AMMONITES OF THE SUBFAMILY ZAPALIINAE FROM THE LOWER TITHONIAN OF ESTANCIA MARÍA JUANA, VACA MUERTA FORMATION (PORTADA COVUNCO MEMBER), NEUQUÉN BASIN, ARGENTINA

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Abstract. A new collection of ammonites from the Picunleufuense Zone (standard base of the Andean Tithonian) of the locality Estancia María Juana (southern Neuquén Basin, Argentina) has provided abundant and well preserved material of new transients of *Indansites picunleufuense* and *Choicensisphinctes platyconus*. These transients are described and a detailed review of the early evolution of the *Indansites* lineage is presented. The meaning of changes in rib density, variations within the microconchs (males) and the length of the bodychamber in *Indansites picunleufuense* are discussed. It is concluded that the changes in rib density which characterize the successive macroconchs of the transients indicate changes in the rate of shell-growth. The more densely ribbed phragmocone of later transients would have had lower growth rates, which would also explain their smaller adult size. The microconchs show high variation in adult size suggesting high plasticity in the size-age maturation, most likely caused by influence of seasonal environmental conditions. A large small-macroconch-like lapetted microconch, coming from the close locality Picún Leufú, is interpreted as a new case of sex-change.

INTRODUCTION

In the last years, it has become evident that, during the Tithonian the only ataxioceratids in the Neuquén Basin (NB; Fig. 1) are represented by the subfamilies Torquatisphinctinae Tavera, 1985, Zapaliinae Parent, Schweigert, Scherzinger, and Garrido, 2017, and Ataxioceratinae Buckman, 1921 (genus *Paraboliceras* Uhlig, 1910) (Parent 2003; Parent et al. 2006, 2011a, 2011b, 2013a, 2015, 2017a, 2017b; Garrido et al. 2018). Nevertheless, some genera (e.g. *Aulacosphinctes*, *Virgatosphinctes*, *Pseudinvoluticeras*) of

the Himalayitidae Spath, 1925 and Virgatosphinctinae Spath, 1923, a subfamily restricted to the Indo-Madagascan region (Enay 2009; Parent et al. 2017a), are still mentioned to include Andean ammonites (e.g. Zeiss & Leanza 2010; Vennari 2016; Iglesia-Llanos et al. 2017). However, the latter are typical representatives of the Zapaliinae. The criteria adopted for these assignations have never been explained, perhaps because they were proposed by Uhlig (1910), Spath (1925), and Weaver (1931), among other old papers. Under these circumstances it is strongly suggested caution in the classification of new specimens and in their use for chronostratigraphic purposes.
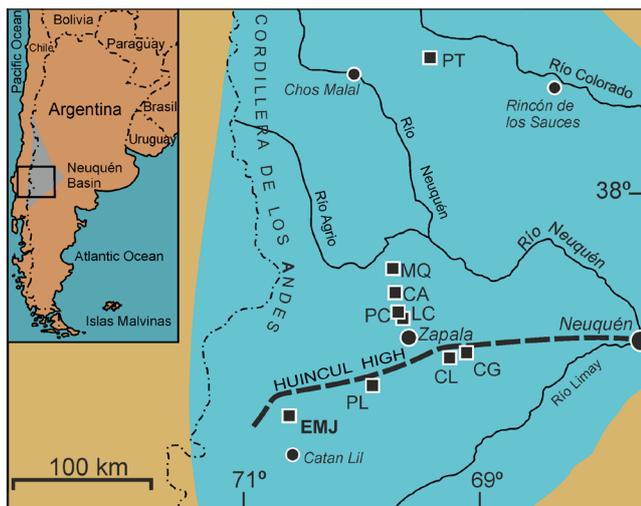
Fig.1 - Southern Neuquén Basin (modified from Garrido et al. 2018) with indication of the localities studied and referred in text: Estancia María Juana (EMJ), Picún Leufú (PL), Cerro Lotena (CL), Cerro Granito (CG), Los Catutos (LC), Portada Covunco (PC), Cañadón de los Alazanes (CA), Mallín Quemado (MQ), Pampa Tril (PT).

The lower Tithonian ammonite fauna of the southern domains of the Neuquén Basin (Fig. 1) seems to show few differences with respect to those of its central and northern regions (see Leanza 1980; Parent et al. 2011a, 2011b, 2013b, 2015; Garrido et al. 2018 and references therein). The genus *Indansites* Vennari, 2016 is one of the main components of the subfamily Zapaliinae, with an abundant record throughout virtually all of the basin, from the lower Tithonian Picunleufuense Zone up to at least the middle Tithonian Internispinosum Zone.

The locality named Estancia María Juana (EMJ) belongs to the region called Fortín Primero de Mayo, the geology of which has been described by Leanza et al. (2003). The Tithonian stratigraphic sequence of this locality and the ammonite fauna of the Portada Covunco Mb. were studied by Parent et al. (2013b). We have restudied this section, expanding the number of ammonite horizons sampled, especially after disclosing the upper part of the sequence, formerly covered. In this section, there are interesting records of *Indansites* and *Choicensisphinctes* Leanza, 1980 in the Picunleufuense standard Zone, in levels which seem to have not been previously recorded in other localities.

The purpose of this paper is to describe these recently collected ammonites and to review the evolution of the early transients of *Indansites* in the Picunleufuense standard Zone, which is the base of the Andean Tithonian.

STRATIGRAPHIC FRAMEWORK

The Picún Leufú Subbasin (PLSB) in the southern Neuquén Basin (Fig. 1) shows specific geological, stratigraphical and palaeontological features which have been studied by several authors (e.g. Groeber 1929; Leanza & Leanza 1979; Leanza 1992; Leanza & Hugo 1997; Leanza et al. 2003 with references therein, Spalletti et al 2000; Garrido & Parent 2013; Parent et al. 2011a, 2013b). The marine Tithonian is mainly represented by the Vaca Muerta, Carrín Curá, and Picún Leufú formations. The two latter units pass gradationally from the bituminous sandy shales and calcareous sandstones of the Vaca Muerta Fm into near-shore sandstones and carbonate, tidally dominated, rimmed-shelf facies (Leanza & Hugo 1997; Leanza et al. 2003; Armella et al. 2007). The lower Tithonian, typically represented in the PLSB by the Portada Covunco Mb. of the Vaca Muerta Fm. (Parent et al. 2013a), is well characterized by an ammonite association widely recorded through the entire basin, lying below the Zitteli [including the "Mendozanus"] Zone (Parent et al. 2011a).

As noted above, the studied section of EMJ was already described in Parent et al. (2013b). The log-section shown in Fig. 2 is more detailed after disclosing of the previously covered upper part. Equivalences between former levels (Parent et al. 2013b: fig. 2) and the notation used herein (Fig. 2) are: levels EMJ-1-2 merged into EMJ-2; EMJ-3 unchanged; EMJ-4-5 (plus covered portion) splitted into EMJ-4-10; and EMJ-6 splitted into EMJ-10-12. The rock and ammonite succession, and accessory molluscs recorded is as follows, from below, with the new levels' notation:

Level EMJ-1: 1.5 m of fine-grained sandstones. No macrofossils.

Level EMJ-2: 2 m of sandy shales. Ammonites: *Indansites picunleufuense* [M&m] transient alpha, abundant *Choicensisphinctes platyconus* [M&m] (see Parent et al. 2013b); abundant oysters. Gastropods: *Exelissa? arcuatoconcava* Gründel & Parent, 2001, *Dicroloma?* sp.

Level EMJ-3: 0.2 m bank of sandstones. No macrofossils.

Level EMJ-4: 8 m of sandy shales. Ammonites (from the lower 2 m): abundant fragmentary *I. picunleufuense* [M&m] transient alpha, *C. platyconus* [M&m]. Oysters.
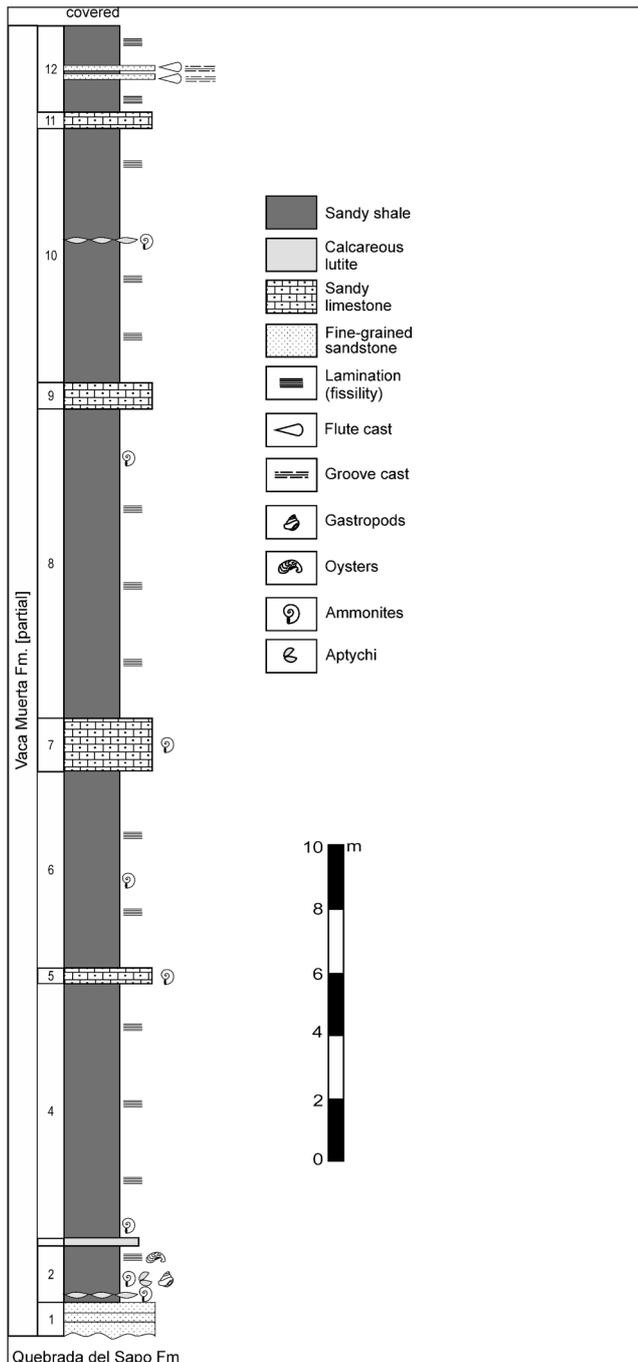
Fig. 2 - Log of the studied section of the lower part of the Vaca Muerta Fm., Portada Covunco Mb. in Estancia María Juana. Total thickness 41.8 m. Levels EMJ-1-10 belong to the lowermost Tithonian Picunleufuense Zone (see Fig. 3).

Level EMJ-5: 1 m thick bank of sandy limestones. Ammonites: crushed specimens of *Choicensisphinctes* sp.

Level EMJ-6: 6 m of sandy shales. Ammonites: *Indansites picunleufuense*, *Choicensisphinctes* sp.

Level EMJ-7: 1.8 m of sandy limestones. Ammonites: abundant *I. picunleufuense* (transient beta?), *C. platyconus*.

Level EMJ-8: 9.8 m of sandy shales. Ammonites (upper part): *I. picunleufuense* and *C. platyconus*.

Level EMJ-9: 1.0 m of sandy limestones. No macrofossils.

Level EMJ-10: 8 m of sandy shales. Ammonites: *I. picunleufuense* (transient EMJ-10, see below), *C. platyconus*.

Level EMJ-11: 0.4-0.5 m bank of sandy limestones. No macrofossils.

Level EMJ-12: more than 3 m (covered) of sandy limestones and shales. No fossils.

The levels EMJ-1-10 belong to the Picunleufuense Zone. The lower part (levels EMJ-1-4) can be assigned to the *picunleufuense* alpha Hz. (Fig. 3). Levels EMJ-6?-7 could be assigned to the *picunleufuense* beta Hz. (see discussion below). Levels EMJ-8-10 are younger than the *picunleufuense* beta Hz. (see discussion below). Levels EMJ-11-12 cannot be dated as they lack fossils.

SYSTEMATIC PALAEONTOLOGY

Conventions. The material described is housed at the Museo Provincial de Ciencias Naturales "Prof. Dr. Juan A. Olsacher", Zapala (MOZ-PI). Bodychamber is abbreviated with Bc and phragmocone with Ph; macroconch (female): [M], microconch (male): [m]. Measurements are indicated as follows: diameter (D), diameter at the last adult septum (D_{ls}) and diameter at adult peristome (D_p), all given in millimeters [mm]; umbilical width (U), whorl width (W), whorl height (H_1), and whorl ventral (or apertural) height (H_2), all given as dimensionless proportions of D; length of bodychamber (L_{BC}) in degrees [°]. Number of primary (P) and ventral (V) ribs per half whorl. Levels of occurrence of the specimens denoted by the level number in Fig. 2 and the prefix EMJ (Estancia María Juana). Zones and biohorizons referred to Fig. 3.

Composition of the fauna. The only ammonite genera recorded in the studied section are *Indansites* Vennari, 2016 and *Choicensisphinctes* Leanza, 1980. Their relative abundance changes through the section:

(1) In level EMJ-2 *Choicensisphinctes* dominates (95%) over *Indansites* (5%). *Choicensisphinctes* occurs mainly as macroconchs (70%); there are only six microconchs (30%) from a total of 20 specimens. The few specimens of *Indansites* are fragmentary, apparently macroconchs.

(2) In level EMJ-10 the proportions revert, *Choicensisphinctes* occurs as a minority (9%) with respect to *Indansites* (91%). All the specimens of both genera collected in this level are macroconchs.

Tethyan Primary Standard		Neuquén Basin		
Stage	Zone	Zone	Horizon	
TITHONIAN (Upper) — Durangites		Koeneni	*planulatum*	
			koeneni	
			striolatus	
Microcanthum		Alternans	*azulense*	
			bardense	
			vetustum	
(Middle) — Ponti		Internispinosum	*catutosensis*	
			"quinchoai"	*Indansites zapalensis*
			internispinosum α	
Fallauxi		Proximus		
			falculatum	*Ind.* n. sp. aff. *picunleufuense*
Semiforme		Zitteli [Mendozanus]	*erinoides*	
			perlaevis	
(Lower) — Darwini			*malarguensis*	*Indansites malarguensis*
Hybonotum		Picunleufuense		*Indansites picunleufuense* tr. EMJ-10
			picunleufuense β	*Indansites picunleufuense* tr. beta
				Indansites picunleufuense tr. PT-8
			picunleufuense α	*Indansites picunleufuense* tr. alpha
KIMM. (Upper)	Beckeri			

Fig. 3 - Reference Andean chronostratigraphic ammonite zonation and biohorizons (based on Leanza 1981 and Parent et al. 2015), correlated with the Tethyan Primary Standard Scale (Geyssant in Cariou & Hantzpergue 1997). Dotted lines indicate non-standard zones. Succession of representatives of the genus *Indansites* as discussed in Parent et al. (2011a, 2015, 2017a) and present report.

The Picunleufuense Zone (lower Tithonian) ammonite fauna of the studied locality is composed exclusively of Andean genera (*Indansites* and *Choicensisphinctes*). Nevertheless, in other close localities of the PLSB, e.g. Picún Leufú, Cerro Lotena-Cerro Granito and Carrín Curá (Fig. 1), the fauna is richer including the remaining genera widely recorded in central and northern areas of the NB, mainly *Catutosphinctes*, *Cieneguiticeras*, and *Physodoceras* (see Leanza 1980; Parent et al. 2011a, 2013a). Only the latter is cosmopolitan, whereas the other two are endemic to the Andean Realm.

The settlement of the first ammonites entering the Neuquén Basin during the early flooding (Picunleufuense Zone) must be studied from the faunas of the *picunleufuense alfa* and *beta* biohorizons (Fig. 3) which are the earliest records of the Andean Tithonian. These horizons are represented throughout virtually all the basin, in the base of the Vaca Muerta Fm. (e.g. Fig. 2). However, a detailed analysis of the early Tithonian geography and physiography and the local faunas of many key localities of the basin must be considered together for this kind of study. This study is in progress under the hypothesis that the early settlements of ammonites in the NB consisted of non-indigenous species with similar ecological requirements, i.e. a biome (sensu Dommergues & Marchand 1988). These species, coming from different areas (Tethys, Antarctica?, Indo-Madagascan region), should have been established in the Palaeopacific basins, which were separated from the NB by the volcanic arc emplaced with Andean orientation (Fig. 1). The evolution of some of these species, early established in the NB, would have lead to the development of local lineages, giving origin to an Andean biota (a fauna dominated by eudemic lineages, sensu Callomon 1985). For progressing in this study, several features of the NB must be considered that should have affected the distribution of the fauna and, importantly, the migrations. The most important of these features seem to be: (1) the tendency to the isolation of the basin due to the tectonic-eustatic dynamics affecting the transarc gateways, (2) the large area covered by the basin divided into two main domains (the elongated Mendoza Shelf and the Neuquén Embayment) which must have imposed different environmental conditions, and (3) the irregular bottom topography.

Order **Ammonitida** Fischer, 1882
Suborder **Ammonitina** Fischer, 1882
Superfamily Perisphinctoidea Steinmann, 1890
Family Ataxioceratidae Buckman, 1921
Subfamily Zapaliinae Parent, Schweigert,
Scherzinger and Garrido, 2017

Genus *Indansites* Vennari, 2016
Type species: *Subplanites malarguensis* Spath, 1931; by original
designation.

Remarks. *Indansites* consists of a lineage, which ranges from the basal Andean Tithonian Picunleufuense Zone up to at least the upper Middle Tithonian Internispinosum Zone (Fig. 3; see Parent et al. 2017a). Its representatives are characterized as compressed to more or less inflated serpenticones, strongly sexually dimorphic, with a well-defined macroconch sculpture-ontogeny: sharp bifurcating ribs (inner whorls), narrowly splayed secondaries with the posterior one twisted backwards (subadult phragmocone), trifurcating in virgatotome s.str. style (adult phragmocone), and through the bodychamber progressively stronger trifurcate to fascipartite passing to stronger, irregular primaries towards the peristome.

Close resemblance, sometimes indistinguishable, between earliest *Indansites*, namely *I. picunleufuense* and some representatives of *Lithacoceras* Hyatt, 1900 from the southern Tethys (see Parent et al. 2006, 2011a, 2011b, 2017a) is a clear indication of the origination of *Indansites* from *Lithacoceras*. Differentiation of *Indansites* as a separate lineage from that of *Lithacoceras*, however, is supported definitely by the different evolutionary trends developed in separated basins. The evolutionary trend of *Indansites* was summarized and illustrated by Parent et al. (2017a). The detailed record of the succession of transients of *I. picunleufuense* in the Picunleufuense (standard) Zone is analyzed in detail below, based on the newly collected material.

Indansites picunleufuense (Parent, Garrido, Schweigert & Scherzinger, 2011)

Figs 4-10

1999   *Lithacoceras (Virgalithacoceras)* cf. *acricostatum* Ohmert & Zeiss – Parent & Capello, p. 349
2001   *Euvirgalithacoceras malarguense* (Spath) – Gründel & Parent, p. 14, fig. 2
2003   *Euvirgalithacoceras malarguense* (Spath, 1931) – Parent, p. 147, figs. 6A, 7C-E
2006   "*Lithacoceras*" n. sp. aff. *malarguense* (Spath, 1931) – Parent et al., p. 257, figs. 2, 3A-B
2007   "*Lithacoceras*" n. sp. aff. *malarguense* (Spath, 1931) – Parent & Cocca, p. 26
*2011a *Lithacoceras picunleufuense* n. sp. – Parent et al., p. 53, figs. 6-12
2011b   *Lithacoceras picunleufuense* Parent et al., 2011 – Parent et al., p. 26, fig. 3
2013a   *Lithacoceras picunleufuense* Parent et al., 2011 – Parent et al., p. 11, fig. 5A
2013b   *Lithacoceras picunleufuense* Parent et al., 2011 – Parent et al., p. 28
2015   *Lithacoceras picunleufuense* Parent et al., 2011 – Parent et al., p. 17, figs. 6-11
2016   *Indansites malarguensis* (Spath, 1931) – Vennari, pl. 1, figs. 1-3, pl. 2, figs. 1-5, pl. 3, fig. 1
2017a   *Indansites picunleufuense* (Parent et al., 2011) – Parent et al., p. 509, fig. 2A-C
2018   *Indansites picunleufuense* (Parent et al., 2011) – Garrido et al., p. 6, figs. 4-9, 10A-B.
2019   *Indansites malarguensis* (Spath, 1931) – Aguirre-Urreta et al., p. 354, fig. 8J-K

Material (new specimens from the studied section): one complete adult [m] from level EMJ-2 (MOZ-PI-2293); 7 incomplete specimens from level EMJ-7 (MOZ-PI-1889/1-7); 10 more or less complete adult [M] and 10 juvenile or incomplete [M] phragmocones from level EMJ-10.

Description. (1) Microconch from level EMJ-2 (Fig. 4): A finely preserved adult microconch, moderately involute ($U/D = 0.35$ from $D = 46$ mm up to the peristome) with higher than wide whorl section ($W/D = 0.28$ from $D = 46$ mm up to the peristome). Primary ribs bi- and trifurcating in the phragmocone and polyfurcating in the bodychamber. The bodychamber begins at $D_{ls} = 51$ mm and is unusually short, only 70° long. Maximum diameter at peristome $D_p = 59$ mm. Lappets short.

(2) Macroconchs from level EMJ-7: Phragmocones ($D = 60-80$ mm) showing compressed and evolute whorls. Densely ribbed from inner whorls: $P = 21-26$ through $D = 33-80$ mm.

(3) Macroconchs from level EMJ-10 (Figs 5-7): Moderately large, compressed and evolute serpenticonic conchs. The ontogeny can be conveniently described as four stages:

- Inner whorls (Fig. 5A), about $D < 20-30$ mm, evolute, oval in whorl section. Primary ribs sharp and prosocline ($P = 16-23$), bifurcating in upper flank; one or two per whorl joined on the umbilical shoulder.

- Middle whorls (Figs 5A$_1$-A$_4$, 6B-C), from about $D = 30$ mm, very evolute, with subrectangular, higher than wide whorl section, venter rounded, and flattish flanks. At about $40 < D < 90$ mm (subadult phragmocone) the ribbing is very dense: $P = 30-44$, consisting of fine slightly flexuous ribs, bi-
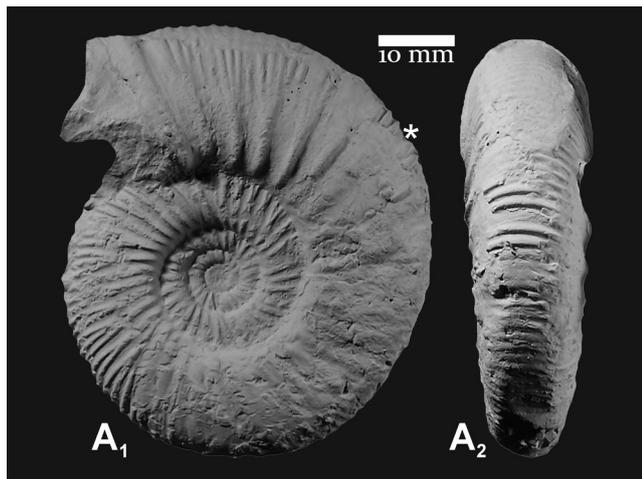
Fig. 4 - *Indansites picunleufuense* transient alpha, complete adult microconch (MOZ-PI-2293); Estancia María Juana, level EMJ-2, *picunleufuense alpha* Hz., Picunleufuense Zone. Asterisk at last septum.

furcating and occasionally trifurcating in the upper third of flank.

- End of the phragmocone and beginning of the bodychamber (Figs 6-7), D_{ls} = 80-110 mm. Primary ribbing becomes gradually less dense, displaying a stage of trifurcates in virgatotome s.str. style.

- Adult bodychamber (Figs 6-7) evolute with oval to subrectangular, higher than wide whorl section, slightly uncoiled towards the peristome. Primary ribs stronger and more widely spaced than in the phragmocone, bi- or trifurcating in the upper

third of the flank, with some intercalaries. Adult size at peristome shows moderately high variation, D_p = 120-220 mm; the length of the adult bodychamber ranges 270-340° long.

Remarks. The microconch from level EMJ-2 (Fig. 4) of the *picunleufuense* alpha Hz. (Parent et al. 2013) is medium-sized and very similar to the microconchs from the same biohorizon from Picún Leufú (see Parent et al. 2011a: figs. 7C and 9E).

The specimens from level EMJ-7 (as well as poor material from level EMJ-6) consist mainly of densely ribbed adult phragmocones which are closely comparable with macroconch phragmocones of the transient beta from Picún Leufú (Parent et al. 2011a: figs. 11-12). Although the material is not very well preserved, the rib density in the phragmocone, higher than in the transient alpha suggests that they most likely belong to the transient beta of the species.

The macroconchs from the level EMJ-10 are all widely umbilicate with compressed whorl section and densely finely ribbed phragmocone (Figs 5-8). Ribbing density shows a fall from D = 80-110 mm associated with the development of the short virgatotome s.str.-stage diagnostic of the species. The complete dominance of this morphotype in level EMJ-10, overlying the levels EMJ-6-7 which yield specimens comparable to the less densely ribbed variants of transient beta, strongly suggests this
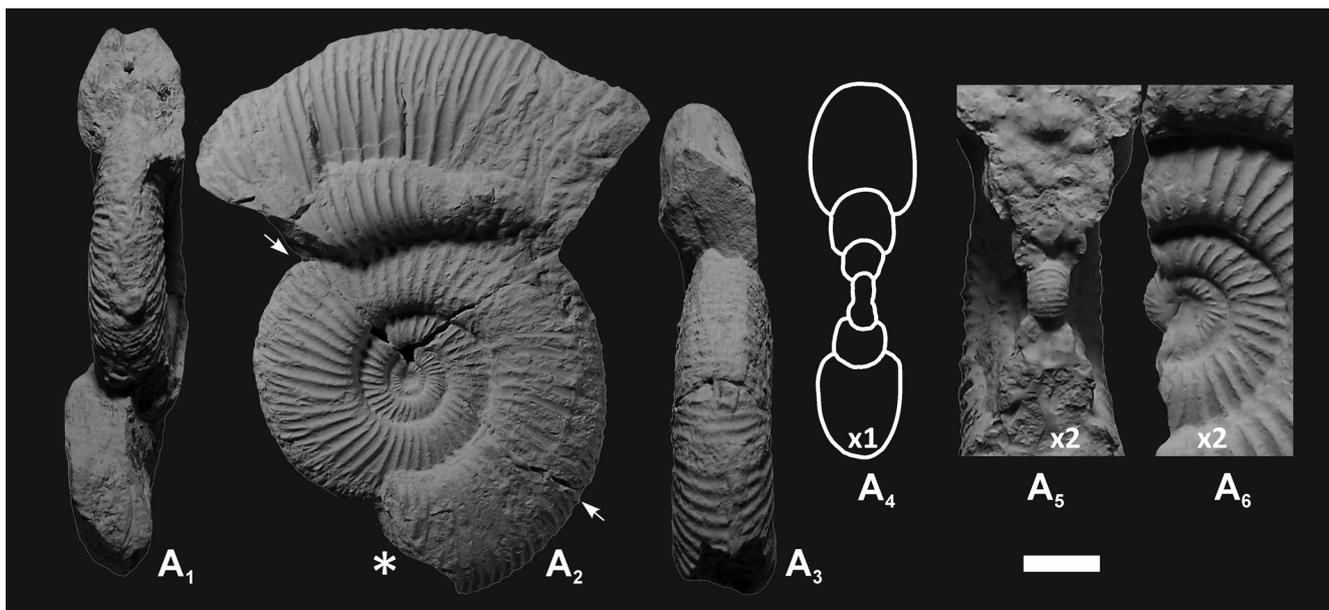
Fig. 5 - *Indansites picunleufuense* (Parent et al., 2011) transient EMJ-10; Estancia María Juana, level EMJ-10, Picunleufuense Zone. Juvenile macroconch (MOZ-PI-2410/1) with incomplete bodychamber. A_1-A_3) ventral (overturned), lateral and apertural views (x1); A_4) cross section of the phragmocone (x1) through the line indicated by arrow-heads in A_2; A_5-A_6) inner whorls (x2). Asterisk indicating the last septum. Bar is 10 mm for A_1-A_4, 5 mm for A_5-A_6.
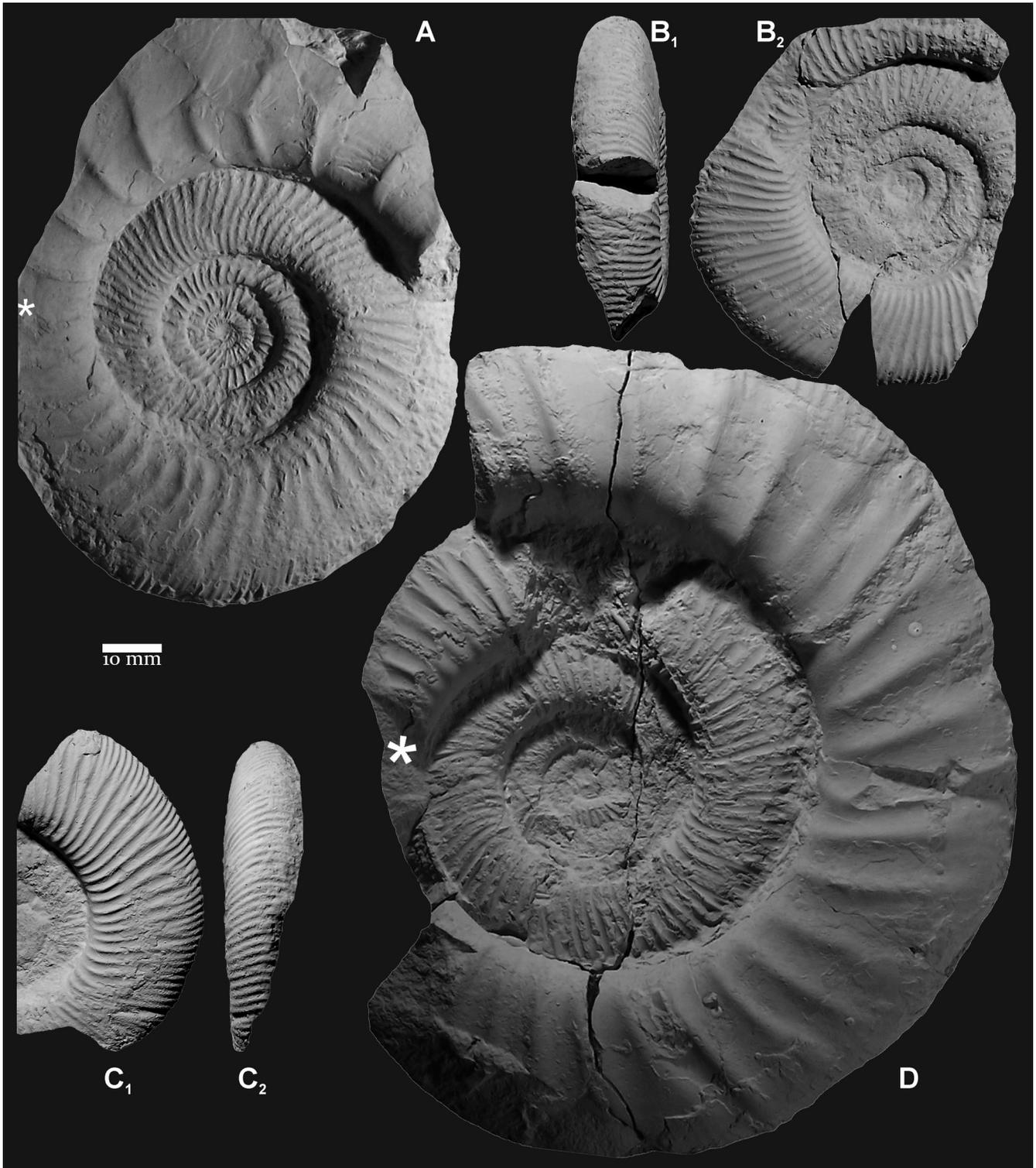
Fig. 6 - *Indansites picunleufuense* (Parent et al., 2011) transient EMJ-10; Estancia María Juana, level EMJ-10, Picunleufuense Zone. A) adult [M] with part of bodychamber (MOZ-PI-2382). B) [M] phragmocone (MOZ-PI-2435). C) [M] phragmocone (MOZ-PI-2410/2). D) Complete adult [M] (MOZ-PI-2482). All x1. Asterisk at last septum.

morphotype represents a transient younger than the transient beta. Unfortunately, no associated micro-conchs have been recorded yet – they would be very important for a more complete characterization of the species in the context of a strongly sexually

dimorphic lineage. Differences between transient EMJ-10 and the holotype of *I. malarguensis* are in the wider subtrapezoidal whorl section (Burckhardt 1903: pl. 4: 2) and the occurrence of several strong constrictions in the latter, although closely resem-
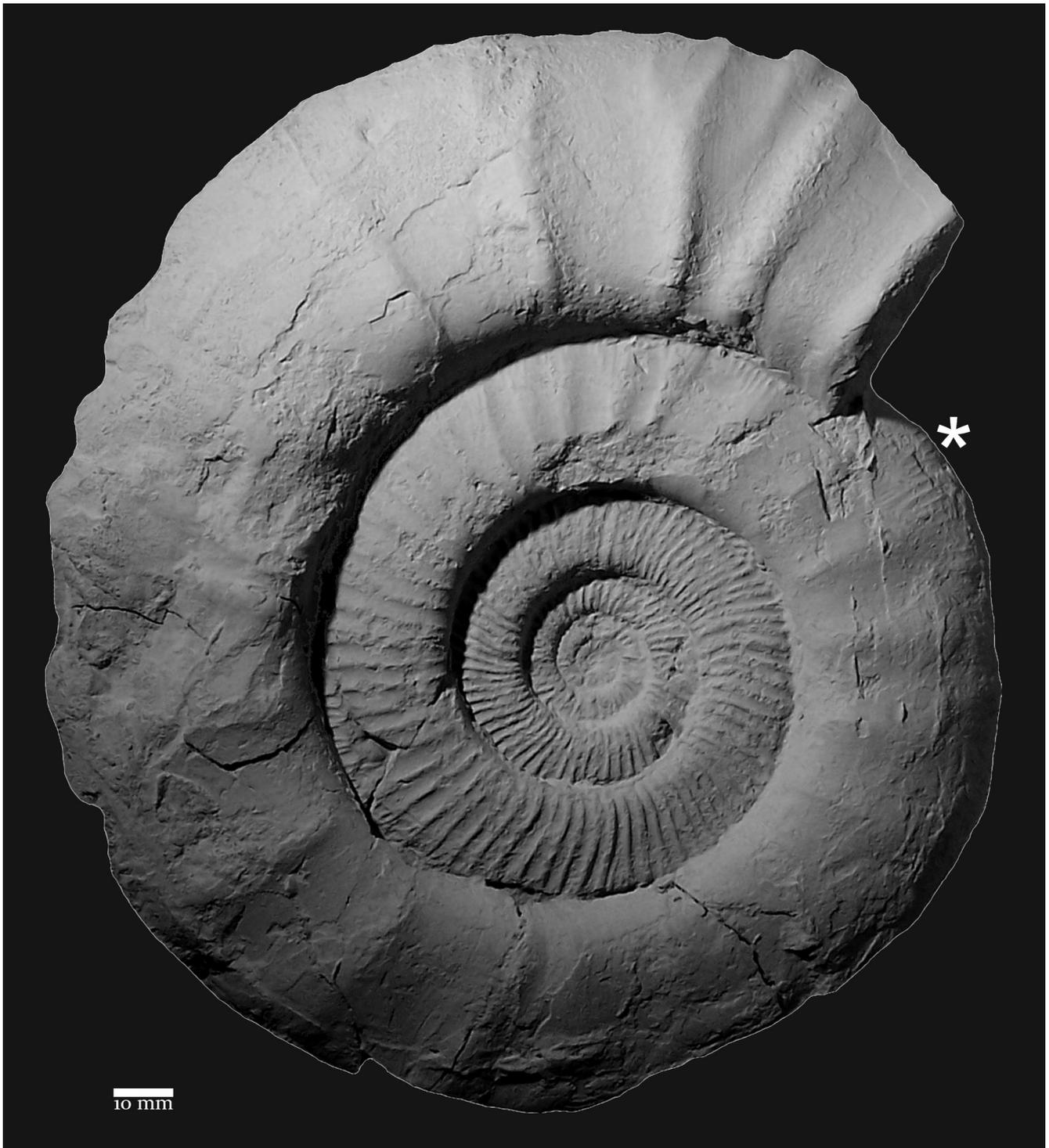
Fig. 7 - *Indansites picunleufuense* (Parent et al., 2011) transient EMJ-10; Estancia María Juana, level EMJ-10, Picunleufuense Zone. Complete adult [M] (MOZ-PI-2484). Asterisk at last septum.

bling each other in rib-density ontogeny (Fig. 8A). These differences and the older stratigraphic age of the transient EMJ-10 (Fig. 3) seem to be significant enough for excluding the possibility to include the latter in *I. malarguensis.*

The specimens of *I. picunleufuense* figured under *I. malarguensis* by Vennari (2016) have been di-

scussed in Parent et al. (2017a) and Garrido et al. (2018). The specimen figured in Aguirre-Urreta et al. (2019: fig. 8J-K) is a refiguration from Vennari (2016).

Transients of Indansites picunleufuense. The species was originally defined from two mean morpho-
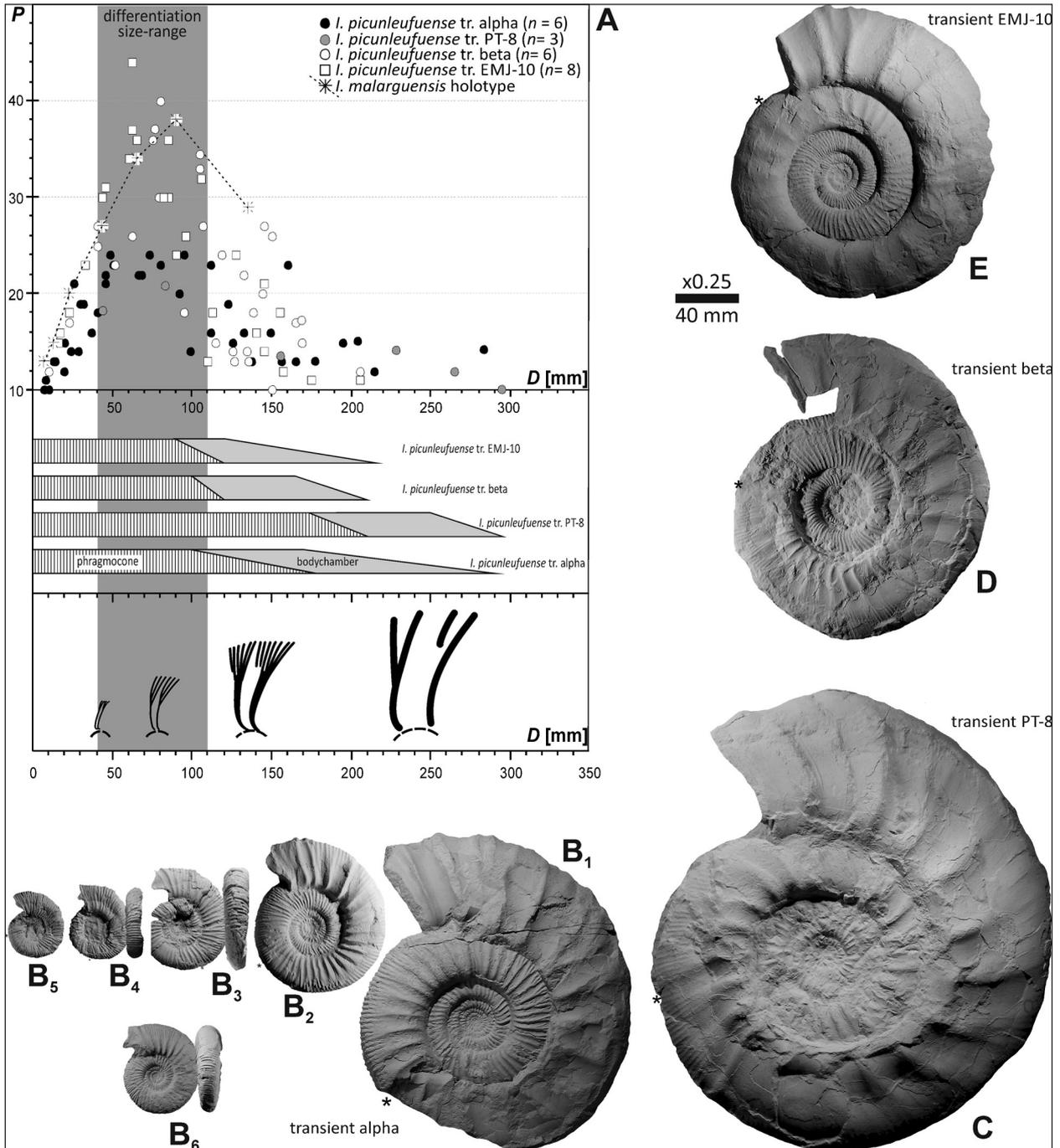
Fig. 8 - *Indansites picunleufuense* (Parent et al., 2011), Picunleufuense Zone. Summary of morpho-ornamental and adult size changes observed in the lineage represented by the four successive transients alpha, PT-8, beta, EMJ-10, illustrated by mean adult-macroconchs (plus microconchs of transient alpha) and data from published specimens from Casa Pincheira, Pampa Tril, Mallín Quemado, Picún Leufú, and E. María Juana. A) Ribbing ontogeny represented by the plot P versus D; adult size ranges (maximum and minimum values of D_{ls} and D_p); and ontogenetic sequence of rib-types of the species. The gray area indicates the size-range within which the later transients beta and EMJ-10 differ by the higher rib-density from the older transients alpha and PT-8. The holotype of *Indansites malarguensis* (Spath) included for comparison. B) Transient alpha (type transient of the species); B_1: complete adult macroconch (MOZ-PI-11239) from the *picunleufuense alpha* Hz. in Pampa Tril (see specimen natural size in Figs 9-10); B_2-B_5: complete adult microconchs from Picún Leufú (modified from Parent et al. 2011a) showing the broad range of adult size; B_6: specimen from level EMJ-2 in Fig. 4. C) Transient PT-8 (characterized by its larger size and lower density of ribbing through the ontogeny), complete adult macroconch from Pampa Tril (modified from Parent et al. 2015). D) Transient beta (characterized by high to medium rib-density in adult phragmocone and smaller adult size), complete adult macroconch from the *picunleufuense beta* Hz. in Pampa Tril (modified from Parent et al. 2015). E) transient EMJ-10 (characterized by the higher rib-density in adult phragmocone and very compressed whorl section through juvenile ontogeny), complete adult macroconch shown in Fig. 7 from level EMJ-10. - All x0.25 including axes of graphs and rib types (A). The asterisk indicates the last adult septum. Some specimens turned left or right for homogeneous visualization. The number of specimens considered for each transient is indicated by n.

Fig. 9 - *Indansites picunleufuense* (Parent et al., 2011) transient alpha, Picunleufuense Zone, *picunleufuense alpha* Hz., Pampa Tril. Lateral view of a complete adult macroconch (MOZ-PI-11239); apertural view in Fig. 10. Asterisk at last septum.

Fig. 10 - *Indansites picunleufuense* (Parent et al., 2011) transient alpha, Picunleufuense Zone, *picunleufuense alpha* Hz., Pampa Tril. Apertural view (x1) of a complete adult macroconch (MOZ-PI-11239); lateral view in Fig. 9.

types in close stratigraphic succession, interpreted as phyletic transients in the evolution of the lineage in the lower part of the Picunleufuense Zone (Fig. 3): transient alpha (the older and type transient) and transient beta (see Figs 8-10). Above as well as between the biohorizons of these two transients occur other morphotypes, some of which show more or less distinctive variations (Figs 8B-E, 9-10). For example, in Pampa Tril a large and coarsely ribbed morphotype occurs between the biohorizons of the transients alpha and beta (Parent et al. 2015: figs. 5, 8C, 9-10). These specimens are herein labelled "transient PT-8" in reference to the level of occurrence. The specimens from level EMJ-10 described above are provisionally labelled "transient EMJ-10" in reference to their level of occurrence in the studied section. These specimens show a higher rib density, a more compressed whorl section and come from a higher stratigraphic position than transient beta. Further local transients could be distinguished from the succession of different morphotypes in the sequence of the Picunleufuense Zone of Mallín Quemado (Garrido et al. 2018) where several levels with adult macroconchs have been sampled.

The main difference between the successive transients of the present species is essentially the rib-density in the size-range $D = 40$-110 mm, which corresponds to the subadult-adult macroconch phragmocone (Fig. 8A). In this size-range, the transient alpha (as well as the local transient PT-8, which is additionally significantly larger) shows a variation within $P = 18$-24, whereas in the transients beta and EMJ-10 (present specimens) the rib-density varies within $P = 18$-44 (Fig. 8A). In the later transients, the ontogenetic stage of high density of the ribbing is observable from the innermost whorls, at least from $D = 5$-8 mm (compare Fig. 5 herein and Parent et al. 2011a: fig. 10A with Parent et al. 2015: fig. 6A). It is worth noting that the ontogenetic sequence of rib-types shown in Fig. 8A is characteristic of the species, observed in all the transients. On the other hand, the whorl section is wider and more rounded in the early transients, becoming more compressed, higher than wide in the late transients (Figs 5, 6B-C).

The specimens from Mallín Quemado level MQ-IV-7 assigned by Garrido et al. (2018: figs. 7-8) to the transient beta, seem to be better assigned to the slightly younger transient EMJ-10. On the other hand, the slightly older specimen of transient beta

from Mallín Quemado level MQ-IV-5 (Garrido et al. 2018: fig. 6) is very similar to those of transient EMJ-10. However, since it is associated with typical specimens of transient beta, it is a good example of the mode of phyletic evolution of the lineage based on changes in the spectra of patterns of variation.

Meaning of rib density. As described above, the differentiation of transients alpha, beta and EMJ-10 of *I. picunleufuense* is based on the rib-density in the phragmocone of the dominant adult macroconch morphotype in the sample. The described changes of rib-density do not correlate with significant changes in the relative umbilical diameter (U/D) as it would expected by the laws of covariation (Westermann 1966). In this sense, the rib-density is a valuable taxonomic character so that it is important to discuss its interpretation in terms of the growth of the shell. The number of ribs per half whorl, P (Fig. 8A), is determined by the distance between each pair of consecutive ribs. This distance, representing the amount of shell formed, may vary indicating higher or lower growth rates. Assuming a rather constant amount of time required for the formation of the shell segment between each pair of ribs (Dommergues 1988; Landman et al. 2012), P becomes a measure for the growth rate of the shell (cf. Webster & Palmer 2016). This means that the higher the rib density, the lower the rate of shell growth. In the case of *I. picunleufuense,* the juvenile phragmocone in the transients beta and EMJ-10 had thus lower growth rates than the transients alpha and PT-8.

Sexual dimorphism. The largest microconch known comes from Picún Leufú. It was formerly considered a small adult macroconch (Parent et al. 2011a: fig. 9D), but after additional preparation it appeared to be a large lappeted microconch (Fig. 8B$_2$). The range of adult size in the microconchs of the earliest representatives of this species is thus very broad (Fig. 8B$_2$-B$_5$). This could be attributed either to different times of maturation, to different rates of growth, or both. However, considering that all specimens develop the same ontogenetic sequence of ribbing at fixed diameters we assume that the specimens have matured at different biological ages (cf. Bayer 1972; Matyja & Wierzbowski 2000; Parent et al. 2008; Schweigert & Kuschel 2017).

The smaller adults are paedomorphic by early halt of growth at maturation, i.e. progenesis (Mc-

Namara 1986; Parent 1997), as in most Ammonitina. Interestingly, broad ranges of variation in adult male size is an usual phenomenon in many Recent coleoids (e.g. Hanlon et al. 2002; Wada et al. 2005; Iwata et al. 2018), commonly induced by ecologial factors conditioning the time of maturation and reproduction. Microconchs (males) of *I. picunleufuense* transient alpha can be collected in great abundance, associated with macroconchs (females) from a single bed (the *picunleufuense alpha* Hz.) in Picún Leufú (Parent et al. 2011a), indicating the specimens should be not affected by significant amounts of variation produced by geographic distribution and/or phyletic evolution. Thus, the observed variation of adult size could be explained either by local fluctuations of environmental/ecological conditions, e.g. maturation season, or by intraspecific genetic variation.

On the other hand, the above mentioned large lappeted microconch from Picún Leufú (Fig. 8B$_2$) shows a strong ribbing on the last part of the bodychamber, matching that of the macroconchs at comparable diameters. This specimen may be interpreted as a case of sex-change, in which a juvenile female transformed into a male in the premature stage. Similar cases have been described in Parent et al. (2008) for aspidoceratids and some perisphinctids.

Length of bodychamber. The very short bodychamber (L_{BC}= 70°) of the microconchiate male (Fig. 4) from level EMJ-2 is unusual, within this species in particular, and among ataxioceratids in general. Microconch perisphinctoids (as well as haploceratoids) tend to have shorter bodychamber than the corresponding macroconchs, but rarely less than half a whorl. The present microconch from level EMJ-2 seems to have the shortest bodychamber yet found, even shorter than the specimen studied by Callomon & Chandler (1994: pl. 8: 4), a microconch? of *Tmetoceras scissum* (Benecke, 1865) from the Aalenian of England. The question raised by Callomon & Chandler (1994: 28) whether or not the shell was completely external, takes special relevance here with the present specimen. Unfortunately, the preservation of our specimen does not allow searching for evidences in the external surface of the shell that could give indication of attachment or intimate contact of an external part of the soft-body, like an external nacreous layer or other modifications (see details in Doguzhaeva & Mutvei 1989).

However, the unusually short bodychamber of our lappeted microconchiate male could be explained by the model proposed by Klug et al. (2015: 265). According to this model, the pair of lappets could be interpreted as the terminal shell-segment for accommodating at least the cephalic portion of the animal. This "shell-segment" could have been secreted rapidly and economically (at low metabolic cost) considering the low amount of aragonite necessary compared to a complete "tubular" shell-segment.

Genus *Choicensisphintes* Leanza, 1980

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

Choicensisphinctes platyconus Parent, Garrido, Schweigert & Scherzinger, 2011

Fig. 11

2001   *Choicensisphinctes*? sp. – Gründel & Parent, fig. 2
2003   *Euvirgalithacoceras malarguense* (Spath, 1931) – Parent, p. 147, figs. 6B-C, 7A-B
2006   *Choicensisphinctes* cf. *windhauseni* (Weaver, 1931) – Parent et al., p. 254, fig. 5A-B
*2011a   *Choicensisphinctes platyconus* n. sp. – Parent et al., p. 66, figs. 14-21
2011b   *Choicensisphinctes platyconus* Parent et al., 2011 – Parent et al., p. 29, fig. 6A-B
2015   *Choicensisphinctes platyconus* Parent et al., 2011 – Parent et al., p. 19, figs. 12-16, 17B, non 28A
2016   *Pseudinvoluticeras primordialis* n. sp. – Vennari, p. 108, pl. 8, figs. 1-10
2017a   *Choicensisphinctes platyconus* Parent et al., 2011 – Parent et al., fig. 3A-C
2018   *Choicensisphinctes platyconus* Parent et al., 2011 – Garrido et al., p. 9, figs. 10C, 11
2019   *Pseudinvoluticeras primordialis* Vennari, 2016 – Aguirre-Urreta et al., fig. 8E

Material: One complete adult macroconch and one fragmentary specimen from level EMJ-10.

Description. Evolute ($U/D = 0.40$) with suboval, higher than wide whorl section ($W/H_1 = 0.75$) through the ontogeny from $D = 15$ mm onwards. Sculpture ontogeny shows three stages:

(1) inner whorls up to about $D = 70$ mm with fine primary ribs (increasing $P = 13$ to 34 through $D = 5$ to 70 mm), bifurcating in narrowly splayed secondaries;

(2) adult phragmocone and beginning of bodychamber (up to about $D = 120$ mm) with prosocline primaries ($P = 33$ at $D = 90$ mm) dividing in the upper half to upper third of flank into three to five finer secondaries. These later become very weak and almost interrupted on the venter, thus forming a wide ventral band;

(3) last half whorl of bodychamber with strong primaries, widely spaced and divided into three to five weak secondaries; towards the peristome polyfurcation is irregular with several intercalaries. The bodychamber begins at $D_{ls} = 93$ mm and is at least 240° long; the peristome seems to be preserved at the maximum $D = 165$ mm.

Remarks. The present specimens differ from the holotype of the species, a macroconch of the earliest transient from the *picunleufuense alpha* Hz., by their more evolute coiling and finer ribbing, retaining a dense ventral ribbing throughout the bodychamber. The closest resemblance is with the evolute transient of this species from the *picunleufuense beta* Hz. in the present locality (Parent et al. 2013b: fig. 4), Picún Leufú (Parent et al. 2011a: fig. 21A) and Pampa Tril (Parent et al. 2015: figs. 17B).

It has been demonstrated (Garrido et al. 2018: 20) that *Pseudinvoluticeras primordialis* Vennari, 2016 is merely a junior synonym of *C. platyconus*. Indeed, the holotype of the former (Vennari 2016: pl. 8: 1) is exactly identical to the paratype-II of the latter (Parent et al 2011a: 66, fig. 15A) – both of them are microconchs with lappets.

Conclusion

The Picunleufuense Standard Zone in the southern Neuquén Basin is consistently well-developed forming the lower part of the Portada Covunco Mb. at the base of the Vaca Muerta Fm. This ammonite zone shows a dense record of fossiliferous levels, in which stands out the occurrence of several transients of *I. picunleufuense*, most of which widely recorded throughout the Neuquén Basin.

The successive transients of *I. picunleufuense* (tr. alpha, tr. PT-8, tr. beta, tr. EMJ-10) are most clearly distinguished by the rib density of the subadult-adult phragmocone of the macroconchs (Fig. 8). The succession of macroconchs of these transients shows a morphocline of increasing rib-density in the phragmocone with a moderate reduction of the adult size. As the increase of rib-density indicates decreased growth rates, the reduction of the adult size would be a consequence of a phase of lower growth rate. The factors which may have driven these phenotypic changes (environmental and/or genetical) remain to be studied.

Fig. 11 - *Choicensisphinctes platyconus* Parent et al., 2011, complete adult macroconch (MOZ-PI-2451); Estancia María Juana, level EMJ-10, Picun-leufuense Zone. Apertural (A₁), lateral (A₂) and ventral (A₃) views. - Asterisk at last septum.

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