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Additional Tithonian and Berriasian ammonites from the Vaca Muerta Formation in Pampa Tril, Neuquén Basin, Argentina

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Keywords: ammonites, sexual dimorphism, Tithonian, Berriasian, Neuquén Basin, Vaca Muerta Formation.

Abstract. The ammonite fauna of the Tithonian–Berriasian of the Vaca Muerta Formation in Pampa Tril has been recently described in detail. New important specimens and additional information are presented in this paper. The phyletic evolution of *Choicensisphinctes*, passing from *C. platyconus* to *C. erinoides* is confirmed, as well as the sexual dimorphic correspondence of this latter with *C. mendozanus*. A microconch of the genus *Krantziceras* is described for the first time. New specimens of *Substeueroceras koeneni* identical to the paralectotype, along with material already described from the *koeneni* Hz. (Koeneni Zone), point to the fixation of this horizon as the type horizon of the species. New specimens of *Subthurmannia boissieri* from the Damesi Zone match clearly the range of variation of this species in Spain, thus providing an element for time-correlation with the Tethyan standard scale. Additional material from the *internispinosum* alpha Hz. confirms the origin of *W. internispinosum* from *C. proximus* by the inception of an evolutionary innovation in the juvenile ontogeny.

INTRODUCTION

The stratigraphy and the ammonite fauna of the Vaca Muerta Formation in the Pampa Tril area (Fig. 1) has been described in detail in a previous paper (Parent *et al.*, 2015, including complete list of references).

The Vaca Muerta Fm in Pampa Tril reaches 421.6 m in thickness in Pampa Tril, covering the interval Tithonian–Lower Valanginian (Andean sense). The Vaca Muerta Fm overlies the Tordillo Fm (Kimmeridgian continental sandstones) and underlies the Quintuco Fm (Lower Valanginian greenish gray claystones). It consists of a succession of shales with several relatively thin intercalations of calcareous shales and fine-grained sandstones. Four lithofacies are differentiated: (1) bituminous shale, (2) sandy shale, (3) calcareous shale, and (4) fine-grained sandstone. The sequence reflects an upward-shallowing marine environment with euxinic-anoxic passing to dysoxic conditions, and increasing input of terrigenous epiclastics along an outer ramp. The fauna of the succession is composed mainly of ammonites, followed by bivalves, gastropods, reptiles, fishes, and nautiloids; ammonites occur in abundance throughout the sequence, mainly in the calcareous and sandstone levels. Nine ammonite families are represented in the fauna, including 35 genera.

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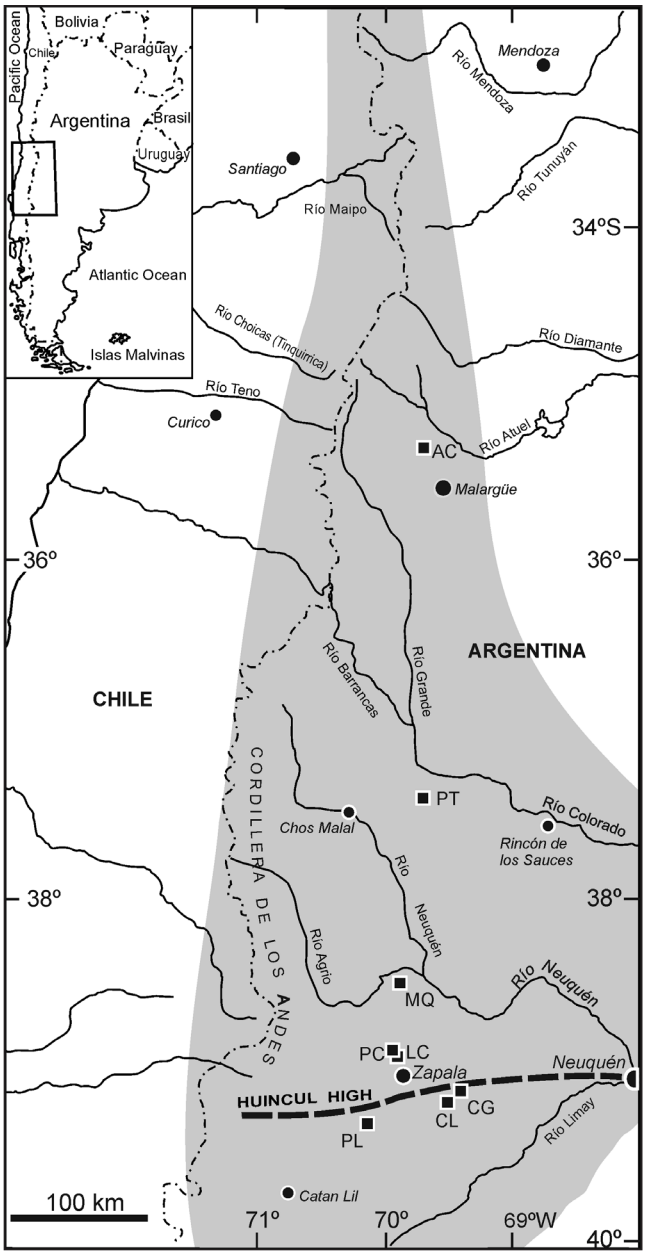

Fig. 1. Neuquén (or Neuquén-Mendoza) Basin (gray area), west-central Argentina, with indication of the locality Pampa Tril (PT) and other localities mentioned in the text

PL: Picún Leufú, CL: Cerro Lotena, CG: Cerro Granito, LC: Los Catutos, PC: Portada Covunco, MQ: Mallín Quemado, AC: Arroyo Cieneguita

The well controlled stratigraphic distribution of the succession of ammonite-assemblages has allowed the establishment of a confident chronostratigraphic subdivision of the column at zonal level and the recognition of fourteen ammonite biohorizons (Parent *et al*., 2015: figs. 5, 86) – here summarized in Fig. 2.

Since the study of Parent *et al*. (2015) new samples have been obtained, and these new ammonites, belonging to species described in that paper, provide additional information about the systematics, sexual dimorphism and chronostratigraphy. These new plus additional specimens as well as new data are presented and discussed in this paper. In addition, new results (Garrido, Parent 2017) from the locality Mallín Quemado (Fig. 1) provide support for the time-correlation of the lower part of the Noduliferum Zone with the Jacobi Zone as formerly proposed from the study of the Pampa Tril fauna.

SYSTEMATIC PALAEONTOLOGY

The material described is housed at the Museo Prof. Olsacher, Zapala (MOZ-PI). Macroconch (female): [M], microconch (male): [m]. Levels of occurrence of the specimens denoted by the level number and the prefix PT (Pampa Tril), referred to Fig. 2 (this report) adapted from Parent *et al*. (2015: fig. 5) restricted to the interval Tithonian-Berriasian. All species considered below have already been described comprehensively in a previous study (Parent *et al*., 2015).

Order Ammonitida Fischer, 1882

Suborder Ammonitina Fischer, 1882

Superfamily Perisphinctoidea Steinmann, 1890

Family Ataxioceratidae Buckman, 1921

Subfamily Zapaliinae Parent, Schweigert, Scherzinger & Garrido, 2017

Remarks. – This subfamily comprises five genera of mainly Tithonian ammonites: *Zapalia* Leanza & Zeiss (1990), *Indansites* Vennari, 2016, *Choicensisphinctes*, *Krantziceras*, and *Platydiscus* Parent *et al*., 2011b. The palaeogeographic distribution of the subfamily was rather broad, right through the Palaeopacific border of southern South America and probably reaching the Caribbean area. It was clearly separated from the distribution of the Virgatosphinctinae Spath, 1923 (sensu Énay, 2009), which are confined in the southern Tethys (mainly India, Madagascar, east Africa).

Genus *Choicensisphinctes* Leanza, 1980

Type species. – *Perisphinctes choicensis* Burckhardt, 1903; by original designation.

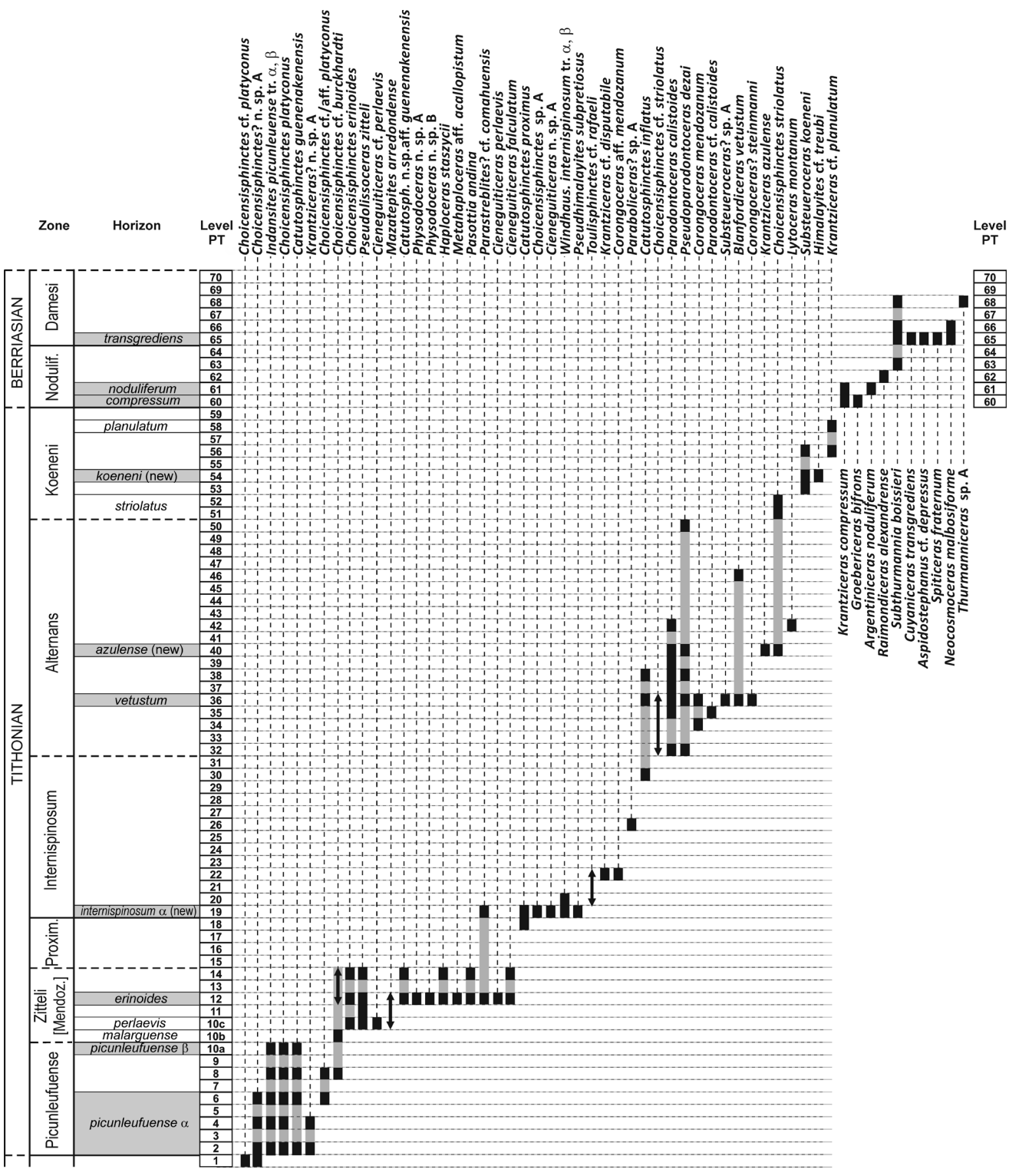

Fig. 2. Distribution of the ammonite fauna in the studied section of Pampa Tril through levels PT-1 to PT-70, including the species studied in this paper

Solid bars indicate normal in-situ records; gray bars the virtual recorded range; arrowheaded lines indicate the estimated position of loosely collected specimen(s). Horizons recognized firmly indicated by gray boxes, tentatively by blank boxes. Broken lines indicate non-standard zones. Abbreviations: Mendoz. (Mendozanus), Proxim. (Proximus), Nodulif. (Noduliferum)

Choicensisphinctes platyconus Parent, Garrido, Schweigert & Scherzinger, 2011
Fig. 3

Remarks. – An adult macroconch from level PT-8, Picunleufuense Zone. This specimen is sufficiently complete and well preserved to complete the picture of the evolutionary succession of morphological transients of this species within the Picunleufuense Zone (see Parent *et al.*, 2015: figs. 12–17). Similar specimens already occur in level PT-6 as rare variants, and in level PT-8 this becomes the typical morphotype.

The inner whorls are moderately evolute with a subrectangular whorl section, higher than wide. The sculpture is composed of fine, prosocline, bi- or rarely trifurcated ribs. The outer whorls of the phragmocone are more inflated, with primaries much stronger than the fine ventral ribs; in the adult phragmocone occur some polyschizotomic ribs

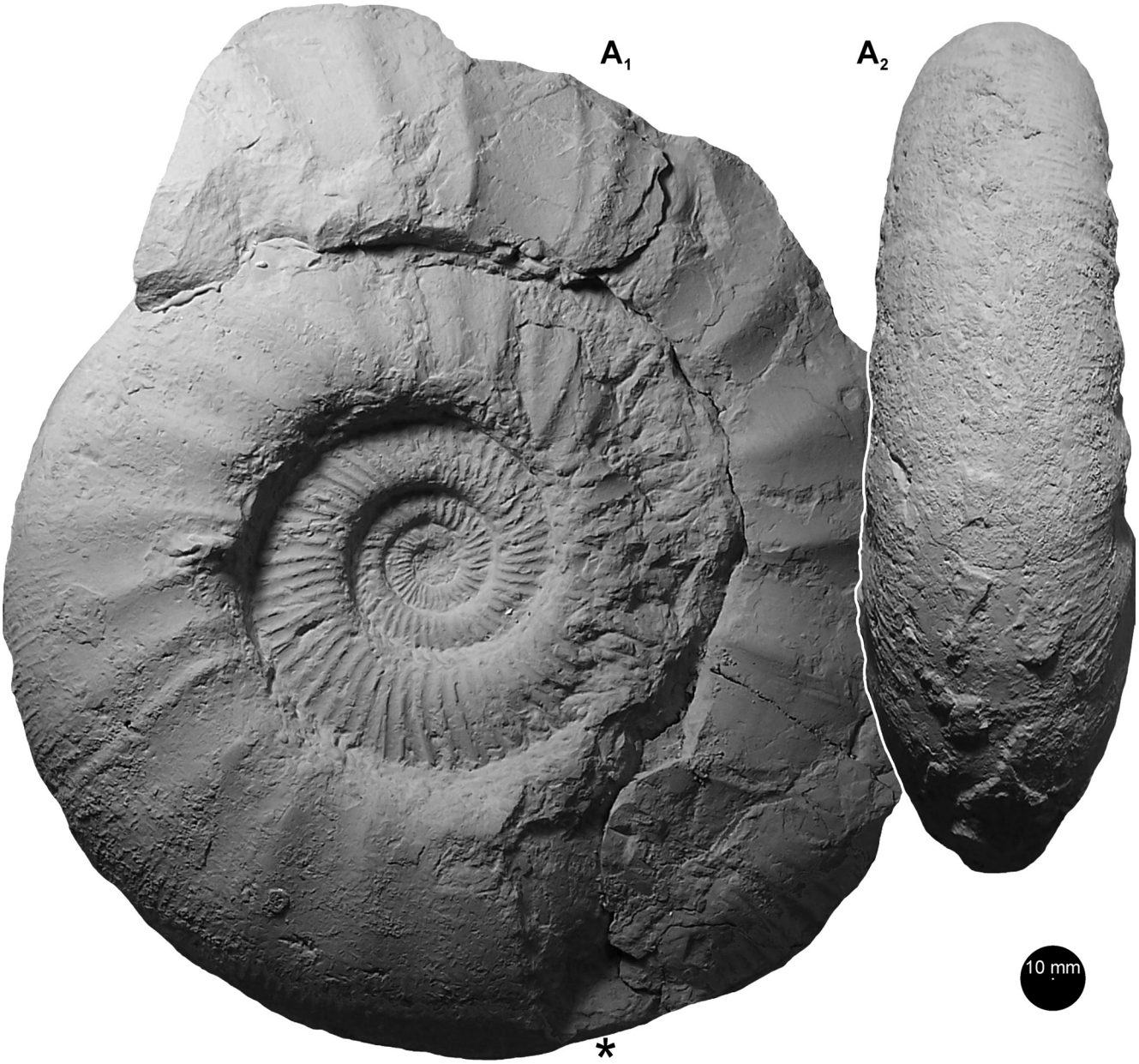

Fig. 3. *Choicensisphinctes platyconus* Parent, Garrido, Schweigert & Scherzinger, level PT-8, Picunleufuense Z., almost complete adult [M] (MOZ-PI 7908). The asterisk indicates the last septum. Natural size (×1)

typical of the genus. The bodychamber, beginning at a shell diameter of 139 mm, is similar to that of the holotype (Parent *et al.*, 2011a: fig. 14A), with strong and widely separated primaries ending close to the ventro-lateral shoulder; the venter is smooth and rounded.

Choicensisphinctes erinoides (Burckhardt, 1903)
Fig. 4A, B

Remarks. – The microconch in Fig. 4A is refigured from Parent *et al*. (2015: fig. 29A) with additional preparation to show the inner whorls and the characteristic ribbing of the bodychamber. The importance of this specimen is that it closely resembles the lectotype of *Virgatites mendozanus* Burckhardt, 1911, which is assumed to be the corresponding microconch of *C. erinoides*. Thus, this is additional documentation of the sexual dimorphic correspondence which is well represented in other localities like Arroyo Cieneguita (Parent *et al.*, 2011b).

The specimen in Fig. 4B represents a more compressed and involute variant of the species in the *erinoides* Hz. which has not been recorded previously. It seems to be a small adult macroconch having a narrow umbilicus and an uncoiled bodychamber, but the bodychamber is too incomplete for a definitive dimorphic assignation. It is interesting to note that identical small adult macroconchs occur in equivalent levels in Cerro Lotena and Cerro Granito, associated with large macroconchs identical to the holotype of *C. erinoides* which is a macroconch phragmocone.

Genus *Krantziceras* Parent, Scherzinger & Schweigert, 2011

Type species. – *Krantziceras compressum* Parent *et al.*, 2011b; by original designation.

Krantziceras azulense (Leanza, 1945)
Fig. 5A, B

Remarks. – The adult macroconch in Fig. 5A (level PT-40, *azulense* Hz., Alternans Zone) has been recently figured in Parent *et al*. (2015: fig. 34A), but the matrix formerly obscuring the umbilicus has been removed. Thus, the innermost whorls are visible now and can be compared with those of the specimen in Fig. 5B which is considered as the corresponding microconch, coming from the same level. The microconch is an adult specimen as shown by the incipient uncoiling at the beginning of the bodychamber, and the variocostation. The inner whorls are identical to those of the macroconch. The ribs become stronger from the end of the phragmocone, especially on the venter, and are bifurcated and wider-spaced. This is the first documentation of sexual

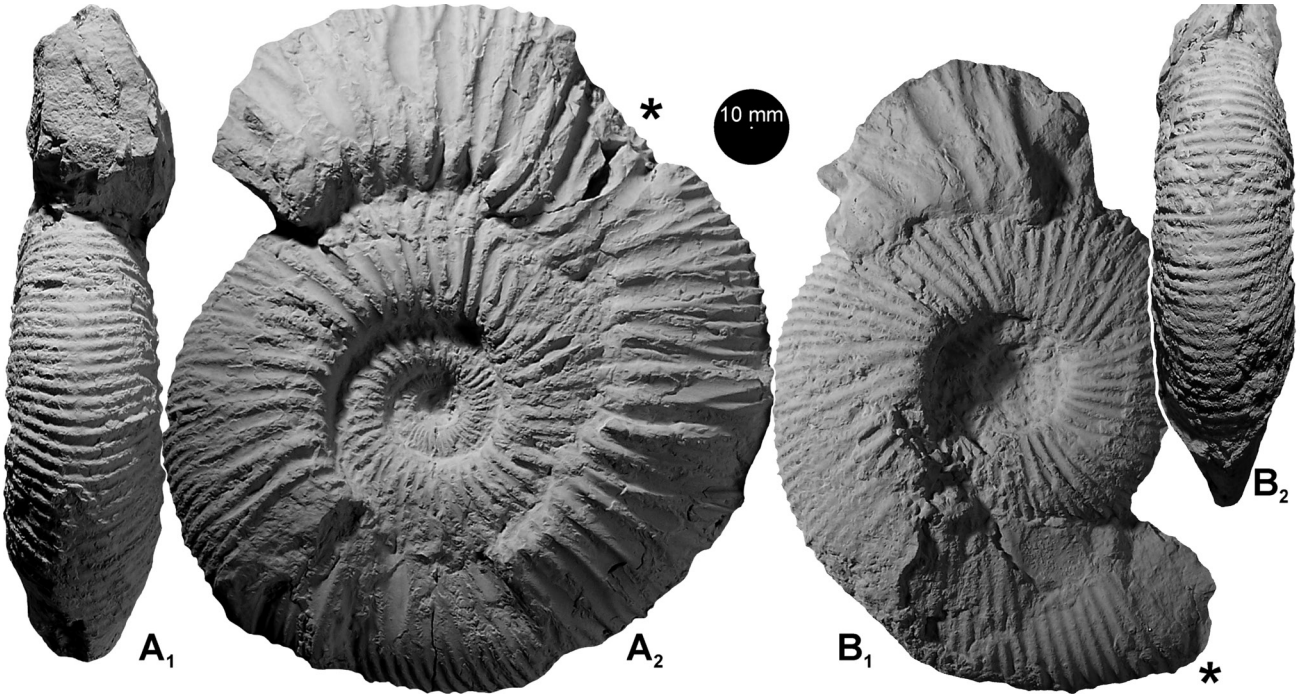

Fig. 4. *Choicensisphinctes erinoides* (Burckhardt, 1903), level PT-12, *erinoides* Hz., Zitteli [Mendozanus] Zone

A – almost complete adult [m] (MOZ-PI-8453); B – adult [M?] phragmocone with a portion of bodychamber (MOZ-PI-8452). Natural size (×1). The asterisk indicates the last septum

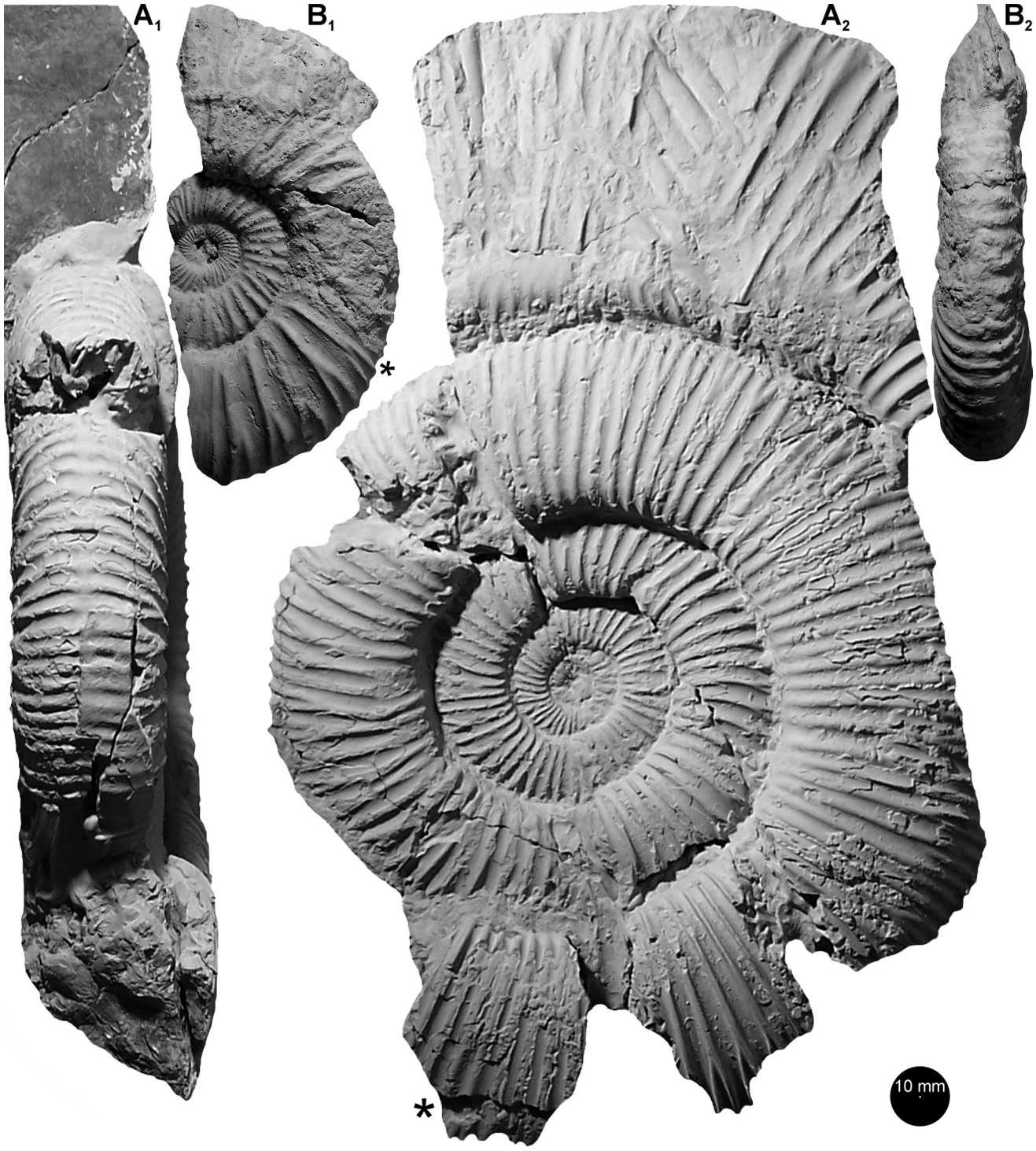

Fig. 5. *Krantziceras azulense* (Leanza, 1945), level PT-40, *azulense* Hz., Alternans Z

A – nearly comple adult [M] (MOZ-PI 8493); B – adult microconch with part of bodychamber (MOZ-PI 8493/2). All in natural size (×1). The asterisk indicates the last septum

dimorphism within this long-ranging genus (at least earliest Tithonian to earliest Berriasian).

Family Neocomitidae Salfeld, 1921

Subfamily Berriasellinae Spath, 1922

Genus *Substeueroceras* Spath, 1923

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

Substeueroceras koeneni (Steuer, 1897)
Fig. 6

Remarks. – The specimen in Fig. 6 is an incomplete adult as indicated by the strong uncoiling of the last part of the bodychamber to be preserved. Considering the larger size of the adult macroconchs present at this level PT-54 (*koeneni* Hz.), it is likely that this specimen represents a microconch. The whorls of the phragmocone are identical to those of the paralectotype (Steuer, 1897: pl. 17: 4-5) refigured in Parent *et al.* (2011b: fig. C in App. 2), a compressed and involute, finely ribbed variant. On the other hand, this specimen contributes to a more complete picture of the characteristic assemblage of the bio-horizon. However, considering the full morphological identity with the type specimens it is probable that the type horizon of this species in Arroyo Cieneguita corresponds to the *koeneni* Hz. of the Upper Tithonian Koeneni Zone.

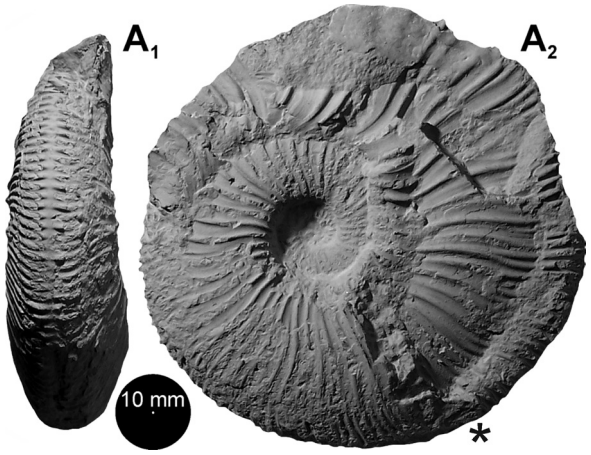

Fig. 6. *Substeueroceras koeneni* (Steuer), level PT-54, *koeneni* Hz., Koeneni Z. Adult specimen with incomplete bodychamber (MOZ-PI 8495/1). Natural size (×1). The asterisk indicates the last septum

Genus *Subthurmannia* Spath, 1939

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

Subthurmannia boissieri (Pictet, 1867)
Figs. 7A–D, 8A–E

Remarks. – The new sample available comes from level PT-68 (Damesi Zone) and is composed of specimens with only the beginning of the bodychamber. The inner whorls show a *Berriasella*-like ribbing style, with indistinctly bifurcated primaries; from 40-50 mm in shell diameter onwards the sculpture passes to a *Subthurmannia*-like ribbing stage consisting of flexuous primaries, bi- or trifurcating from a lamellar (bulla-like) tubercle on the umbilical shoulder and commonly again at mid-flank. The specimens show, from a shell diameter of 20-30 mm, a continuous spectrum of variation, from strongly ribbed morphotypes (Fig. 7) to more finely and denser ribbed morphotypes (Fig. 8). However, the whorl section and the relative umbilical width show very little variation. Between the end of the adult phragmocone and the beginning of the bodychamber (shell diameter 50 to 100 mm) the number of primary ribs per half-whorl ranges 20 to 33; the relative umbilical diameter ranges 0.25 to 0.35; and the relative whorl width ranges 0.20 to 0.30. These measurements were on the whole sample of ammonites from level PT-68, including the specimens studied in Parent *et al.* (2015) from the same stratigraphic level.

The shape of the bodychamber is not well known in the specimens from this level (PT-68), but the phragmocones match perfectly in size and morphology those specimens figured by Tavera (1985: pl. 44: 1–5, pl. 45: 4, as "*Fauriella*") from the Boissieri Zone of Cehegín, Spain.

The present sample must be considered as a snapshot of this species during a probably very short time-interval represented by only a single, 0.3 m-thick event-like bed within the succession. As already noted in Parent *et al.* (2015) the present specimens fit well with the diagnosis of the genus *Subthurmannia* (Wright *et al.*, 1996: 55), and in particular with the original description of *Ammonites boissieri* Pictet (1867: 79–80, pl. 15: 1, lectotype), assuming some natural degree of variation in the strength and density of ribbing.

Family Himalayitidae Spath, 1925

Genus *Windhauseniceras* Leanza, 1945

Type species. – *Perisphinctes internispinosus* Krantz, 1926; by original designation.

Windhauseniceras internispinosum (Krantz, 1926)
Figs. 9B,C–12

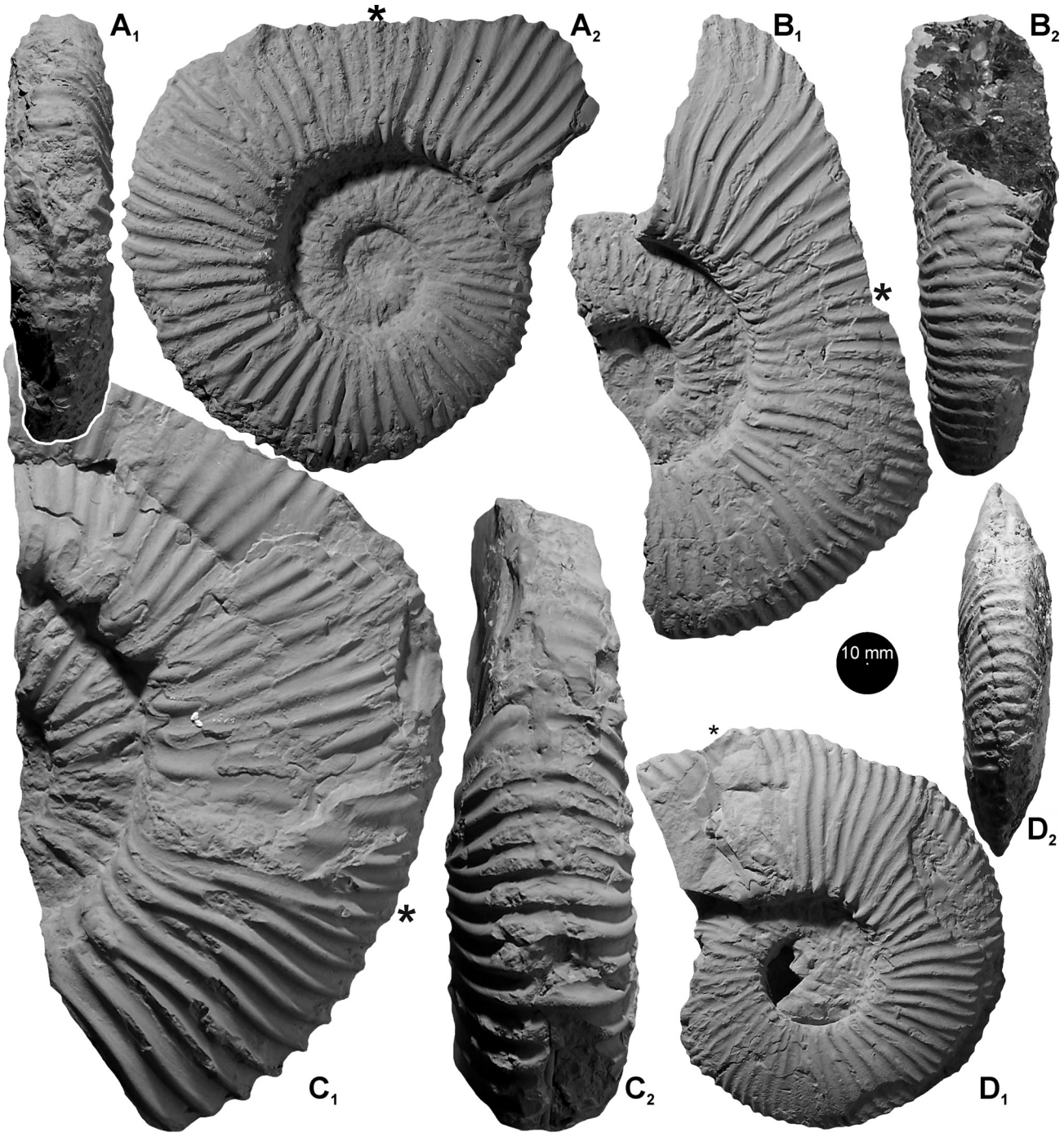

Fig. 7. *Subthurmannia boissieri* (Pictet) [M], level PT-68, Damesi Zone

A–C – adult specimens with the beginning of the bodychamber (MOZ-PI-8160, 8157, 8161); D – subadult phragmocone (MOZ-PI-8150). All natural size (×1). Asterisk at last septum

Remarks. – *W. internispinosum* clearly seems to have originated from *Catutosphinctes proximus* (Steuer, 1897) through a short transition well recorded in the *internispinosum* alpha Hz. (Fig. 12). After a juvenile evolutionary innovation consisting of the development of a more or less marked tuberculate or bullate stage in specimens which re-

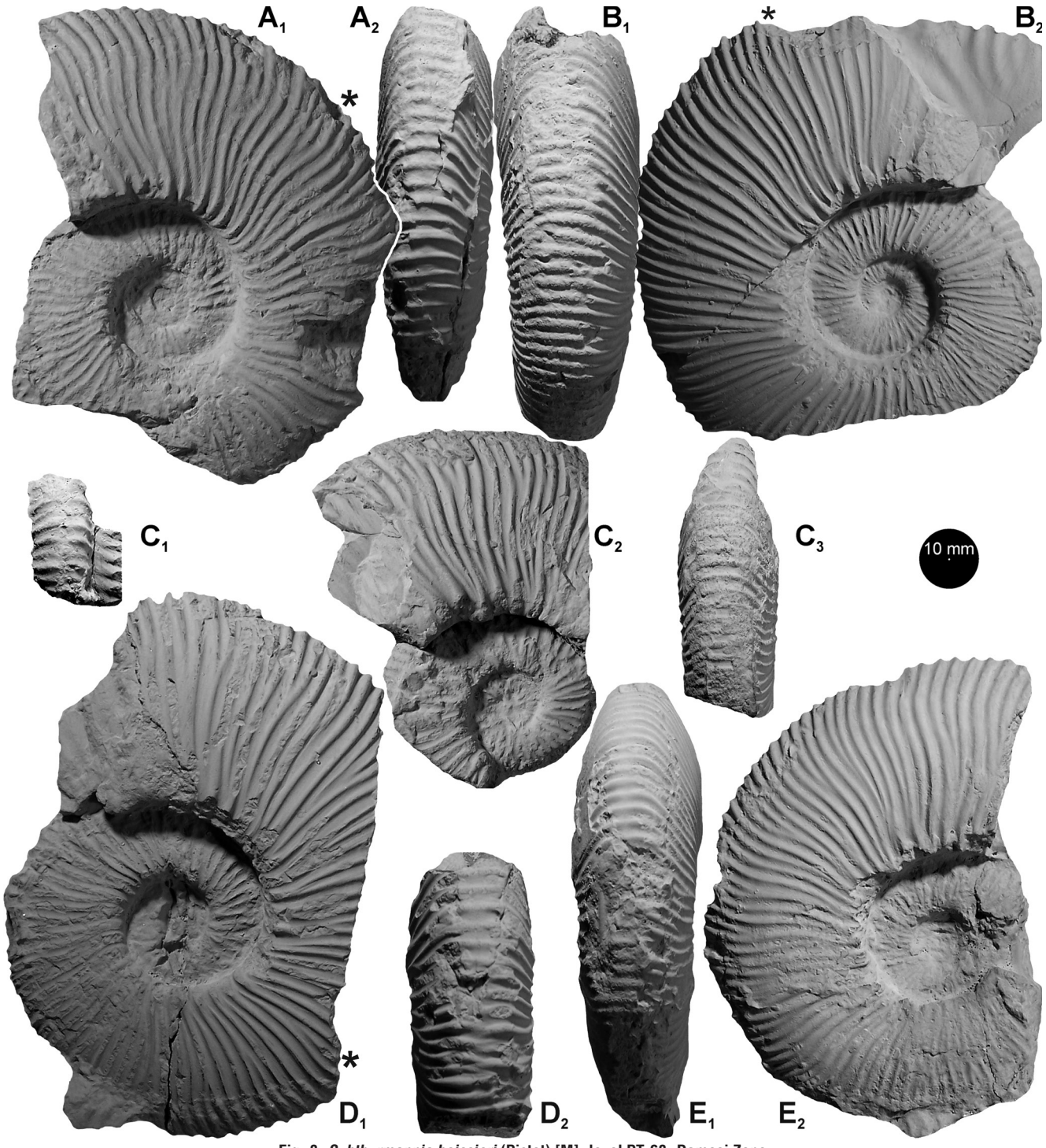

Fig. 8. ***Subthurmannia boissieri*** **(Pictet) [M], level PT-68, Damesi Zone**

A–B – adult specimens with the beginning of the bodychamber (MOZ-PI-8168, 8158); C – adult phragmocone (MOZ-PI-8155); C_1: ventral view of the penultimate whorl; D–E – adult specimens with the beginning of the bodychamber (MOZ-PI-8154, 8173). All natural size (×1). Asterisk at last septum

tain the aspect of *Catutosphinctes* in their outer whorls (Parent *et al.*, 2015: fig. 74), the phyletic evolution of this species leads to larger macroconchs (transient beta). These latter have more depressed inner whorls and an adult phragmocone and bodychamber with a higher than wide whorl section.

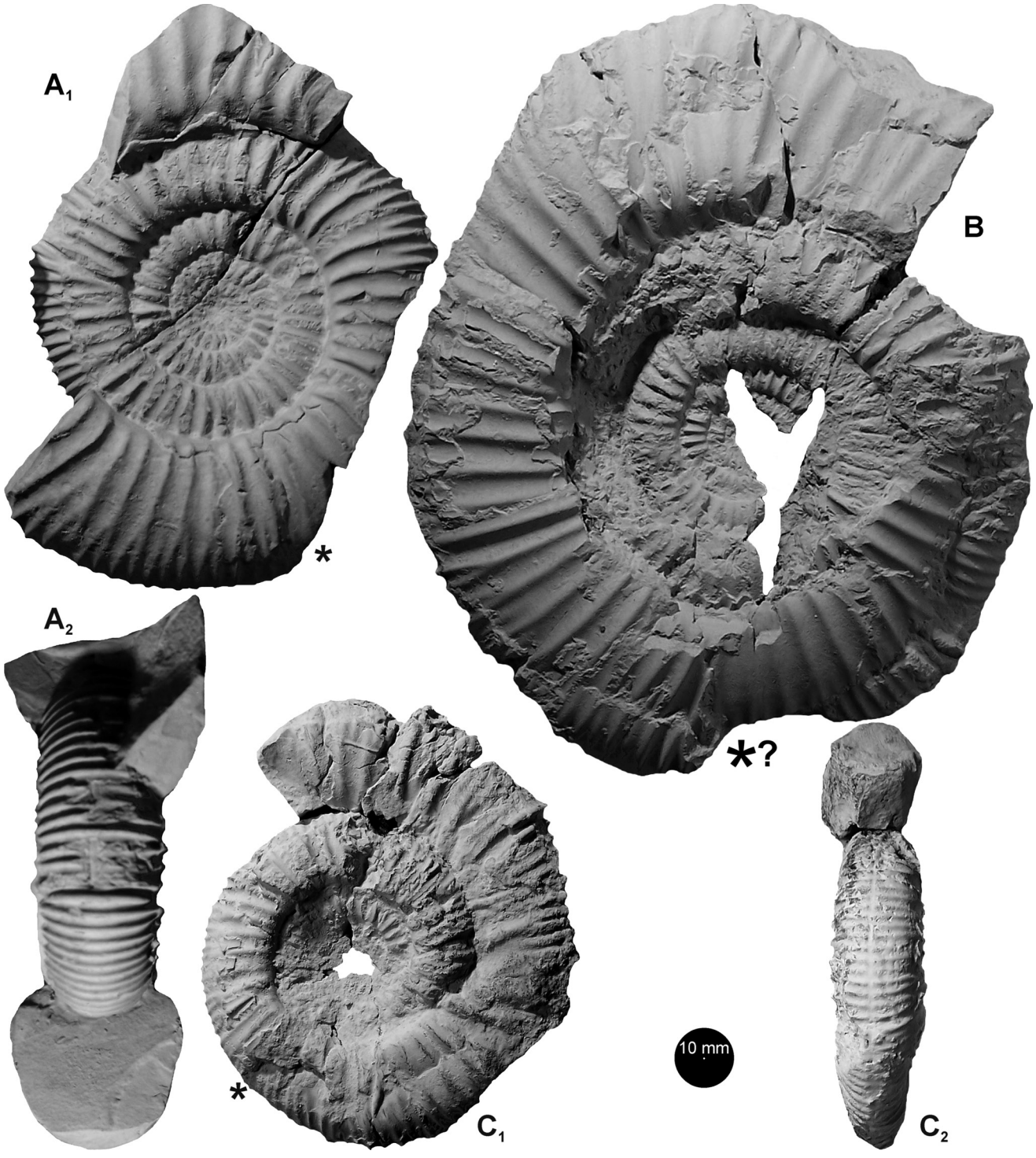

Fig. 9. A: *Catutosphinctes proximus* (Steuer, 1897); B–C: *Windhauseniceras internispinosum* (Krantz) transient alpha, level PT-19, *internispinosum* alpha Hz., Internispinosum Z

A – almost complete adult [M] (MOZ-PI-8026), level PT-19, *internispinosum* alpha Hz., Internispinosum Z; B – almost complete adult [M] (MOZ-PI-8036); early form with *Catutosphinctes*-like outer whorls; C – complete adult [m] (MOZ-PI 8432/1). All natural size (×1). Asterisk at last septum

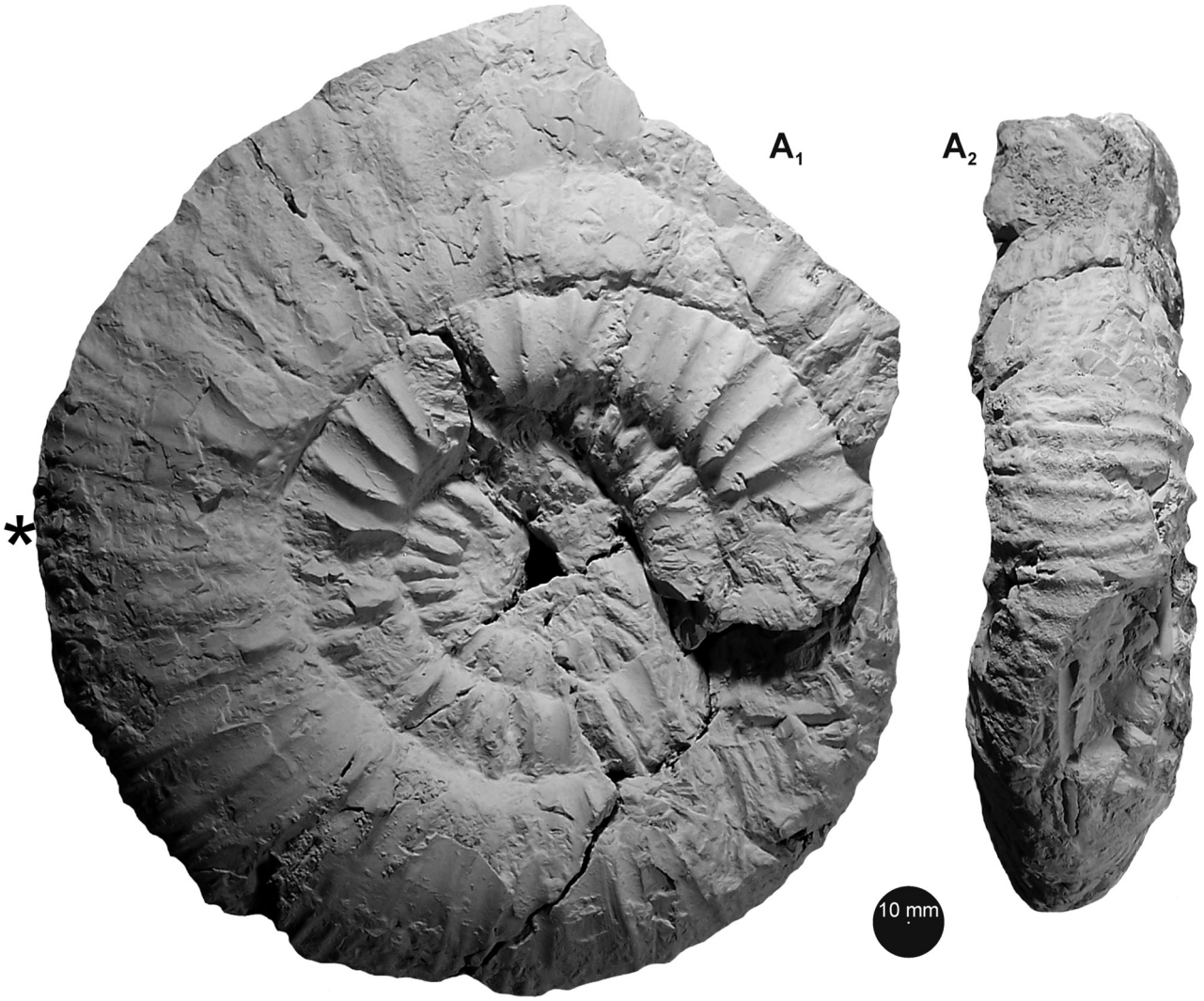

Fig. 10. ***Windhauseniceras internispinosum*** **(Krantz) transient alpha [M], level PT-19,** ***internispinosum*** **alpha Hz., Internispinosum Z, almost complete adult macroconch (MOZ-PI 8050). Natural size (×1). The asterisk indicates the last septum.**

The morphological transition between *W. internispinosum* and *C. proximus* as represented in the level PT-19 (*internispinosum* alpha Hz.), is herein illustrated by a typical *C. proximus* [M] (Fig. 9A), a transitional sexual dimorphic pair with *Catutosphinctes*-like outer whorls (Fig. 9B-C), and a typical *W. internispinosum* transient alpha [M] (Fig. 10). The adult macroconch of transient beta in Fig. 11 (refigured from Parent *et al*., 2015: fig. 75, with additional preparation) shows the migration of the strong ribbing and tubercles towards larger diameters with respect to the older transient alpha.

The intermediate specimens cannot be clearly assigned to one of the two genera, much less if found in isolation. The transition observed in the level PT-19 could be considered just as intraspecific variation, so that the separation into two different species is nothing but a convenient taxonomic decision for practical purposes. This situation may be frequent in the fossil record but hard to determine if the material is not sampled bed-by-bed. On the other hand, it is very likely that in other localities the process of the gradual origin of the species *W. internispinosum*, which may have spanned hundreds or thousands of years, could be recorded in other instance, or time-interval, where the spectrum of variation could be dominated by the one or the other morphotype. In the case of the material of level PT-19 both extremes of variation are rather balanced in terms of the number of macroconch specimens, and intermediate specimens are less abundant.

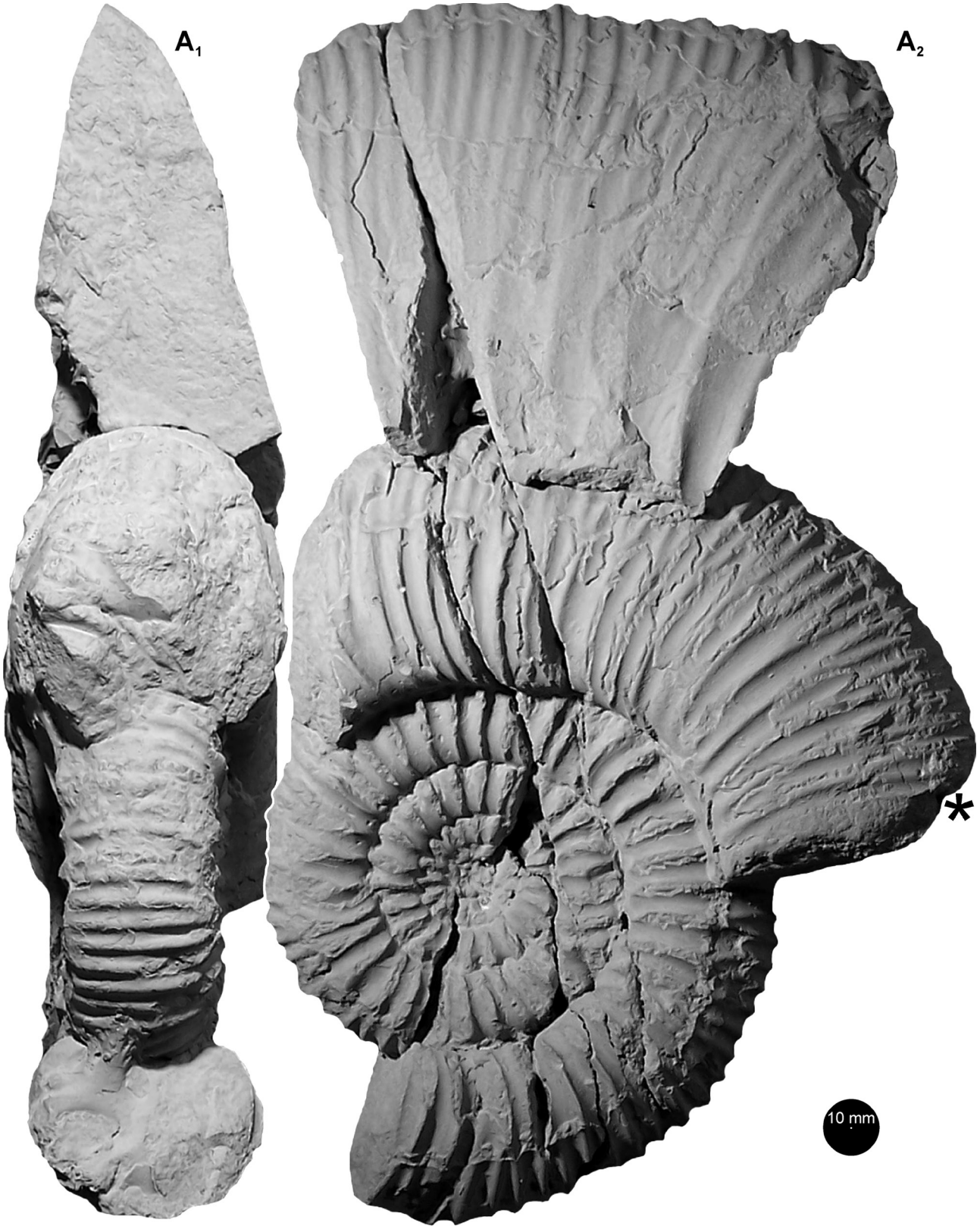

Fig. 11. ***Windhauseniceras internispinosum*** **(Krantz) transient beta [M], level PT-20, Internispinosum Z, almost complete adult with bodychamber (MOZ-PI 8465). Natural size (×1). The asterisk indicates last septum**

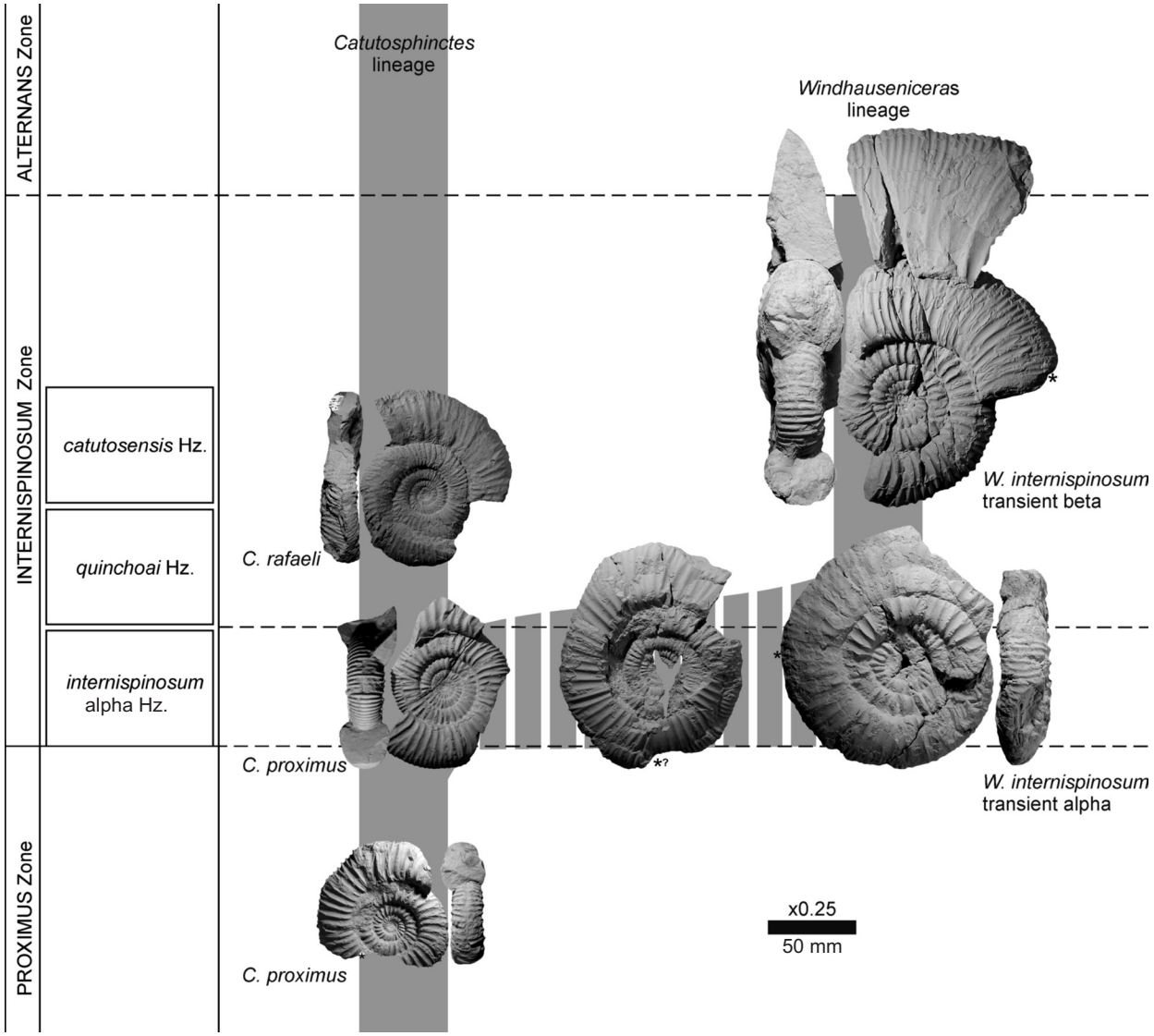

Fig. 12. Representation of the origin of the genus *Windhauseniceras* from *Catutosphinctes proximus* in the basal Internispinosum Zone (the three specimens of the *internispinosum* alpha Hz. are shown in Figs. 9-10 in natural size). During the time-interval recorded by the *internispinosum* alpha Hz. there coexisted typical individuals of *C. proximus* with intermediate forms (*Windhauseniceras*-like inner whorls and *Catutosphinctes*-like outer whorls) and others with juvenile and adult morphology of the early transient alpha of *W. internispinosum*. The relevant segment of the *Catutosphinctes* lineage is illustrated with an early *C. proximus* [M] from Portada Covunco (Parent *et al.*, 2013: fig. 12C) and *C. rafaeli* [M] from Mallín Quemado. The specimen of *W. internispinosum* transient beta (shown in natural size in Fig. 11) is completely differentiated. All specimens macroconchs, ×0.25

CHRONOSTRATIGRAPHY

Evidence for time-correlation between the Andean Upper Tithonian-Lower Berriasian interval and the Tethyan Primary Standard Chronostratigraphic ammonite zonation has been discussed in detail in Parent *et al.* (2015). The ammonites recorded in the interval *planulatum-compressum* horizons (see Fig. 2) are mainly of the genus *Krantziceras* which occurs with *Groebericeras bifrons* Leanza, 1945. Within the faunas of the upper Microcanthum-Durangites zones of southern Spain (Tavera, 1985), stand the conspicuous ammonites belonging to the genera "*Andalusphinctes*" and "*Neoperisphinctes*". These ammonites are comparable with *Krantziceras*, especially with *K. planulatum* (Vennari *et al.*, 2012), suggesting a similar latest Tithonian age for the *planulatum* Hz. in the uppermost Koeneni Zone.

On the other hand, the association of *G. bifrons* with *K. compressum* (Fig. 2) strongly suggests an Early Berriasian,

Jacobi Zone age for the *compressum* Hz. which represents the base of the standard Noduliferum Zone. This assumption is based on (1) the studies by Howarth (1992) and Aguirre-Urreta & Álvarez (1999) which assign *G. bifrons* to the Early Berriasian, (2) the conclusion above that the underlying ammonite bio-horizon, the *planulatum* Hz. (in Parent *et al*. 2015), should be latest Tithonian, and (3) in the locality Mallín Quemado (see Fig. 1) Garrido & Parent (2017) have recently recorded *G. bifrons* from the Noduliferum Zone associated with *Substeueroceras permulticostatum* (Steuer, 1897), a species very close to, or a late transient of *Substeueroceras koeneni* which is characteristic of the Koeneni Zone. Furthermore, this latter association occurs below levels with *Subthurmannia* sp. A (in Garrido, Parent, 2017).

CONCLUSIONS

Important new data gathered from new ammonites from the Vaca Muerta Fm in Pampa Tril permit the making of the following advances in the knowledge of the Tithonian and Berriasian ammonite faunas of the Neuquén Basin:

1. *C. platyconus* evolves phyletically through the Picunleufuense Z. with a slowly changing morphology, mainly dominated by compressed evolute morphotypes, up to the lower Zitteli [Mendozanus] Z., from where it shifts to more inflated and involute morphotypes, which are classified as *C. erinoides*.
2. The spectrum of variation of the macroconchs of *C. erinoides* in the *erinoides* Hz. comprises large, involute and inflated morphotypes with short, bold primaries on the bodychamber up to much smaller and involute variants. The microconchs are much less abundant and all the known specimens are very similar to or match the lectotype of *Virgatites mendozanus*.
3. The sexual dimorphism of *K. azulense* is characterized by microconchs one third the size of, and thus significantly smaller than the corresponding macroconchs, with stronger bifurcated ribbing. Due to the slowly changing macroconch morphology of the lineage from the Picunleufense Z. up to the Noduliferum Z., a similar trend in the microconchs can be expected.
4. The predominant morphotype of *S. koeneni* in the *koeneni* Hz. is identical to the paralectotype of the species, suggesting it could be the type horizon of the species, since both the lectotype and the paralectotype come from the same horizon: level Cieneguita-IV in Arroyo Cieneguita.
5. Additional material from the *internispinosum* alpha Hz. confirms the origin of *W. internispinosum* from *C. proximus* by the inception of an evolutionary innovation in the juvenile ontogeny.
6. Identification of Andean material of the Damesi Zone with the Tethyan representatives of *S. boissieri* is reinforced by new specimens showing a spectrum of variation that matches assemblages of morphotypes in the Boissieri Zone of Spain.

New material recently described from the Quintuco Fm in Mallín Quemado provides additional evidence in support of the time-correlation of the lower Noduliferum Zone with the Jacobi Zone as formerly proposed from the study of the Pampa Tril fauna.

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