tubercles, with two secondaries from consecutive primaries converging into a single ventral tubercle. The corresponding spines of the umbilical and lateral tubercles are conical with pointed end; the ventral spines are rather claviform. The very short body-chamber ( $L_{BC} = 77^\circ$ ) begins at  $D = 27$  mm; it shows some degree of uncoiling and is somewhat more compressed than the phragmocone, ending with long lateral peristomatic lappets.

*Transient  $\beta$*  (Figs. 5, 7C). Female. The whorl section and involution show no differences with the older transient, but the adult size is significantly smaller (based on the diameter at the last adult septum,  $D_{ls}$ ). The sculpture is in general similar but with a lower density of umbilical and ventral tubercles (smaller values of  $T_U$  and  $T_V$ ) all through from about  $D = 25$  mm onwards.

Male. It differentiates from the female inner whorls from about  $D = 15$  mm, developing a sculpture closely resem-

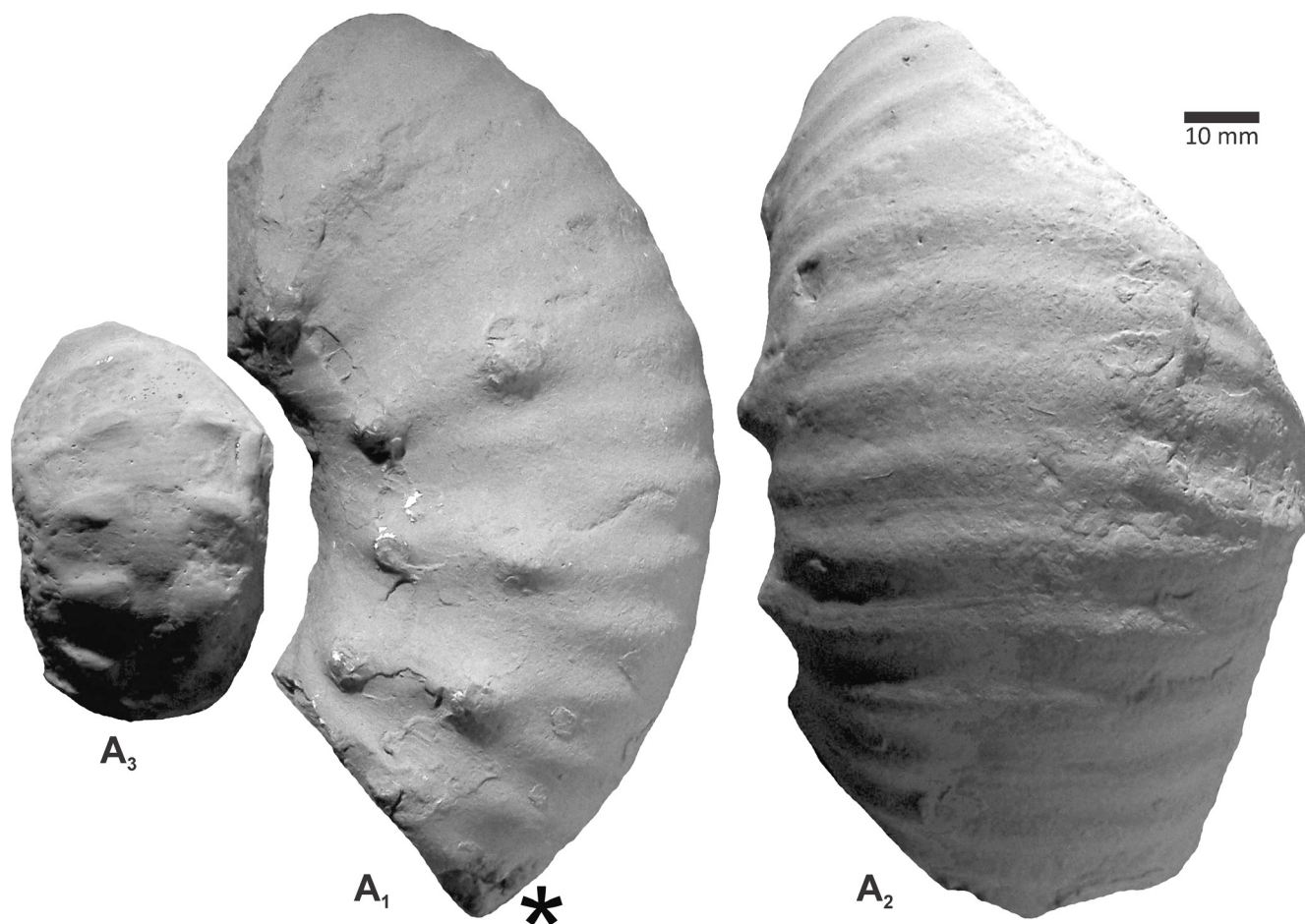


Fig. 12. *Pseudhimalayites steinmanni* (Haupt, 1907), level CL-60, *internispinosum*  $\alpha$  Hz., basal Internispinosum Zone

A. Fragmentary adult female body-chamber (MOZ-PI-7533); A<sub>3</sub> – plaster cast of the venter of the preceding whorl. Natural size ( $\times 1$ ). The asterisk indicates the last septum

bling that of the male of *P. andinus* tr.  $\alpha$ , but the ventral tubercles are smaller and wider spaced on the otherwise smooth venter. Adult body-chamber  $L_{BC} = 160^\circ$ .

**Remarks and comparison.** The lateral bituberculation with later occurrence of umbilical tubercles, and the additional ventral tubercles (bullae) of *P. andinus* are diagnostic of the genus. It differs from *Pseudhimalayites* n. sp. A by its earlier onset of umbilical tubercles and the occurrence of ventral tubercles in the juvenile and adult phragmocone.

The specimen in Fig. 6B is an adult phragmocone as indicated by the merging of the ventral tubercles into ventral ribs and the incipient uncoiling. It is classified as a mesoconch, a female that became mature at smaller size than the larger specimen in Fig. 6A. The latter is an adult macroconch female phragmocone, also showing the merging of the ventral tubercles into ventral ribs throughout the last whorl.

The specimen of transient  $\beta$  perfectly matches in size, sculpture and shell shape ontogeny with the specimens of the *falculatum* Hz. of Arroyo Cieneguita (Parent *et al.*, 2011b, fig. 37A, B). The present specimen of the transient  $\beta$  (Fig. 7B) was collected from the level CL-56 which can be assigned to the *falculatum* Hz. (for details see below). This close correspondence between coeval ammonites from distant localities shows that the differences with the earlier representatives of the species are not originated in local or punctual variations.

*Simocoscoceras pszczolkowskii* Myczyński, 1989 from Cuba and *Simocoscoceras pszczolkowskii apulcoensis* Villaseñor, Olóriz, González-Arreola, 2003 from Mexico are practically indistinguishable from the male of the transient  $\beta$  from Arroyo Cieneguita (Fig. 13E). The Cuban specimen was collected associated with *Pseudolissoceras zitteli*, suggesting the Zitteli Zone. The Mexican specimen was said to

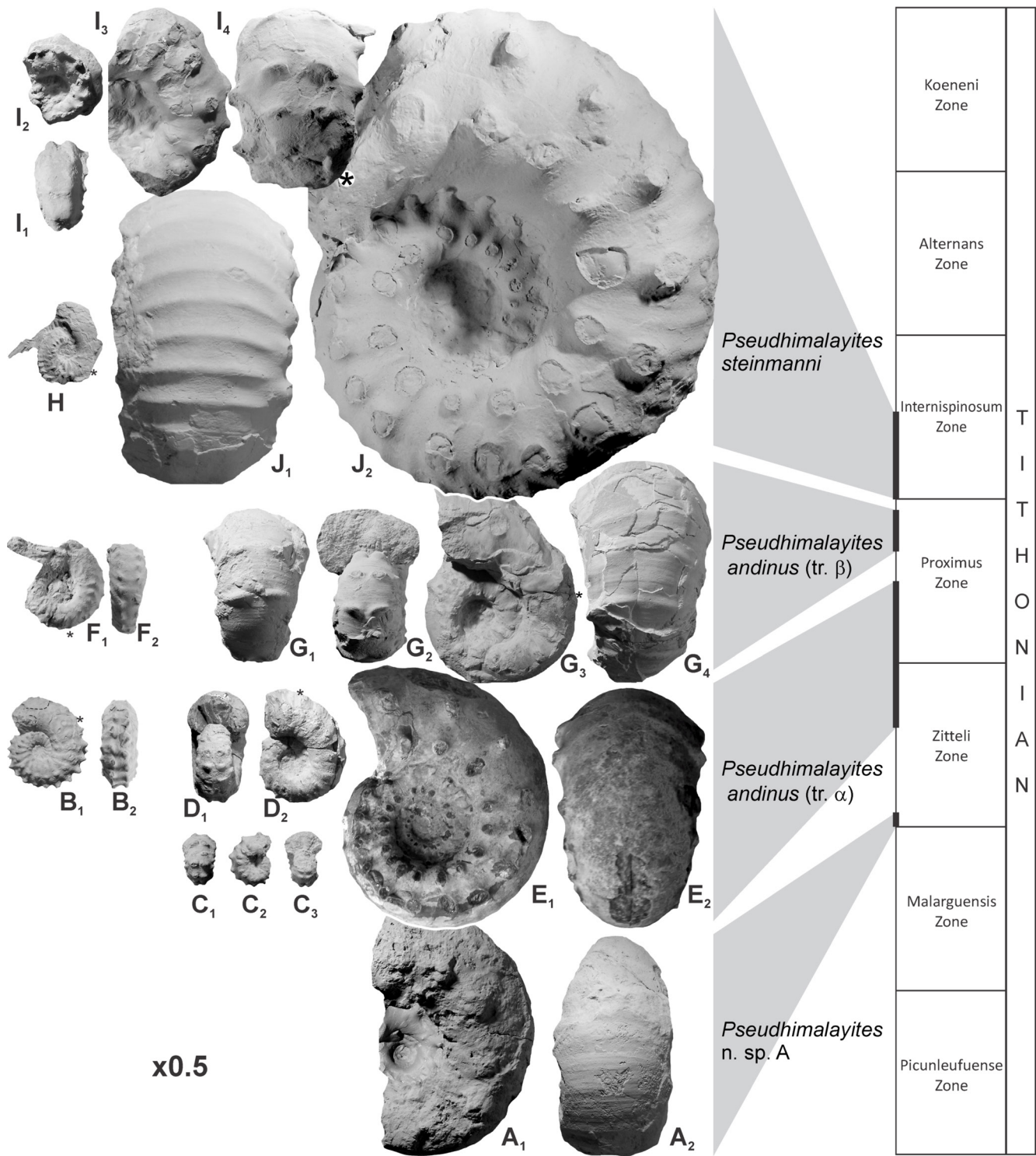


**Fig. 13. Evolution of the Andean *Pseudhimalayites* lineage**

Selected specimens showing the changes in the ontogeny of females and adult males. **A–C, E, G–I.** From Figs. 4–8 and 11 herein; **D.** Juvenile female (MOZ-PI-7228), Zitteli Zone, Pampa Tril; **F.** Modified from Parent *et al.* (2011b: fig. 37C); **J.** Modified from Parent *et al.* (2013: figs. 24C and 25A<sub>2</sub>). All ×0.5

come from the Semiforme Zone, rather equivalent to the Zitteli Zone; its ribbing seems weak, but this is a by-product of the poor preservation as can be seen by remains of well-formed ribs in the fig. 4B of Villaseñor *et al.* (2003).

**Distribution and age.** The specimens of the transient  $\alpha$  come from levels CL-33-37, 41 and 43. The ammonite fauna in this interval includes *Pseudolissoceras zitteli*, *Cieneguiticeras perlaevis* (Steuer, 1897), *Indansites* n. sp. aff. *picunleufuense* (Parent *et al.*, 2011a), *Choicensiphinctes* cf. *erinoides*, early *Catutosphinctes proximus* (Steuer, 1897), *Physodoceras* n. sp. B, and *Toulisphinctes* cf. *rafaeli*; upper Zitteli Zone. In the matrix of the specimens from level CL-33 occurs the small gastropod *Sinuarbullina melehuensis* Gründel, Parent, 2001.

The specimen of transient  $\beta$  comes from level CL-56, and is associated with: *Catutosphinctes proximus* (late transient), *Aspidoceras quinchaoi* Zeiss, Leanza, 2010 (as *Aspidoceras euomphalum* Steuer, 1897), *Physodoceras*? n. sp. B, *Toulisphinctes* cf. *rafaeli*, the earliest representatives of *Windhausenicerias internispinosum* (Krantz, 1926), *Coronogoceras* aff. *huarpense* Parent, Garrido, 2021, and *Cieneguiticeras falculatum* (Steuer, 1897) (Parent, Garrido 2021: 58). This association is very similar to the assemblage which characterizes the *falculatum* Hz. in Arroyo Cieneguita.

In addition to the type locality *Pseudhimalayites andinus* occurs in some other localities of the basin, in the form of specimens morphologically and stratigraphically intermediate between the two transients:

1. Portada Covunco (Parent *et al.*, 2013, fig. 25B), a juvenile female specimen from the middle Proximus Zone that can be assigned to transient  $\alpha$ .
2. Cañadón de los Alazanes (Parent, 2001, fig. 8I, J), a juvenile? fragmentary body-chamber similar to the adult phragmocone of late representatives of transient  $\beta$ .
3. Mallín Quemado (Garrido *et al.*, 2018, fig. 14), a well-preserved, adult female phragmocone from the Zitteli Zone, very likely transient  $\alpha$ .
4. Pampa Tril (Fig. 13D), transient  $\alpha$  (discussed above).
5. Arroyo Cieneguita (Parent *et al.*, 2011b: fig. 37A–C), transient  $\beta$  (discussed above).
6. Bardas Blancas: section described by Gerth (1925), where he cited *Aspidoceras* from his level 13 of some 120 m in thickness. Krantz (1928, p. 47) provided a list of the ammonites from that level: *Pseudolissoceras zitteli*, *Neochetoceras waageni* Zittel, 1870 (= *Cieneguiticeras perlaevis* (Steuer, 1897) (as), *Simoceras* aff. *volanense* Oppel, 1863 (= *Volanoceras krantzense* Cantú-Chapa, 1990) (as), and *Pseudhimalayites steinmanni*. Even considering the huge thickness of the level 13, the first three species have concurrences in the Zitteli Zone (see also

Schweigert *et al.*, 2002); hence, this interval can be assumed also for the record of *Pseudhimalayites*, which most likely would belong to *Pseudhimalayites andinus*.

The species has also been recorded in the Caribbean area by the male specimens assigned to *Simocosmoceras pszczolkowskii* Myczyński, 1989 from Cuba and Mexico discussed above. In the Semiforme Zone of the Southern Tethys the genus is represented by *Pseudhimalayites kondai* Vigh, 1984 and *P. subpretiosus* (see below).

### *Pseudhimalayites steinmanni* (Haupt, 1907)

Figs. 5, 8–12; App. 1

- \*1907. *Aspidoceras steinmanni* n. sp. – Haupt, p. 189, pl. 7, fig. 1 (lectotype)
- ?1931. *Aspidoceras steinmanni* Haupt – Weaver, p. 434, figs. 339, 340
- non 1978. *Pseudhimalayites steinmanni* (Haupt) – Olóriz, p. 328, pl. 22, fig. 4
- non 1985. *Pseudhimalayites steinmanni* (Haupt) – Checa, p. 112, pl. 20, figs. 2–5
- non 1985. *Pseudhimalayites steinmanni* (Haupt) – Benetti, Pezzoni, p. 502, fig. 1
- non 1990. *Pseudhimalayites steinmanni* (Haupt) – Benetti *et al.*, p. 34, pl. 1, figs. 9–10
- non 1992. *Pseudhimalayites steinmanni* (Haupt) – Westermann, pl. 81, fig. 3
- \*1997. *Pseudhimalayites steinmanni* (Haupt) – Schweigert, pl. 2 (lectotype)
- non 2012. *Pseudhimalayites steinmanni* (Haupt) – Villaseñor *et al.*, pl. 1, figs. 18–20
- 2013. *Pseudhimalayites subpretiosus* (Uhlig) – Parent *et al.*, p. 39, figs. 24C, 25A
- 2015. *Pseudhimalayites subpretiosus* (Uhlig) – Parent *et al.*, p. 80, fig. 80A, B
- 2021. *Pseudhimalayites subpretiosus* (Uhlig) – Parent, Garrido, p. 58 (level CL-60)

**Lectotype.** The lectotype of *Aspidoceras steinmanni* Haupt (1907, pl. 7, fig. 1) was re-figured by Schweigert (1997, pl. 2). The collection of a practically identical specimen (Fig. 8A) with the same lithology allows us to identify its type horizon, which is most likely located in the uppermost Proximus Zone, at the top of level CL-59 (Fig. 2). This level differs in its lithology from the overlying level CL-60 which represents the *internispinosum*  $\alpha$  Hz. (Fig. 3) and has yielded most of the sample of *P. steinmanni* studied herein.

**Material.** One adult female with incomplete phragmocone (MOZ-PI-7279) from level CL-59. Seven adult and subadult female specimens (MOZ-PI-1286, 7528, 7529/1-2,

7530, 7533, and 7626) from level CL-60. Two complete male specimens from levels CL-62 (MOZ-PI-7612) and CL-79 (MOZ-PI-8349).

**Description.** Female. Widely variable adult size as indicated by the last adult septum which ranges through  $D = 68$ – $180$  mm. Stout and involute, heavily ornamented throughout the ontogeny for  $D > 10$  mm. Innermost whorls poorly known, globose and smooth for  $D < 3$  mm. The whorl section at  $5 < D < 15$  mm is suboval, slightly wider than high, becoming more depressed in the middle whorls, and more compressed towards the adult body-chamber. The sculpture is mainly preserved from about  $D = 10$  mm; it is composed of three rows of tubercles and weak ribs that become somewhat stronger in the ventral area of the body-chamber.

The umbilical spines are hollow, conical, and relatively sparse throughout the ontogeny, oscillating between 6 to 8 per half whorl. The lateral spines are larger, hollow, slightly more numerous, oscillating between 6 and 9 per half whorl; in the phragmocone they end spatulate while covered by the umbilical wall of the next outer whorl. The ventral bullate tubercles, are 7–8 per half whorl in the early ontogeny, gradually decreasing in number towards the adult body-chamber; from the adult phragmocone they become weaker and the ventral pairs gradually merge to form an uninterrupted rib.

The adult body-chamber bears only lateral and umbilical spines, which are both strong, connected one-to-one by a wide rib; the ventral area is covered by wide ribs only. The adult size at the peristome can be only estimated since none of our adult specimens preserves any signs of the peristome. It could range from about  $D = 120$  to more than 210 mm, assuming a half whorl body-chamber.

Male. Much smaller, adult size at peristome  $D_p = 28$ – $33$  mm; and at the base of the body-chamber is  $D_{ls} = 21$ – $22$  mm. Innermost whorls poorly known, globose and smooth for  $D < 5$  mm. From about  $D = 5$  mm there are small lateral spines which persist up to base of the adult body-chamber. Ventral tubercles observable from  $D = 13$  mm onwards, somewhat larger than the laterals with which they are connected by a rib born in the umbilical shoulder directed backwards. In the outer part of the phragmocone the lateral tubercles migrate towards the mid-flank, leaving space for a very short development of umbilical tubercles. The three rows of tubercles fade off from the end of the adult phragmocone. The adult body-chamber ( $L_{BC} = 120$  and c.  $170^\circ$ ) is smooth and slightly uncoiled; with long and narrow peristomatic lapets.

**Remarks and comparison.** The sexual dimorphic correspondence between the studied specimens cannot be proved by our incomplete comparison of the inner whorls. However, we have confidence in the association described

because of additional strong evidence: (1) undoubtedly the male specimens (Fig. 11B, C) show the morphology and sculpture diagnostic of the morphogenus *Simocoscocer*as Spath as do the females of *Pseudhimalayites*, (2) all females and the male from level CL-62 come from a very short stratigraphic interval, and (3) the females and males show the same morpho-ornamental relationships described for *P. andinus*.

In the Caribbean area (Cuba and Mexico) the genus is represented by specimens older than *P. steinmanni*, but closely comparable to *Pseudhimalayites* n. sp. A and *P. andinus* as discussed above.

The female of *P. steinmanni* is larger and stronger ornamented than the nearly coeval *Pseudhimalayites carchelejensis* Parent, Ramos-Agustino, Scherzinger, Schweigert, 2023 from the Ponti Zone of Southern Spain. The male of the latter bears prominent ventrolateral (or ventral) tubercles in the adult phragmocone, and the female has no ventral tubercles in the adult phragmocone or at comparable size.

In the Semiforme Zone of the Southern Tethys (approximately time-equivalent to the Zitteli Zone of the Andes) the genus is well represented as an ancillary element within the ammonite assemblages (e.g., Olóriz, 1978; Cresta, Pallini, 1984; Benetti, Pezzoni, 1985; Checa, 1985; Kutek, Wierzbowski, 1986; Benetti *et al.*, 1990; Fözy *et al.*, 1994; Cecca, 1999; Fözy, Scherzinger, 2013; Nannarone, Bilotta, 2021). Many of the reported occurrences were assigned to *P. steinmanni* or to species of *Simocoscocer*as, respectively. However, most of these ammonites must belong to *P. kondai* and *P. subpretiosus* (see discussion in Fözy *et al.*, 2022), since *P. steinmanni* is confined to the Internispinosum Zone, roughly equivalent to the Mediterranean Ponti Zone.

**Distribution and age.** The species is known only from the basal levels of the Internispinosum Zone at Cerro Lotena (present material) and Pampa Tril. Most of the specimens figured or cited as *P. steinmanni* from the Zitteli and Proximus zones actually belong to *P. andinus* as discussed above.

## BIOGEOGRAPHY AND EVOLUTION OF PSEUDHIMALAYITES

The aspidoceratid ammonite genus *Pseudhimalayites* developed during the interval Early Oxfordian–latest Early Tithonian in the Southern Tethys (Schweigert, 1997; Parent *et al.*, 2023). In the Andean basins the genus is currently known only from the Tithonian records described above, the earliest one from the base of the Zitteli Zone and the latest in the middle of the Internispinosum Zone (Fig. 13). Thus, according to the current knowledge the genus would have originated in the Southern Tethys during the Early

Oxfordian, and the Early Tithonian Andean lineage originated from that main lineage.

There is no Tithonian record of the genus *Pseudhimalayites* from Southeast Asia, the Indo-Madagascan realm, or Antarctica that could suggest a Transpacific, or via-Mozambique Corridor migration. However, there exist some few records from the Caribbean area (Myczyński, 1989; Villaseñor *et al.*, 2003, 2012) that, as discussed above, resemble *Pseudhimalayites* n. sp. A and *P. andinus*. This situation suggests that the first representatives of *Pseudhimalayites* could have arrived to the Southeastern Pacific through the Caribbean Corridor, during the latest Malarguensis Chron, or late Darwini Chron of the Tethyan time-scale (Fig. 14).

The evolutionary patterns of the Andean lineage mainly consist of changes in the adult female size (Fig. 5H) and the

timing of onset-offset of the rows of spines during the ontogeny (Figs. 5G):

- The adult size of *P. andinus* tr.  $\alpha$  is  $D_{ls} = 80\text{--}110$  mm (considering the possible mesoconch in Fig. 6B it would be  $42\text{--}110$  mm). *P. andinus* tr.  $\beta$  becomes smaller ( $D_{ls} = 55\text{--}65$  mm), and *P. steinmanni* reverts to evolve a larger adult size ( $D_{ls} = 50\text{--}180$  mm).
- *Pseudhimalayites* n. sp. A develops the umbilical and lateral tubercles from  $D = 15\text{--}20$  mm, and the subadult phragmocone lacks ventral spines. In both transients of *P. andinus* the umbilical and lateral tubercles develop earlier, from  $D = 5\text{--}10$  mm, and the ventral tubercles persist up to the adult phragmocone. The inner whorls of *P. steinmanni* are not discernible; the offset of the three rows of tubercles is produced at a larger size, but this could be due to the larger size they reach.

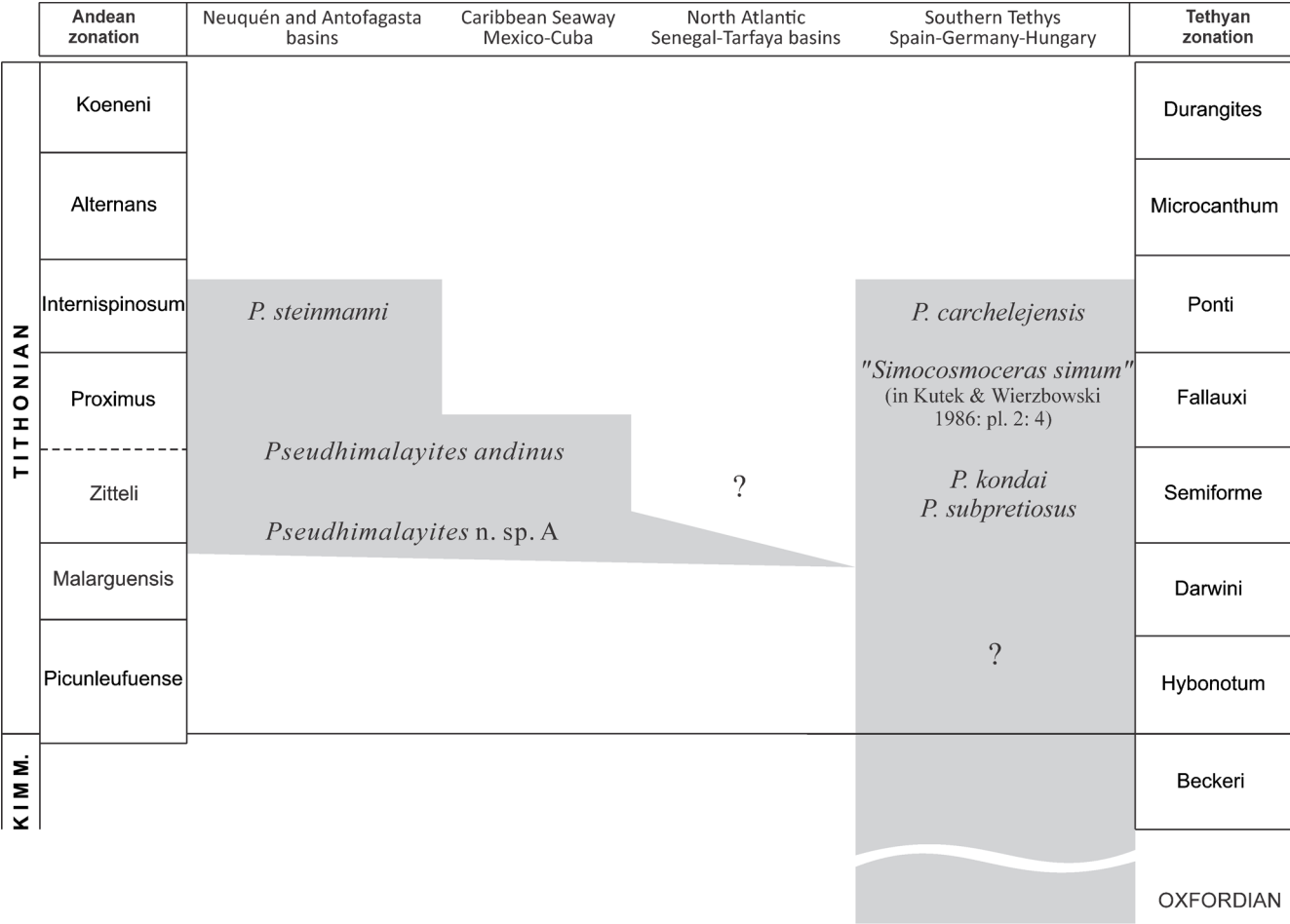


Fig. 14. Spatio-temporal model representing the origin and evolution of the Andean lineage of *Pseudhimalayites* from the main lineage of the Southern Tethys

The migration must have been during the late Darwini Chron through the Caribbean area where the genus is known by few records. Source of data in text and Parent *et al.* (2023)

- The males show a stable adult size at the peristome and show little sculptural changes, with the main trend being to lose the sculpture in the adult body-chamber, ventrally in *P. andinus* tr.  $\beta$ , and later completely in *P. steinmanni*.

The evolution of the Andean lineage shows significant differences with respect to that which is known in the Southern Tethys. We have no information about *Pseudhimalayites* in the Hybonotum and Darwini zones there, but the representatives of the Semiforme Zone are different from *Pseudhimalayites* n. sp. A., showing instead a closer resemblance to *P. andinus*. The latest Tethyan form, *P. carchelejensis*, is well differentiated from *P. steinmanni* as discussed above.

These differences between the two parallel lineages must have been produced by the episodes of partial or total isolation of the Neuquén Basin from the Palaeopacific Ocean (Spalletti *et al.*, 1999, 2000; Spalletti, 2013), leading to a progressive evolutionary differentiation, perhaps with only little (Proximus Zone) or no genetic exchange (Internispinosum Zone) between populations from the Tethys and the Neuquén Basin.

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## Appendix 1

## BIOMETRIC FEATURES OF THE STUDIED SPECIMENS

|                                        | <i>D</i> [mm] | <i>U/D</i> | <i>W/D</i> | <i>H<sub>i</sub>/D</i> | <i>T<sub>U</sub></i> | <i>T<sub>L</sub></i> | <i>T<sub>V</sub></i> | Ph, Bc,<br>Ph-Bc | adult or<br>juvenile | Remarks                                  | Figure  |
|----------------------------------------|---------------|------------|------------|------------------------|----------------------|----------------------|----------------------|------------------|----------------------|------------------------------------------|---------|
| <i>Pseudhimalayites</i> n. sp. A       |               |            |            |                        |                      |                      |                      |                  |                      |                                          |         |
| MOZ-PI-7523 (CL-13) - [M]              | 85.00         | 0.31       | 0.47       | 0.38                   | 6                    | 6                    | 0                    | Ph               | adult?               |                                          | 4       |
|                                        | 61.00         | 0.28       | 0.62       | 0.43                   | —                    | —                    | —                    | Ph               |                      |                                          |         |
|                                        | 36.00         | 0.28       | —          | —                      | 3                    | 5                    | —                    | Ph               |                      |                                          |         |
| <i>Pseudhimalayites andinus</i>        |               |            |            |                        |                      |                      |                      |                  |                      |                                          |         |
| MOZ-PI-4050 (CL-33) - [M] tr. $\alpha$ | 94.00         | 0.37       | 0.59       | 0.37                   | 8                    | 8                    | 3                    | Ph               | adult                |                                          | 6A      |
|                                        | 63.00         | —          | —          | —                      | 9                    | 8                    | 8                    | Ph               |                      |                                          |         |
|                                        | 46.00         | —          | —          | —                      | 9                    | 8                    | —                    | Ph               |                      |                                          |         |
|                                        | 33.00         | —          | —          | —                      | 9                    | 8                    | —                    | Ph               |                      |                                          |         |
| MOZ-PI-7524 (CL-33) - [M] tr. $\alpha$ | 42.00         | 0.32       | 0.60       | 0.36                   | 12                   | 9                    | 11                   | Ph-Bc            | adult                |                                          | 6B      |
| MOZ-PI-4903 (CL-37) - [m] tr. $\alpha$ | 29.00         | 0.32       | 0.43       | —                      | 8                    | 9                    | 11                   | Bc               | adult                | $L_{BC} = 77^\circ$<br>$D_{ls} = 27$ mm  | 6C      |
|                                        | 23.00         | 0.29       | 0.43       | —                      | 5                    | 10                   | 11                   | Ph               |                      |                                          |         |
|                                        | 16.00         | 0.23       | —          | —                      | 0                    | 9                    | —                    | Ph               |                      |                                          |         |
| Holotype [m] tr. $\alpha$              | 29.50         | 0.34       | 0.38       | 0.34                   | 8                    | 8                    | 10                   | Bc               | adult                | (1)                                      |         |
|                                        | 20.00         | 0.23       | 0.58       | —                      | —                    | —                    | —                    | Ph               |                      |                                          |         |
| MOZ-PI-7525 (CL-41) - [M] tr. $\alpha$ | 18.00         | 0.29       | 0.65       | 0.42                   | 7                    | 8                    | 7                    | Ph               |                      |                                          | 7A      |
| MOZ-PI-7615 (CL-56) - [M] tr. $\beta$  | 65.00         | 0.36       | 0.62       | —                      | 7                    | 8                    | 3                    | Bc               | adult                |                                          | 7C      |
|                                        | 53.00         | 0.36       | 0.66       | 0.36                   | 7                    | 8                    | 5                    | Ph-Bc            |                      |                                          |         |
|                                        | 37.00         | 0.29       | 0.66       | —                      | 6                    | 6                    | 5                    | Ph               |                      |                                          |         |
| <i>Pseudhimalayites steinmanni</i>     |               |            |            |                        |                      |                      |                      |                  |                      |                                          |         |
| MOZ-PI-7279 (CL-59) - [M]              | 128.00        | 0.36       | 0.59       | 0.31                   | 7                    | 6                    | 9                    | Bc               | juvenile             | $D_{ls} = 90$ mm                         | 8A      |
| MOZ-PI-7626 (CL-60) - [M]              | 67.00         | 0.37       | 0.60       | —                      | 8                    | 8                    | 7                    | Ph-Bc            | juvenile             |                                          | 8B      |
|                                        | 33.00         | 0.27       | 0.45       | 0.36                   | 7                    | 7                    | 7                    | Ph               |                      |                                          |         |
|                                        | 10.00         | —          | —          | —                      | 0                    | 6                    | —                    |                  |                      |                                          |         |
| MOZ-PI-7528 (CL-60) - [M]              | 90.00         | 0.34       | 0.56       | —                      | 7                    | 7                    | 3                    | Bc               | adult                |                                          | 9A      |
|                                        | 68.00         | 0.33       | 0.60       | —                      | 7                    | 7                    | 7                    | Ph-Bc            |                      |                                          |         |
| MOZ-PI-7529/1 (CL-60) - [M]            | 117.00        | 0.36       | 0.50       | —                      | 8                    | 8                    | 4                    | Bc               | adult                |                                          | 9B      |
|                                        | 85.00         | —          | —          | —                      | 7                    | 7                    | 7                    | Ph-Bc            |                      |                                          |         |
| MOZ-PI-7530 (CL-60) - [M]              | 152.00        | 0.36       | 0.46       | —                      | 8                    | 8                    | 0                    | Ph-Bc            | adult                |                                          | 10, 11A |
|                                        | 103.00        | 0.32       | 0.58       | —                      | 6                    | 6                    | 6                    | Ph               |                      |                                          |         |
| MOZ-PI-1286 (CL-60) - [M]              | 180.00        | 0.38       | 0.48       | —                      | 8                    | 8                    | 0                    | Ph-Bc            | adult                |                                          | 13I     |
|                                        | 135.00        | 0.33       | 0.50       | —                      | 7                    | 9                    | 2                    | Ph               |                      |                                          |         |
| MOZ-PI-7612 (CL-62) - [m]              | 33.00         | 0.33       | —          | —                      | 0                    | 0                    | 0                    | Bc               | adult                |                                          | 11B     |
|                                        | 25.00         | 0.28       | —          | —                      | 5                    | 10                   | 9                    | Ph               |                      |                                          |         |
| MOZ-PI-8349 (CL-79) - [m]              | 28.00         | 0.29       | —          | —                      | 3                    | 4                    | 2                    | Bc               | adult                | $L_{BC} = 120^\circ$<br>$D_{ls} = 21$ mm | 11C     |
|                                        | 25.00         | —          | —          | —                      | 6                    | 7                    | —                    | Ph               |                      |                                          |         |
|                                        | 19.00         | 0.24       | —          | —                      | 0                    | 11                   | 13                   | Ph               |                      |                                          |         |
| Lectotype [M]                          | 124.00        | 0.34       | 0.62       | 0.40                   | 7                    | 6                    | 6                    | Bc               | adult                | (2)                                      |         |
|                                        | 95.00         | 0.32       | 0.61       | 0.39                   | 7                    | 7                    | 7                    | Ph               |                      |                                          |         |

Abbreviations and symbols explained in text.

Ph-Bc indicates observations at the base of the body-chamber.

(1): measurements from Leanza, Olóriz (1987); (2): measurements from Schweigert (1997)

