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The ataxioceratid ammonite fauna of the Tithonian (Upper Jurassic) of Casa Pincheira, Mendoza (Argentina)

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Abstract

The Tithonian Ataxioceratids from Casa Pincheira (Mendoza) are described in the framework of a period of global relative high sea level stand, with Andean basins well communicated with Central and Western Tethys. The family Ataxioceratidae is interpreted including the subfamily Torquatisphinctinae Tavera (*Katroliceras* Spath, *Torquatisphinctes* Spath, and *Pachysphinctes* Dietrich). The original specimens of '*Perisphinctes*' *densestriatus* Steuer, *Paraulacosphinctes striolatus* (Steuer), *Paraulacosphinctes? mangaensis* (Steuer), and *Torquatisphinctes proximus* (Steuer) are photographically refigured, and their types are designated. Type specimens are also designated for *Euvirgalithacoceras malarguense* (Spath) and *Choicensisphinctes choicensis* (Burckhardt). The genus *Euvirgalithacoceras* is used for the first time for lowermost Tithonian Andean forms, and *Choicensisphinctes* is suggested as a derivated genus.

Keywords: Ammonites; Tithonian; Andes; Taxonomy; Biostratigraphy

Resúmen

Los Ataxioceratidae tithonianos de Casa Pincheira (Mendoza) se describen en el contexto de un período de nivel marino global relativamente alto, con las cuencas andinas bien comunicadas con las regiones Central y Occidental del Tethys. La familia Ataxioceratidae se interpreta incluyendo a la subfamilia Torquatisphinctinae Tavera (*Katroliceras* Spath, *Torquatisphinctes* Spath and *Pachysphinctes* Dietrich). Los especímenes originales de "*Perisphinctes*" *densestriatus* Steuer, *Paraulacosphinctes striolatus* (Steuer), *Paraulacosphinctes? mangaensis* (Steuer) y *Torquatisphinctes proximus* (Steuer) son refigurados fotográficamente y los especímenes tipo designados. Se designan especímenes tipo para *Euvirgalithacoceras malarguense* (Spath) y *Choicensisphinctes choicensis* (Burckhardt). El género *Euvirgalithacoceras* es usado por primera vez para formas andinas del Tithoniano Inferior basal, y *Choicensisphinctes* es sugerido como un género derivado del primero.

Palabras clave: Amonites; Tithoniano; Andes; Taxonomía; Bioestratigrafía

1. Introduction

Ammonites from Casa Pincheira, Mendoza (Fig. 1), near Mina La Valenciana in the middle part of the Malargüe River, have been formerly described by Steuer (1897), Behrendsen (1922), Burckhardt (1900) and Gerth (1925), among others. Burckhardt (1900) described a very consistent succession from three localities of southwestern Mendoza–Casa Pincheira, Cajón del Burro–Río Choicas or Tordillo, and Paso Montañés (Fig. 1)—which he used to propose the first biostratigraphic classification of the Andean Tithonian, currently named the '*Virgatosphinctes*' *mendozanus, Pseudolissoceras zitteli,* and '*Aulacosphinctes*' *proximus* biozones. The type locality of these biozones seems situated in the area between Cajón del Burro and Río Choicas or Tordillo (Leanza, 1980, 1981a,b).

The *Mendozanus* biozone has been long considered the oldest Tithonian rock unit of the Neuquén–Mendoza basin, roughly of Darwini zone age (Leanza, 1980, 1981a,b; Zeiss, 1968), but a recently discovered assemblage indicates that the earliest Tithonian may be

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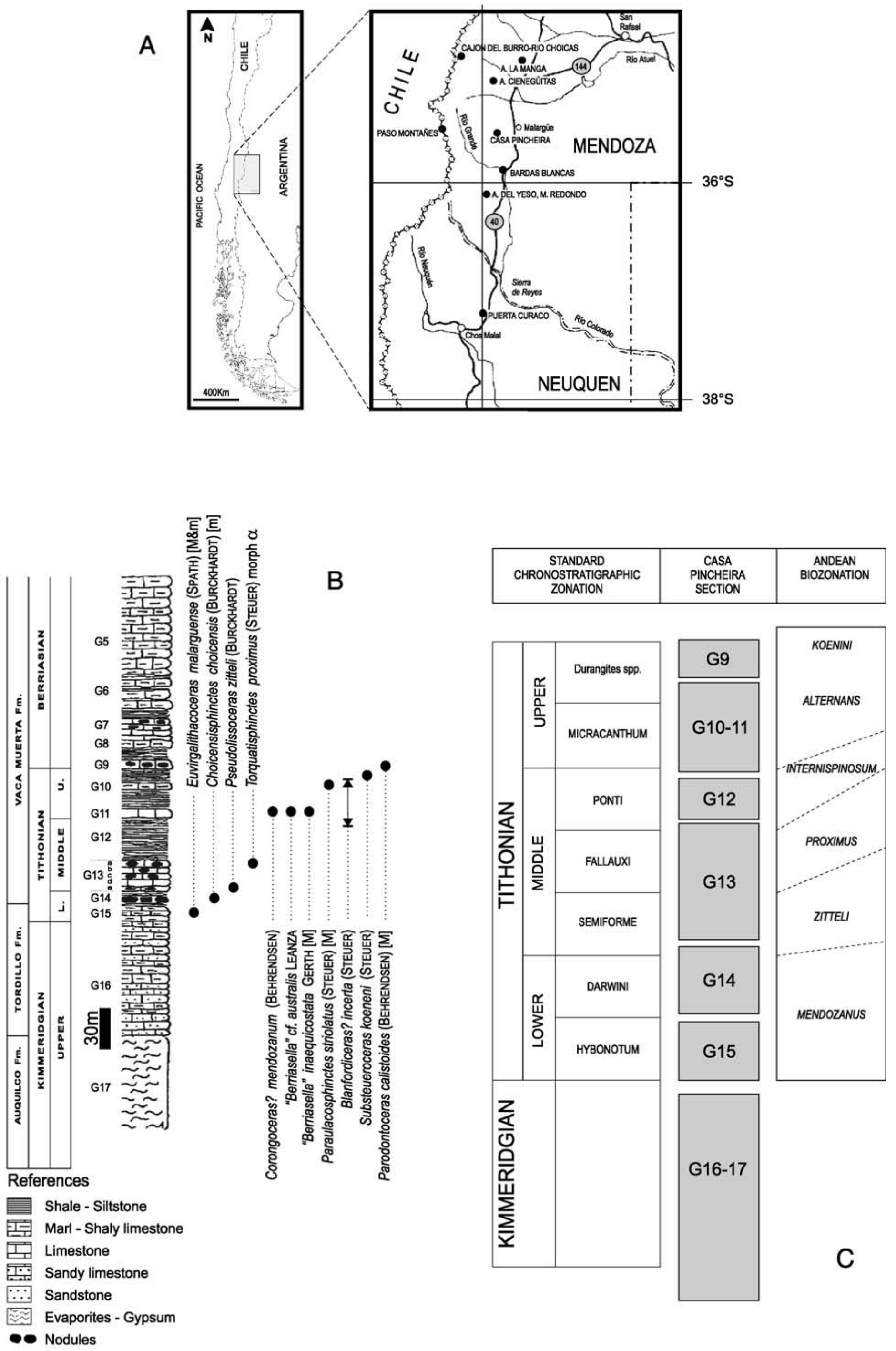

Fig. 1. A: Geographic location of Casa Pincheira and other localities cited in text. B: Log-section of Casa Pincheira and distribution of important ammonoids. C: Biostratigraphy and age of the Casa Pincheira section. Gray boxes indicate the estimated chronostratigraphic ranges (ages) of the beds. Dotted inclined lines delimiting biozones represent the variation of age at different localities of the Neuquén–Mendoza basin where ranges of the guide species are not the same. Log-section, ammonoid occurrences, and biostratigraphy slightly modified after Parent and Capello (1999).

represented by Ataxioceratids of Hybonotum zone age (Parent and Capello, 1999). The ammonite fauna that leads to this interpretation and other Tithonian Ataxioceratidae with direct Tethyan and/or Indo-Malgach affinities, are here described. All come from Casa Pincheira.

The Late Jurassic was a period of relatively high sea level stand (see Hallam, 1988), a condition that created shallow epeiric seas and attached ramp shelves settings around Gondwana. These basins were consequently well communicated among one another and with the Tethys and adjacent areas, which allowed for easy exchange and global homogenization of marine faunas (principally neritic organisms). In this context, the Andean fauna may be described under Tethyan generic taxa in accordance with the congruent morphologic resemblance among them, though local and endemic forms exist. The assumption of these faunal similarities as direct faunal affinities allows close correlations to be made with the Tethyan chronostratigraphic standard scale. This same approach has been used for the Andean Oxfordian faunas of Argentina and Chile (Gygi and Hillebrandt, 1991; Hillebrandt and Gröschke, 1995; Chong et al., 1984; Parent, 1998a), the Kimmeridgian (Förster and Hillebrandt, 1984), and the Tithonian (Callomon, 1993, p. 269; Enay et al., 1996; Parent and Capello, 1999). Similar assumptions were made in recent studies of Mexican and Cuban faunas by Olóriz et al. (1993, 1999), Myczynski et al. (1998) and Villaseñor et al. (2000). Nevertheless, the extended phenomenon of homoeomorphism must be considered to avoid circular arguments on correlation.

2. Stratigraphy of the studied area

The Kimmeridgian–Tithonian Upper Jurassic of the Malargüe area (Fig. 1) is well developed and exposed at several localities. The Kimmeridgian sediments are, apparently, mostly of continental nature and included in the Auquilco and Tordillo formations. Groeber (1952, p. 353 et seq.) stated that a marine ingression invaded the western margin of South America during the Early Tithonian, as documented by the beds with '*Virgatosphinctes pseudolictor*' [= *Euvirgalithacoceras malarguense* (Spath)]. The Tithonian sedimentary sequence at the studied area is analogous to that of the greatest part of the basin, which progresses, from bottom to top, as follows: (1) sandy, bioclastic limestones with ammonites, bivalves, and gastropods of the lowermost Tithonian, frequently poorly preserved; (2) a probably condensed succession of dark bituminous shales and limestones, sometimes with concretions containing well-preserved ammonites of the *Mendozanus* biozone; (3) dark marls and limestones with evident signs of condensation at the base and concretions at some levels, as well as reptilian bones and ammonites of the *Zitteli* and *Proximus* biozones; and (4) a thick succession of shales with limestone banks intercalated with ammonites of the *Internispinosum, Alternans,* and *Koeneni* biozones. Above this follows a thick succession of limestone-dominated Berriasian rocks. In the upper *Proximus* biozone, a thin lithographic limestone bed with aptychi resembles those of the Zapala region, as recently described by Leanza and Zeiss (1990, 1992, 1994). Extensive data about and analysis of regional stratigraphy, biostratigraphy, and paleontology may be found in Burckhardt (1900), Gerth (1925), Leanza (1980, 1981a,b, 1993), Leanza and Hugo (1977) and Leanza et al. (1977).

The section of Casa Pincheira was described, and the age of the fauna discussed by Parent and Capello (1999). In Fig. 1, the limits of the Andean biozones and age of the beds of the section of Casa Pincheira are slightly modified from those of Parent and Capello (1999), in accordance with recently obtained results. The identification of *Lithacoceras (Virgalithacoceras)* cf. *acricostatum* Ohmert and Zeiss (Parent and Capello, 1999) with '*V. pseudolictor*' [= *E. malarguense* (Spath)] leads to the inclusion of bed G15 into the *Mendozanus* biozone, because '*V. pseudolictor*' has been included in the guide assemblage since the original definition of the biozone by Burckhardt (1900, 1903). This is further evidence of how the boundaries of biozones depend on the taxonomy of the guide species or assemblage of species, in contrast to the stability of the boundaries of standard chronostratigraphic (ammonite zones) classification.

The local succession represents the progradation of a shallow platform onto a slope, as may be interpreted by the succession of sandy limestones (bed G15), condensed marls with nodules (bed G14), and shales and marly limestones (G13–G9). This interpretation fits well with paleogeographic data and reconstructions given by Leanza et al. (1977) and Riccardi et al. (1992). Evidence of high energetic conditions in the lower part of the section comes from bed G15, which consists of light coloured sandy limestones with abundant minute gastropods and shell debris of gastropods, bivalves, and ammonites. Bed G15 is palinologically barren (M. Quattrocchio, pers. comm., 01-03-99).

3. Systematic description

The studied specimens belong to the collection of the Laboratorio de Paleontología y Biocronología (LPB) of the Instituto de Fisiografía y Geología (Universidad Nacional de Rosario); the few additional specimens illustrated to supplement descriptions come from the Cerro Lotena section (39°10′S, 69°40′W), Neuquén, and belong to the Museo Olsacher, Zapala (PIV). Some of the studied species were defined by Steuer (1897), who illustrated them with drawings. Type specimens were not designated, and interpretation of his species by subsequent authors was subjective and created much confusion. The original specimens studied by Steuer (1897) were mostly collected by Bodenbender, who sent the specimens to the University of Göttingen, Germany. Photographic illustrations of the Bodenbender collection's pertinent specimens are included here, and the types are designated. All photographs were prepared courtesy of Hans Jahnke, Institut und Museum für Geologie und Paläontologie der Georg-August-Universität at Göttingen (MGAU).

Measured characters (dimensions) used as biometric variables are as follows (Fig. 2): diameter (*D*), diameter at the last adult septum (*Dls*), final adult diameter at peristome (*Dp*), umbilical width (*U*), whorl width (*W*), whorl height (H_1), and whorl ventral height (H_2), all given in mm; counts of number of primary (*P*) and ventral (*V*) ribs per half-whorl; and length of bodychamber (*LBC*) in degrees

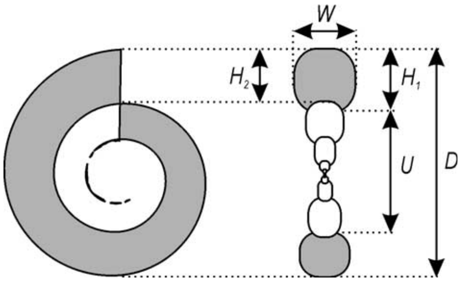

Fig. 2. Dimensions used to quantify morphology and ontogeny of the ammonite shell.

[°]. Estimated measurements are indicated with $(^e)$, and bodychamber is abbreviated as BC and phragmocone as Ph.

The samples are small, and many of the studied specimens are deformed by lateral compression, which prevents a comparative statistical analysis. To improve the utility and precision of graphical comparisons, the measurements from samples have been plotted over the polygons of dispersion (Figs. 4, 10 and 12) as defined by the measurements of the reference or comparative material. When several successive measurements through the ontogeny of particular specimens are available, it was fitted on an ontogenetic trajectory according to a distance-weighted least-squares smoothing (DWLSS) procedure. This procedure is very useful to obtain comparable nonparametric ontogenetic trajectories from particular subjects, even when measures are affected by autocorrelation and statistical and/or stratigraphical heterogeneity. The terminology used for the description of types of ribs and styles of ribbing follows Geyer (1961) and Atrops (1982). The guiding principles of taxonomy are based on the sexual dimorphic ontogeny of shape and sculpture, which is the nearest attainable approach to phenogenetics available from this material. Following this procedure, homeomorphies are expected to be detected with an acceptable margin of security, depending on the quality and quantity of material.

Order Ammonoidea Zittel 1884

Suborder Ammonitina Hyatt 1884

Superfamily Perisphinctaceae Steinmann 1890

Family Ataxioceratidae Buckman 1921

The family Ataxioceratidae is interpreted in the sense of Donovan et al. (1981) but expanded to include the subfamily Torquatisphinctinae Tavera (1985) and restricted to the lineage *Katroliceras* Spath 1924, *Torquatisphinctes* Spath 1924, and *Pachysphinctes* Dietrich 1925; see the subsequent remarks on Torquatisphinctinae.

Subfamily Lithacoceratinae Zeiss (1968)

This subfamily appears well represented in the Neuquén–Mendoza basin through the Upper Kimmeridgian(?)–Upper Tithonian by a relatively continuous succession of more or less well-defined species. At least the following occurrences are documented:

(1) A group of lithacoceratids that is very close, if not identical, to *Lithacoceras ulmense* (Oppel) comes from sections of Mendoza, such as Cajón del Burro–Río Choicas, Portezuelo del Burro, and other localities of Southern Mendoza. These forms were illustrated by Burckhardt (1900, pl. 25, figs. 3–5) as *Perisphinctes involutus* Quenstedt and by Indans (1954) as different species of *Virgatosphinctes* Uhlig 1910. The inclusion of some of the '*Virgatosphinctes*' of Indans (1954) in *Lithacoceras* was suggested by Donze and Enay (1961, p. 27), though Leanza (1980, p. 27) disregarded this possibility. *L. ulmense* (Oppel) is typical of the Upper Kimmeridgian Beckeri zone (Schweigert and Zeiss, 1999).

(2) *E. malarguense* (Spath) of the lowermost *Mendozanus* biozone (Lower Tithonian, Hybonotum zone). See the subsequent description (Figs. 6 and 7).

(3) *Choicensisphinctes choicensis* (Burckhardt) and related morphospecies of the *Mendozanus* biozone (Lower Tithonian Darwini zone). See the subsequent description (Fig. 8).

(4) The holotype of *Perisphinctes densestriatus* Steuer (1921) (Fig. 3) is a Lithacoceratinae very close to some early *Sublithacoceras*, such as the Middle Tithonian *Sublithacoceras* cf. *sphinctum* Donze and Enay (in Olóriz, 1978, pl. 42, fig. 2). There is also some resemblance to *Paraulacosphinctes striolatus* (Steuer), as figured by Leanza (1945, pl. 2, figs. 5 and 8). *P. densestriatus* Steuer is more evolute than *Choicensisphinctes* Leanza but shows the same sculpture on juvenile and subadult whorls, especially the polygyrate ribs preceding the prosocline constrictions (cf. Leanza, 1980, pl. 3, fig. 1a, 2, 3a). Steuer (1897) described the species from a single specimen from Arroyo Cieneguitas (Mendoza). The only specimen figured by Steuer (1897, pl. 15, figs. 8–10; transl. 1921, pl.15, figs. 8–10) as from Arroyo Cieneguitas (Steuer's level 'Cieneguita I') is designated as the holotype by monotype and refigured (Fig. 3A and B). The species association given by Steuer for his level 'Cieneguita I' includes: '*Perisphinctes roubyanus* Fontannes' (unfigured), '*Reineckeia* cf. *stephanoides* Oppel' [= *Windhauseniceras internispinosus* (Krantz)], *Perisphinctes colubrinus* (Reinecke) [= *Torquatisphinctes proximus*], and *Aspidoceras cyclotum* (Oppel). This assemblage indicates Middle Tithonian age, probably Fallauxi to early Ponti zones. Among Andean lithacoceratids strongly resembling *P. densestriatus* Steuer stand some ammonites from uncertain localities of southern Mendoza that were described by Indans (1954) as *Virgatosphinctes densistriatus* (Steuer), *V.* cf. *denseplicatus* (Waagen), *V.* sp., *Perisphinctes aeneas* (Gemmellaro), and *P.* cf. *subhelenae* Spath.

(5) Leanza and Zeiss (1990) cited *Sublithacoceras*? sp. and described *Zapalia fascipartita* nov. gen. et nov. sp. from the lower and upper parts, respectively, of the *Internispinosum* biozone (Middle Tithonian, late Fallauxi to Ponti zones) at Los Catutos, near Zapala (Neuquén). *Z. fascipartita* Leanza and Zeiss is a poorly known but typical lithacoceratid ammonite.

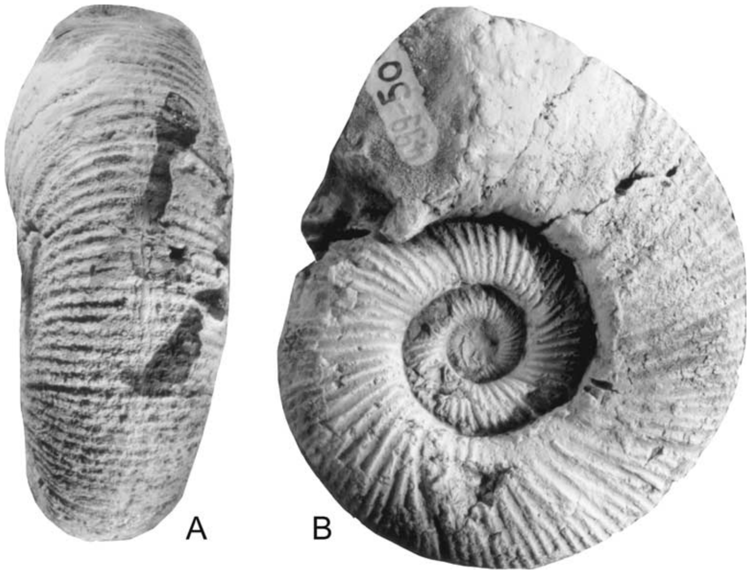

Fig. 3. *Perisphinctes densestriatus* Steuer (1897). Holotype (here designated) originally figured by Steuer (1897, pl. 15, figs. 8–10; transl. 1921, pl. 15, figs. 8–10) from the Tithonian of Arroyo Cieneguitas, level/bed "Cieneguitas I." A: Ventral view (×1), B: lateral view (×1). Actual repository at the Institut und Museum für Geologie and Paläontologie, Georg-August-Universität, number 499-50.

(6) *P. striolatus* (Steuer) is a species that occurs in the lower *Koeneni* biozone (Upper Tithonian, late Microcanthum–Durangites zones) and is very close to *Paraulacosphinctes senex* (Oppel) and *P. transitorius* (Oppel). See the subsequent description.

Genus *Euvirgalithacoceras* Zeiss et al. 1996

Type species *Virgatosphinctes supremus* Sutner in Schneid, 1915 by original designation.

In a comprehensive review, Olóriz (1978) included the group of *Virgatosphinctes riedense* Schneid, 1915 into the new genus *Virgalithacoceras* Olóriz. According to Ohmert and Zeiss (1980, p. 11) *Virgalithacoceras* Olóriz is a macroconch subgenus of *Lithacoceras* (cf. Olóriz, 1978, p. 519). *Virgalithacoceras* Olóriz may be distinguished from *Lithacoceras s.s.* by (1) its wider umbilicus in the inner whorls and (2) the occurrence of virgatotome ribs at the end of the Ph, followed by conspicuous bundles of secondaries connected, at about the middle of the flank, to thick primaries (palmate; cotes palmées sensu Atrops, 1982, p. 30) through the adult BC. Zeiss et al. (1996) believed that *V. riedense* Schneid belongs to *Lithacoceras* s.s. and, therefore, that *Virgalithacoceras* Olóriz should be a synonym of *Lithacoceras* s.s. They proposed for the group of *V. supremus* Sutner in Schneid, which is the remaining '*Virgalithacoceras*,' the genus *Euvirgalithacoceras* Zeiss et al. (1996), indicating that differences with respect to *Lithacoceras* s.s. are the absence of a fascipartite stage of ribbing in *Euvirgalithacoceras* and that microconchs of *Lithacoceras* s.s., grouped in *Silicisphinctes* Schweigert and Zeiss (1999), clearly differ from *Subplanites* Spath, which groups the microconchs of *Euvirgalithacoceras*. Moreover *Lithacoceras* s.s. seems to group mainly Ulmense subzone (Late Kimmeridgian) species, whereas *Euvirgalithacoceras* groups mainly those of the Hybonotum zone, Early Tithonian (Zeiss et al., 1996; Schweigert, 1998; Schweigert and Zeiss, 1999). The latter is more evolute and less densely and finely ribbed than *Lithacoceras* s.s. The difference between the palmate style of ribbing of *Euvirgalithacoceras* and the fascipartite of *Lithacoceras* s.s. lies in the lower point of furcation of the latter; the palmate style begins with a thickened stalk on the lower half of the primary rib prior to its division at the middle or upper third of the flanks (Fig. 6A).

Euvirgalithacocers malarguense (Spath, 1931) [M and m]

See Figs. 1, 4, 5A, 6A–D, and 7A–E, as well as Appendix A.

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* 1900 *Perisphinctes lictor* Fontannes: Burckhardt, p. 43, pl. 24, fig. 4 [lectotype].

? 1900 *P. Tiziani* Oppel: Burckhardt, p. 43, pl. 24, fig. 3.

? 1900 *P. pouzinensis* Toucas: Burckhardt, p. 45, pl. 24, fig. 8.

* 1903 *Perisphinctes* aff. *pseudolictor* Choffat: Burckhardt, p. 36, pl. 4, figs. 1 [lectotype], 2–4.

? 1906 *Virgatites* sp.: Burckhardt, p. 119, pl. 30, fig. 4.

? 1906 *Perisphinctes* sp.: Burckhardt, p. 113, pl. 30, fig. 8.

? 1906 *Virgatites mexicanus* n. sp.: Burckhardt, p. 115, pl. 31, figs. 5–9.

? 1906 *Perisphinctes* cfr. *danubiensis* Schlosser: Burckhardt, p. 112, pl. 32, fig. 1.

? 1906 *Virgatites* sp. ind.: Burckhardt, p. 118, pl. 32, fig. 2.

1931 *Subplanites malarguensis* nom. nov. [*recte* sp. nov.]: Spath, p. 468, 501.

(*continued on next page*)

1954 *Virgatosphinctes* (*Subplanites*?) aff. *pseudolictor* Choffat: Indans, p. 119, pl. 19, figs. 3, 4.
? 1954 *Virgatosphinctes* cf. *raja* Uhlig: Indans, p. 110, pl. 14, figs. 1–3.
1954 *Virgatosphinctes communis* Spath: Indans, p. 108, pl. 15, fig. 6.
? 1964 *Perisphinctes (Dichotomosphinctes) bangei* Burckhardt: Muñoz, p. 9, pl. 2, fig. 3.
? 1964 *S. durangoensis* n. sp.: Muñoz, p. 21, pl. 8, figs. 1–2.
? 1980 *Lithacoceras (Virgalithacoceras) acricostatum* n. sp.: Ohmert and Zeiss, p. 19, pl. 3, fig. 1, pl. 5, figs. 1–2.
1981a *Subplanites malarguense* Spath: Leanza, p. 571.
1981b *S. malarguensis* Spath: Leanza, p. 81.
? 1988 *Discosphinctoides* (?) aff. *D. neohispanicus* (Burckhardt): Poulton et al., p. 106, pl. 5.3: figs. 1–2, 4–9.
? 1993 *Lithacoceras? mexicanus* (Burckhardt): Callomon, p. 267.
1997 *Subplanites* sp.: Kraemer & Riccardi, p. 339, fig. 4(3).
1999 *Lithacoceras (Virgalithacoceras)* cf. *acricostatum* Ohmert and Zeiss: Parent and Capello, p. 349.
1999 *Torquatisphinctes* cf. *laxus* Olóriz: Parent and Capello, p. 349 [a microconch].

Lectotype. The incomplete adult specimen from Casa Pincheira illustrated by Burckhardt (1900, pl. 24, fig. 4; drawing refigured 1903, pl. 4, fig. 1 [referred by Spath, 1931, p. 468, 501]) is here designated and may be in the collection of the Museo de La Plata.

Material. One complete, adult macroconch slightly crushed (LPB 178), five incomplete adults and phragmocones (LPB 180, 183, 185, 191, 407), and two complete adult microconchs (LPB 186, 188) from bed G15, lowermost *Mendozanus* biozone (Hybonotum zone, Early Tithonian).

Descriptions. Macroconch: evolute and compressed with biplicate and virgatotome ribbing on the Ph and palmate on the BC, which is about 365° long. Ventral ribs never interrupt at any developmental stage. There are approximately 2 constrictions per whorl through $D > 10$ mm. At $D = 5-10$ mm, 14–18 strong, prosocline primaries occur per half-whorl, biplicated on the upper third of flanks. Umbilicus is moderately open ($U/D = 0.38-0.40$). At $10 < D < 30$ mm, the whorl section is oval compressed ($W/D = 0.29$), and the umbilicus is slightly narrower, $U/D = 0.34-0.38$. Ribbing is composed of 18–25 fine, slightly flexuous primaries per half-whorl, bifurcated on the upper half of flanks; some simple and rare virgatotome ribs are intercalated. At $30 < D < 100$ mm ($\approx$Dls), the whorl section is high oval to subrectangular compressed ($W/D = 0.20-0.29$); in some specimens, it is subtrapezoidal and widest at the umbilical shoulder. There are 25–35 fine primaries and 42 ventrals per half-whorl, primaries divide at the middle of the flanks, and one virgatotome occurs each 2–5 biplicates. The umbilicus becomes slightly enlarged ($U/D = 0.32-0.44$). On the BC, $100 < D < 165$ mm (= Dp), there are about 23 primaries on the initial half; along the terminal half, there are about 20 palmate primaries with the umbilical stalk thickened and divided into up to 8 secondaries, $V = 97$. Some simple, strong primaries occur terminally preceding the peristome. Uncoiling is evident, and U/D passes from 0.42 at Dls to 0.47 at Dp. The peristome is simple and slightly sinuous.

Microconch: smaller than the macroconch, it differs in the aspect of the adult BC, which develops irregular ribbing with primaries as strong as secondaries. The furcation point is not clearly defined, moving from the inner to the middle third of the flank. Uncoiling is observed through the last half of the BC, which does not show lappets preserved.

Comparison and discussion. The lectotype of *Subplanites malarguense* Spath is a large adult Ph with a portion of BC strongly ribbed, indicating macroconch sexual dimorphic status. The attribution of the species to the genus *Euvirgalithacoceras* rather than to *Lithacoceras* is due to the general aspect of the conch and the diagnostic ontogenetic sequence of bipartite-virgatotome-palmate ribbing with no occurrence of a true fascipartite ribbing stage (confirmed by G. Schweigert, pers. comm., 19/03/99), as is typical of *Lithacoceras* (Zeiss et al., 1996, p. 137). This species was originally included in *Subplanites* by Spath (1931). Indans (1954) placed *Subplanites* as a subgenus of *Virgatosphinctes*, including some forms directly comparable with and here assigned to *S. malarguense* Spath.

Perisphinctes tiziani Oppel and *Perisphinctes pouzinensis* Toucas, as illustrated by Burckhardt (1900), differ slightly in details of costulation with respect to the lectotype of *E. malarguense* Spath, but they could fit the intraspecific range of variation of the latter.

The ammonoid fauna from southern Mendoza studied by Indans (1954) mostly comprises lithacoceratids. This fauna includes forms illustrated as *Virgatosphinctes* (*Subplanites*?) aff. *pseudolictor* Choffat, *V.* cf. *raja* Uhlig, and *V. communis* Spath, all closely resembling *E. malarguense* (Spath) in every detail of ornamentation and morphology, which thus suggests conspecificity. This group of forms intergrades with *Lithacoceras tenuilineatus* Indans, *L. burckhardti* (Douvillé), *V. erinoides* Burckhardt, *V. communis* Spath, and *V. densistriatus* (Steuer), which may be included in *Lithacoceras* (cf. Donze and Enay, 1961, p. 70; Olóriz, 1978, p. 510) and closely resemble the type species *L. ulmense* (Oppel) reviewed by Schweigert (1998) and Schweigert and Zeiss (1999). If chronostratigraphic succession of these two groups of lithacoceratids can be demonstrated for the Neuquén–Mendoza basin, the same transition seen in the Tethys, from *Lithacoceras*-dominated

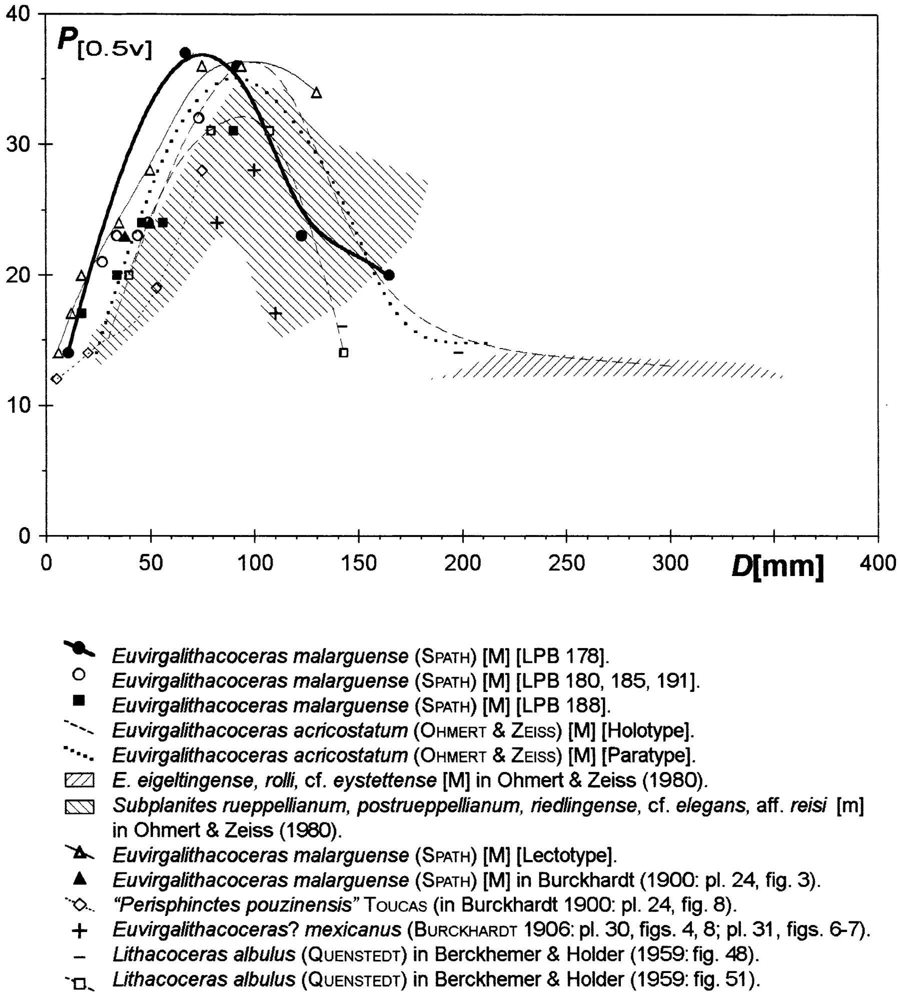

Fig. 4. *Euvirgalithacoceras malarguense* (Spath) [M&m]. Patterns of ribbing compared with the assemblage of *Euvirgalithacoceras* and *Subplanites* described by Ohmert and Zeiss (1980) and other relevant material discussed in text.

faunas in the Beckeri zone (Upper Kimmeridgian) to *Euvirgalithacoceras*-dominated faunas in the Hybonotum zone (Lower Tithonian) should arise.

The specimen from Santa Cruz (Argentina) illustrated by Kraemer and Riccardi (1997, fig. 4 [3]) as *Subplanites* sp. is a macroconch very close if not identical to the macroconch of the present species; they are assumed to be conspecific.

The resemblance to *Lithacoceras? mexicanus* (Burckhardt, 1906, pl. 30, figs. 4, 8, pl. 31, figs. 5–9, pl. 32, figs. 1–2) from Cañón de San Matías, México, is very close, but no adult specimens with a BC of this Mexican form are known. Nevertheless, the age assigned by Callomon (1993, p. 267), slightly adjusted by Villaseñor et al. (2000), is the same proposed for the present material in the Hybonotum zone (Early Tithonian). The general aspect of the sculpture indicates that it could belong to *Euvirgalithacoceras*. '*Perisphinctes (Dichotomosphinctes)*' *bangei* Burckhardt, as figured by Muñoz (1964, pl. 2, 3), and *Substeueroceras durangoensis* Muñoz (1964, pl. 8, 1–2) from Durango are, on morphological grounds, typical *Subplanites*, similar to the present species and *Subplanites* gr. *rueppellianum–postrueppellianum*.

Discosphinctoides aff. *neohispanicus* (Burckhardt, 1919, non *Idoceras neohispanicum* Burckhardt, 1912, p. 111, pl. 29, 1–4, 6, 8), as described by Poulton et al. (1988), is a group of microconchs of the Hybonotum zone of Western Canada with strong similarity to the present microconchs and Ph of the adult macroconch, which suggests conspecificity. Neither the specimens described by Poulton et al. (1988) nor the present ones match the type material of the Mexican '*Perisphinctes*' *neohispanicus* originally described by Burckhardt (1919, pl. 10, figs. 1–5, 7), which are stouter perisphinctids with a dense, fine, primary ribbed BC and thicker ribbed inner whorls, as in *Torquatisphinctes* Spath 1924. Moreover, these specimens seem to come from beds of Darwini zone age (cf. Callomon, 1993). *Lithacoceras*? sp. and *Lithacoceras? (Subplanites?)* sp. of the same age and locality at Canadá (Poulton et al., 1988) are incomplete adult specimens that show affinities with the present adult macroconch.

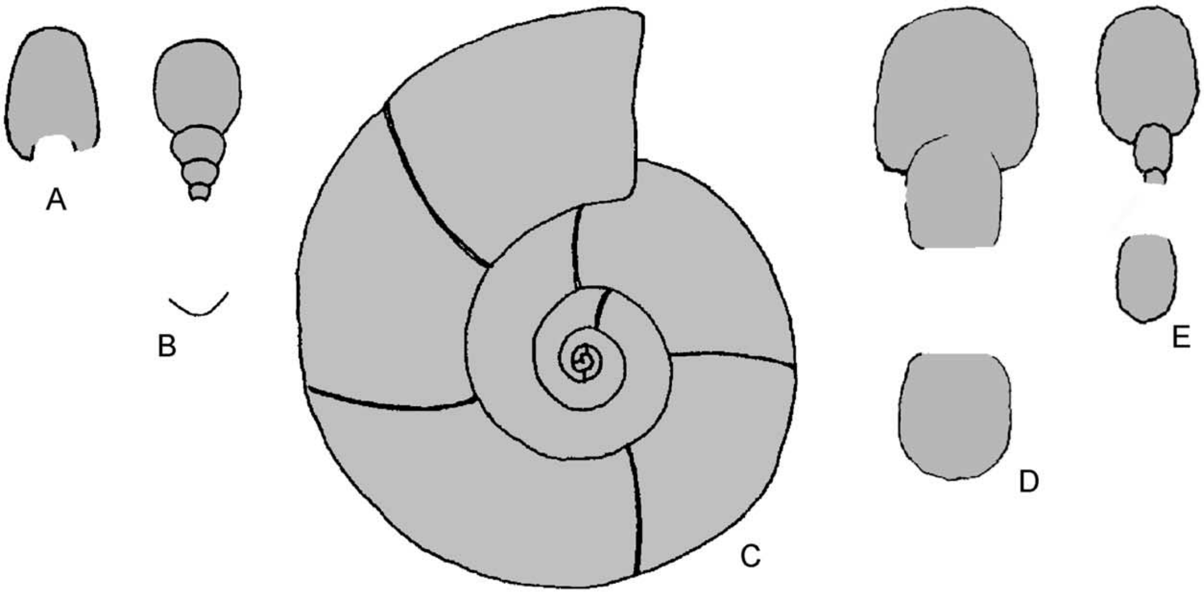

Fig. 5. Cross-sections and lateral view in natural size (×1). A: *Euvirgalithacoceras malarguense* (Spath), end of phragmocone of a subadult macroconch (LPB 191) at about $D = 60$ mm. B: *T. proximus* (Steuer) morph α, adult phragmocone (LPB 187) at $D = 38$ mm. C–E: *Paraulacosphinctes striolatus* (Steuer); C: schematic lateral view of an adult phragmocone (LPB 184) showing the emplacement of constrictions, D: same specimen at $D = 70$ mm, E: complete adult phragmocone (LPB 201) at $D = 43.5$ mm.

Of these specimens, the adult macroconch (Fig. 6A) is almost identical to *Euvirgalithacoceras acricostatum* [M] (Ohmert and Zeiss, 1980, pl. 3, fig. 1, pl. 5, figs. 1–2). It differs in its slightly smaller adult size and the faster growing of ribbing density in the flanks of the Ph (Fig. 4). *Perisphinctes albulus* (Quenstedt) in Berckhemer and Hölder (1959, fig. 51), which may be an *Euvirgalithacoceras* (Olóriz, 1978; G. Schweigert, pers. com., 16-02-98), also strongly resembles it. *Euvirgalithacoceras copei* (Ohmert and Zeiss, 1980) [M] and *Euvirgalithacoceras* aff. *copei* (Ohmert and Zeiss, 1980) [M], as figured by Zeiss (1994, pl. 4), show a close resemblance and differ mainly in their bigger adult size.

Venzo (1959) has figured as *Subplanites* cf. *rueppellianus* (Quenstedt) and *Subplanites scarsellai* Venzo some specimens of the lower Tithonian (?Hybonotum zone) of Ethiopia that do not differ significantly at comparable diameters. The main difference lies in the more densely ribbed last whorls. From Nepal, paleogeographically closer to Ethiopia, Helmstaedt (1969) has figured *Subplanites nepalensis* Helmstaedt and *Subplanites* sp., forms that closely match the present species and differ mainly in the somewhat flexuous primary ribs on the flanks.

C. choicensis (Burckhardt) is stouter, and the ribbing is more irregular on the adult BC and rigid on the Ph. Two shared features of ribbing—the development of palmate ribbing on the adult BC and the occurrence of pairs of close, parallel primaries delineating a narrow constriction—are remarkable and suggest direct phyletic relationships between these two forms, which occur in succession in several localities throughout the Neuquén–Mendoza basin. The second last feature (or structure) is regarded in some morphotypes of species belonging to Lithacoceratinae, including the holotype of *Lithacoceras albulus* (Quenstedt) and the specimen of *Lithacoceras fasciferum* (Neumayr) figured by Berckhemer and Hölder (1959, pl. 9, fig. 48 and pl. 11, fig. 55, respectively).

Age and distribution. The stratigraphic position and age of *Euvirgalithacoceras* in Swabia is well established and thus a solid indication of a Hybonotum zone age for *E. malarguense* (Spath). Additional arguments for the correlation of bed G15 of the Casa Pincheira section are given by Parent and Capello (1999). This could be extended to the rest of the closely comparable forms of Patagonia, México, and Canada discussed previously. Moreover, the Canadian fauna (Poulton et al., 1988) has been dated as Hybonotum zone age independently of this study. The distant paleogeographic location of the Neuquén–Mendoza basin and the Central Tethys has prevented the inclusion of *E. acricostatum* (Ohmert and Zeiss) [M] as a junior synonym of *E. malarguense* (Spath) [M], though the morphological identity suggests these morphospecies may belong to a single biospecies. Moreover, when the respective ammonite assemblages are compared, the present one covers a wide range of the spectrum of morphotypes described by Ohmert and Zeiss (1980) as *E. acricostatum* (Ohmert and Zeiss, 1980, pl. 5, 1) [M], *Euvirgalithacoceras eigeltingense* (Ohmert and

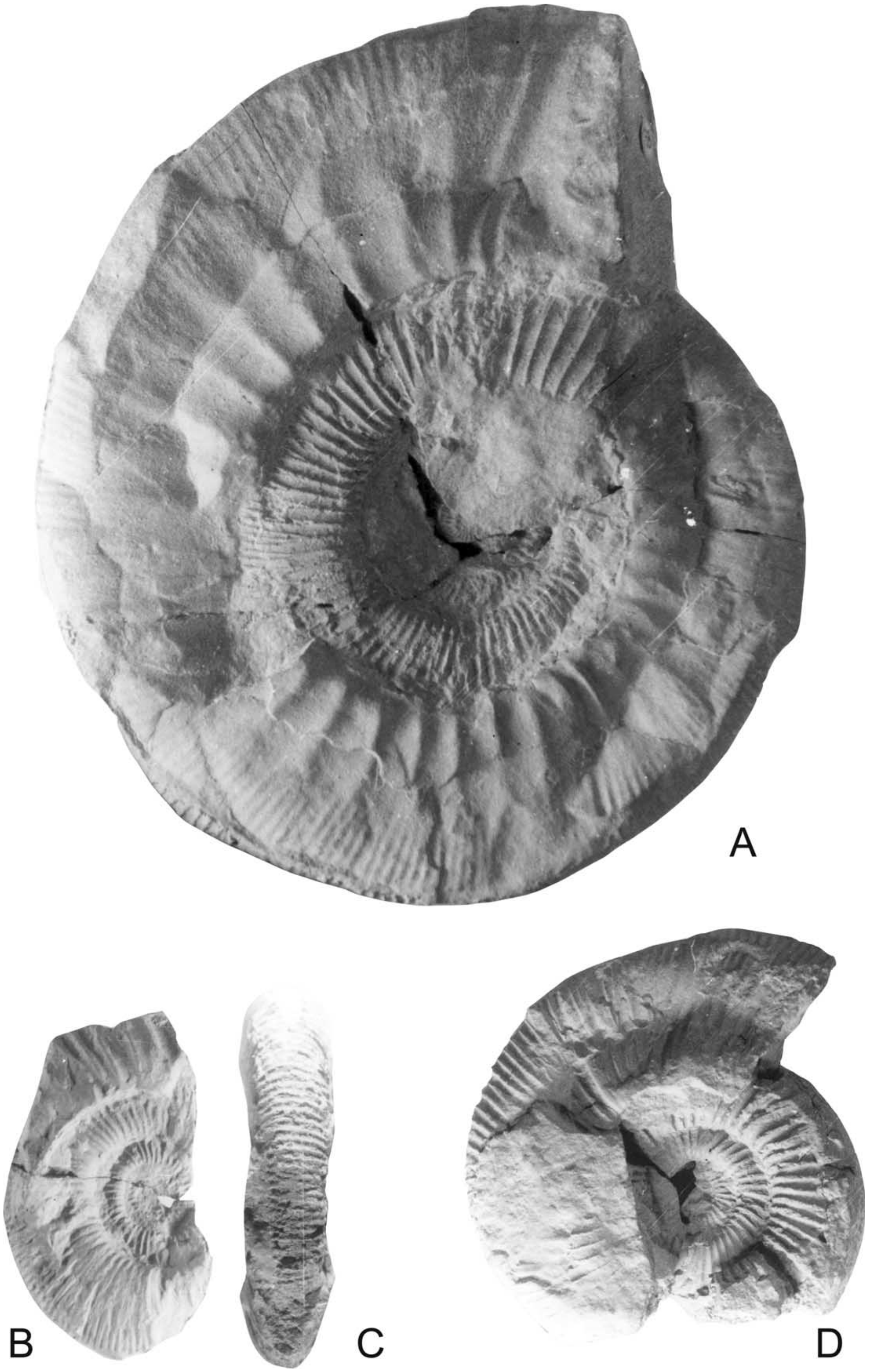

Fig. 6. *Euvirgalithacoceras malarguense* (Spath) [M&m], Casa Pincheira (Mendoza), bed G15. A: Complete adult macroconch (LPB 178). B–C: Lateral and ventral views of an incomplete adult macroconch (LPB 191). D: Lateral view of an almost complete microconch (LPB 188). All natural size (×1).

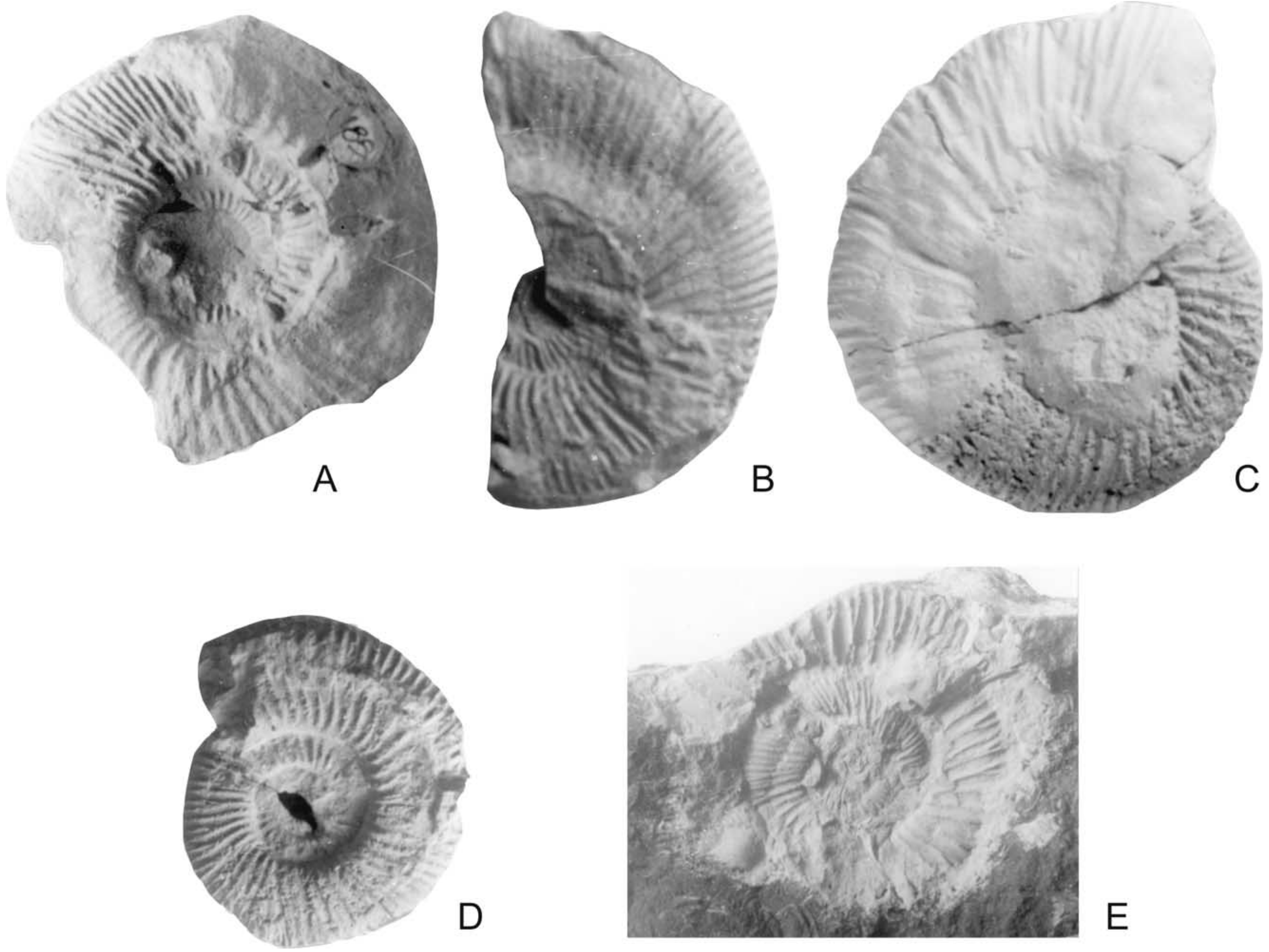

Fig. 7. *Euvirgalithacoceras malarguense* (Spath) [M&m], Casa Pincheira (Mendoza), bed G15. A: Lateral view of a subadult macroconch (LPB 185). B: Lateral view of a phragmocone of a macroconch (LPB 191). C: Lateral view of a complete microconch (LPB 186). D: Lateral view of an almost complete phragmocone (LPB 180). E: Lateral view of an incomplete macroconch(?) showing innermost whorls (LPB 407). All natural size (×1).

Zeiss, 1980), *Subplanites postrueppellianum* (Ohmert and Zeiss, 1980, pl. 13, 3) [m], *S.* sp. (Ohmert and Zeiss, 1980, pl. 12, fig. 5) [m], and *S.* cf. *elegans* (Spath in Ohmert and Zeiss, 1980, pl. 14, fig. 2) [m].

It appears that, along the Western American Pacific basins, Hybonotum zone age populations (seen as conventional morphospecies) developed from a relatively low variable biospecies, whose morphotypes differ little from those of the European Tethyan populations. The main difference is the smaller adult size of these peri-Pacific populations, a pattern seen in other perisphinctids of the Andean Middle and Upper Jurassic (Parent, 1998a,b), such as the late Bathonian *Choffatia subbakeriae* (d'Orbigny) [M], the Middle Oxfordian *Perisphinctes* gr. *kranaus–decurrens* Buckman, and the Upper Oxfordian–Lower Kimmeridgian macroconch *Orthosphinctes* (*Lithacosphinctes*) cf. *evolutus* (Quenstedt). The consistency of this clinal pattern, paedomorphic (Parent, 1998b), receives additional support from these observations and could be a useful biogeographical feature in studying migrational routes and intercontinental correlations.

Genus *Choicensisphinctes* Leanza 1980

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

Remarks. *Choicensisphinctes* Leanza includes stout, moderately evolute, macro- and microconch perisphinctids. Ribbing on the inner whorls is relatively fine, prorsiradiate and biplicate in the upper third of flanks but sometimes irregular, especially at constrictions. On the BC, it develops ataxioceratid habit; true virgatotome ribs with primaries widening on the lower third of flanks may occur occasionally; on the upper half of flanks arise bundles of secondaries, similar to the palmate structure seen in *E. malarguense*. These features strongly suggest the inclusion of the genus in the Lithacoceratinae, and considering the temporal continuity with *E. malarguense*, they may be considered in direct phyletic connection. The species described by Leanza (1980) as *C. choicensis* (Burckhardt), *Ch. choicensis sutilis* Leanza, *Ch. erinoides*

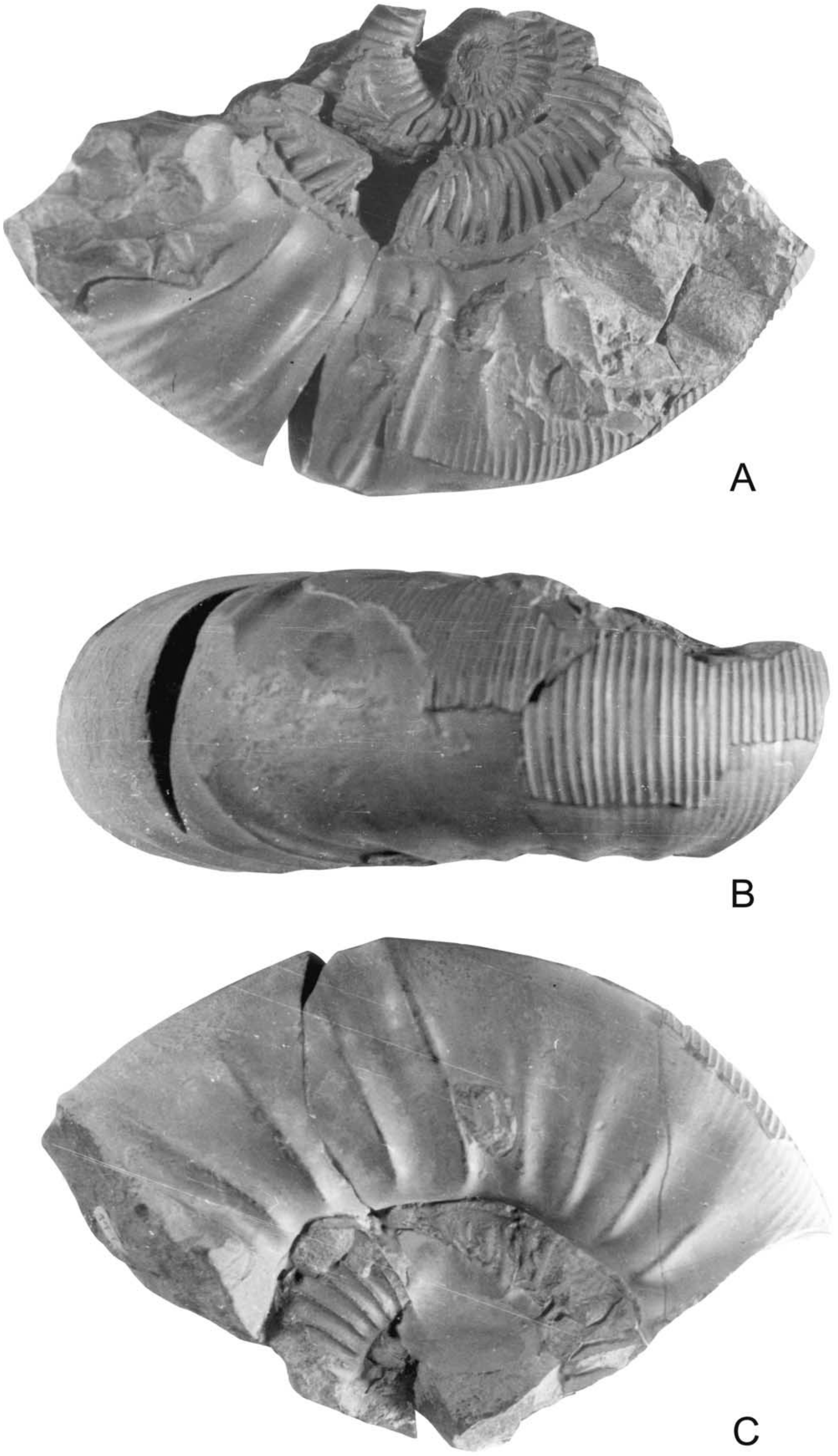

Fig. 8. *Choicensisphinctes choicensis* (Burckhardt), Casa Pincheira (Mendoza), bed G14. Natural size (×1) left lateral (A), ventral (B), and right lateral (C) views of specimen LPB 197 (aperture facing upward facing observer). Note ornamentation slightly attenuated on the inner mould.

(Burckhardt), *Virgatosphinctes burckhardti* (Douvillé), and *Pseudinvoluticeras douvillei* Spath conform to a very homogeneous group with some morphotypes that more or less resemble typical Submediterranean Tethyan lithacoceratids, such as *Franconites vimineus* (Schneid, 1915) and *Dorsoplanitoides bavaricus* Zeiss (1968) from the Darwini–Semiforme zones of Germany. The ammonite figured by Leanza and Leanza (1979, pl. 4, fig. 2) from the *Mendozanus* biozone of Catan Lil (Neuquén) may be included in *Choicensisphinctes* Leanza. The genus has been recorded in Neuquén and Mendoza (Leanza, 1980), San Juan (Lo Forte et al., 1996), and the Austral basin (Kraemer and Riccardi, 1997), and all forms have been assigned to the Lower Tithonian *Mendozanus* biozone. From southern Rancagua, Chile, emerges a specimen close to *Choicensisphintes erinoides* (Burckhardt, 1903) illustrated as *Perisphinctes* aff. *erinus* (d'Orbigny, 1847) by Corvalán (1959, pl. 3, fig.12). (A cast of this specimen was kindly loaned to me by Ernesto Perez d'A, Servicio Nacional de Geología y Minería de Chile.) This specimen shows an intermediate morphology between *Choicensisphinctes* and the Mexican Late Kimmeridgian genus *Procraspedites* Spath sensu Olóriz et al. (1998): a very involute shell with flattened flanks converging to a narrow venter and covered with wide, rounded primaries and several feeble and short secondaries at the upper third of flanks.

Choicensisphinctes choicensis (Burckhardt, 1903) [m]

See Figs. 1 and 8A–C, as well as Appendix A.

*	1903	*Perisphinctes choicensis* Burckhardt, p. 50, pl. 6, figs. 10–12; pl. 8, fig. 6.
	1980	*C. choicensis* (Burckhardt): Leanza, p. 51, pl. 2, fig. 4.
	1980	*C. choicensis sutilis* H. Leanza n. ssp., p. 34, pl. 3, fig. 1, pl. 4, fig. 3.
	1980	*V. burckhardti* (Douvillé): Leanza, p. 30, pl. 5, fig. 2.
	1980	*P. douvillei* Spath: Leanza, p. 23, pl. 3, fig. 5, *non* 3, pl. 4, fig. 2.
	1999	*Choicensisphinctes* cf. *choicensis morfo sutilis* [?m] Leanza: Parent and Capello, p. 349.

Holotype. The specimen drawn by Burckhardt (1903, pl. 6, figs. 10–12 and pl. 8, fig. 6, whorl section), probably an adult with an incomplete BC, is the only one originally included in the species, and thus, it becomes the holotype by monotypy. The type locality is situated between Cajón del Burro and the valley of Río Choicas, Mendoza (Fig. 1).

Material. One virtually complete adult microconch (LPB 197) and fragmentary specimens from bed G14, *Mendozanus* biozone (Darwini zone, late Early Tithonian).

Description. An evolute and robust perisphinctid. The Ph is evolute, the whorl section subquadrate with ventral and umbilical shoulders broadly rounded and a high umbilical wall. Ribbing is fine and sharp, more or less prosocline, and bifurcates at the upper third of flanks. Rib density increases from the innermost whorls to a maximum at the end of the adult Ph: $P = 10–14$ at $4 < D < 30$ mm and $P = 26$ at $Dls = 86$ mm.

The BC is stout with a rounded whorl section, as high as wide ($W/H_1 = 0.98$) and slightly uncoiled. Ribbing changes dramatically (pronounced variocostation) to very strong, broadly spaced primaries ($P = 12$) divided into 6–10 fine secondaries in palmate fashion that cross the venter without any change.

Remarks. Our specimen is more evolute than typical *Choicensisphinctes*, as described by Leanza (1980). This feature and the aspect of ribbing on the BC associate this species with *E. malarguense* (Spath) and suggest that our specimen could be an early representative of the genus, originated in *E. malarguense* (Spath).

The species of *Choicensisphinctes* described by Leanza (1980) occur associated with one another and intergrade morphologically, not differing significantly and thus conforming to a single, variable dimorphic biospecies. *Choicensisphinctes erinoides* (Burckhardt) [M] (= *Perisphinctes* aff. *Erinus* d'Orbigny in Burckhardt, 1900, pl. 25, fig. 1, pl. 26, fig. 3) certainly corresponds with *Choicensisphinctes* gr. *choicensis* (Burckhardt) [m] (including *Ch. choicensis sutilis* Leanza and *P. douvillei* Spath [in Leanza, 1980, pl. 3, fig. 5, pl. 4, fig. 2]) and confirms a sexual dimorphic pair, in that (1) inner whorls of these species are indistinguishable and the sculpture of their BCs only differs in the greater prominence of the primary ribs of *Ch. erinoides*, (2) they come from the same beds and frequently occur associated in other localities, and (3) the paratype of *Ch. choicenisis sutilis* Leanza (1980, pl. 4, fig. 3) shows a lateral peristomatic lappet indicating microconchiate-male sexual dimorphic status. However, it seems convenient to keep these forms as separate morphospecies pending better preserved adult specimens from single beds to compare the whole preadult ontogeny.

Virgatosphinctes cf. *raja* Uhlig (in Indans, 1954, pl. 14, figs. 1–3) resembles the present specimen in the palmate style of ribbing on the BC and broad whorls (cf. Leanza, 1980, p. 32), but a closer resemblance with *E. malarguense* (Spath) was noted previously.

Genus *Paraulacosphinctes* Schindewolf 1925

Type species *Ammonites senex* Oppel 1865 by original designation.

Discussion. Tavera (1985) has revised the genus, created the closely related *Moravisphinctes, Zitteli, Andalusphinctes* (upper Micracanthum zone = Transitorius zone of Tavera (1985)), and *Neoperisphinctes* (Durangites zone), and included all these genera into the Paraulacosphinctinae Tavera (1985). These taxa comprise finely ribbed macroconchs with smooth BCs ending with a simple peristome; the corresponding microconchs are indistinguishable by their inner whorls, but their BCs are

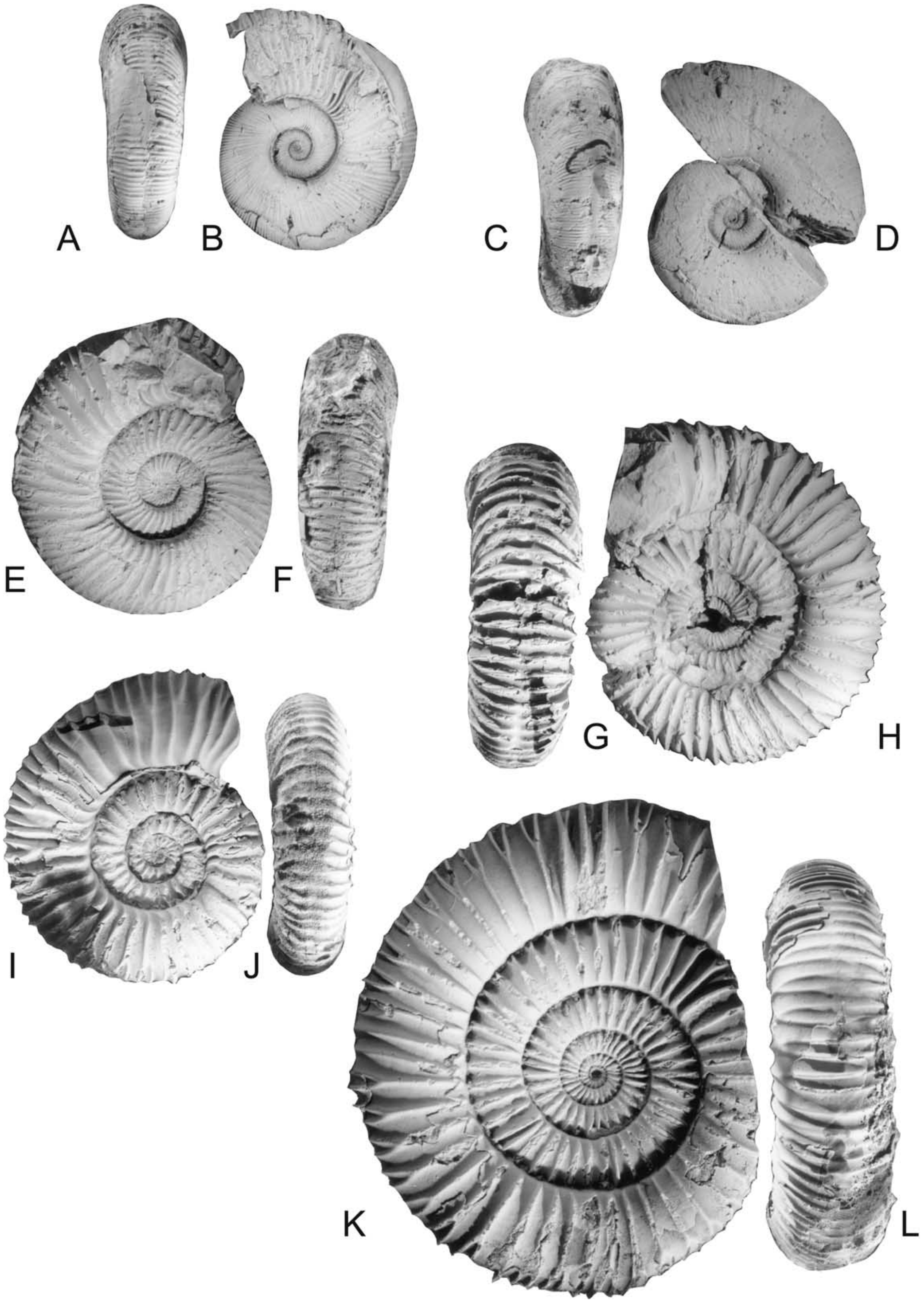

Fig. 9. Lateral and ventral photographic views at natural size (×1) of specimens originally drawn by Steuer (1897). Location of Plate and figures are referred to the original German publication, which is the same as the Spanish edition of 1921. Updated taxonomy, typological status if it corresponds, locality, and collection number of the MGAU are indicated. A–B: *Reineckeia striolata* Steuer [pl. 14, figs. 8–9 – *Paraulacosphinctes striolatus* (Steuer) (M), Lectotype, Arroyo de la Manga, MGAU 499-45]. C–D: *Reineckeia striolatissima* Steuer [pl. 14, figs. 5–6—*P. striolatus* (Steuer) (M), Arroyo de la Manga, MGAU 499-44]. E–F: *Reineckeia transitoria* (Oppel) [pl. 15, fig. 6, ventral view added here—*P. striolatus* (Steuer) (M), Arroyo de la Manga, MGAU 499-49]. G–H: *Reineckeia mangaensis* Steuer [pl. 13, figs. 7–8—?*Paraulacosphinctes striolatus* (Steuer) (m?), Holotype, Arroyo de la Manga, MGAU 499-41]. I–J: *Reineckeia proxima* Steuer [pl. 8, figs. 7–8—*Torquatisphinctes proximus* (Steuer) morph β, Lectotype, Arroyo Cieneguitas (level II), MGAU 499-30]. K–L: *P. colubrinus* (Reinecke) [pl. 15, fig. 11, ventral view added here—*T. proximus* (Steuer) morph α, Arroyo Cieneguitas (level I), MGAU 499-51].

normally densely or coarsely ribbed, ending with peristomes bearing lateral lappets such as those on *Subplanites*.

Reports of *Paraulacosphinctes* and related genera form the Andean Tithonian are scarce, but recent studies on old and new material indicate that the genus, in a broad sense including the morphogenera of Tavera (1985), occurs in the Upper Tithonian of several localities of the Neuquén–Mendoza basin. As Tavera (1985, 79) noted, Krantz (1928) cited *P. striolatus* (Steuer), using the genus for the first time for a form of the AndeanTithonian. Tavera (1985) assigned '*Aulacosphinces*' *hebecostatus* Krantz (1928, pl. 3, fig. 8) and '*A.*' *wanneri* Krantz (1928, pl. 2, fig. 6) to *Zittelia*. Recently, Enay et al. (1996) reported *Moravisphinctes* sp. and *Zittelia* sp. from the Upper Tithonian of the Chicama basin, Northern Peruvian Andes.

Paraulacosphinetes striolatus (Steuer, 1897) [M&?m]

See Figs. 1, 5C–E, 9A–H, 10A–B, and 11A–B, as well as Appendix A.

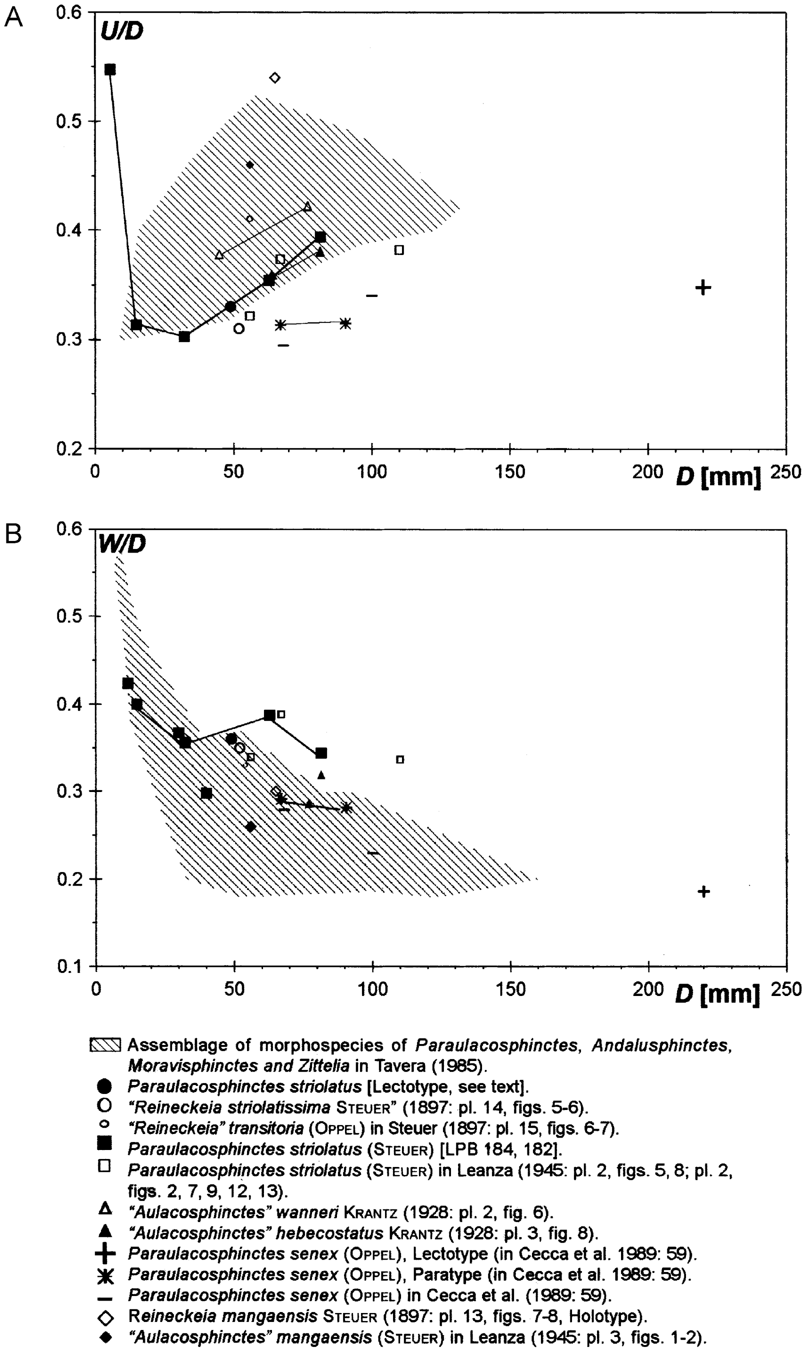

Fig. 10. *Paraulacosphinctes striolatus* (Steuer). Comparative biometric patterns of *U/D* (A) and *W/D* (B) for Andean material and data from Tavera (1985).

Fig. 11. *Paraulacosphinctes striolatus* (Steuer), Casa Pincheira (Mendoza), bed G10. A: Lateral view of an adult phragmocone (LPB 184). B: Lateral view of a phragmocone dissected to show innermost whorls (LPB 182). All natural size (×1).

* 1921 *R. striolata* Steuer [sp. nov.], p. 63, pl. 14, figs. 8–10 [lectotype].
1921 *Reineckeia striolatissima* Steuer [sp. nov.], p. 63, pl. 14, figs. 5–7.
1921 *Reineckeia transitoria* Oppel: Steuer, p. 59, pl. 15, figs. 6–7.
? 1921 *Reineckeia mangaensis* Steuer [sp. nov.], p. 60, pl. 13, figs. 7–8.
1928 *Paraulacosphinctes striolatus* Steuer: Krantz, p. 44.
1928 *Aulacosphinctes wanneri* n. sp., Krantz: p. 42, pl. 2, fig. 6, text-fig. 12.
1945 *Pectinatites* (?) *striolatus* (Steuer): Leanza, p. 24, pl. 2, figs. 5, 8.
1945 *Substeueroceras striolatissimum* (Steuer): Leanza, p. 30, pl. 2, figs. 2, 7, 9, 12, 13.
? 1945 *A. mangaensis* (Steuer): Leanza, p. 21, pl. 3, figs. 1–2.
1945 *Substeueroceras koenini* (Steuer): Leanza, p. 28, pl. 5, figs. 7–8.
1999 *Paraulacosphinctes? striolatisimun* Steuer: Parent and Capello, p. 349.

Lectotype. The Ph wihout BC figured by Steuer (1897; trans. 1921, pl. 14, figs. 8–9) is here designated and refigured in Fig. 9A and B. The type locality is Arroyo de la Manga (Fig. 1), Mendoza, cited by Steuer (1897; trans. 1921, 63) as “La Manga.” Paralectotypes come from different localities.

Material. Five more or less complete Phs (LPB 181–182, 184, 189, 201) from bed G10, upper *Alternans* to lower *Koeneni* biozones (late Micracanthum–early Durangites zones, Late Tithonian).

Description. Innermost whorls are evolute and wider than high with a depressed subrounded whorl section with convex flanks. Sculpture is composed of coarse primary ribs, irregularly bifurcated highest on the flanks; there are two constrictions per whorl. From about $D = 10$ mm, the aspect of the shell changes notably: The whorl section becomes rounded subquadrate with flattened flanks; ribbing changes to fine and dense, primaries are projected and slightly concave toward the aperture and bifurcated or trifurcated irregularly on the middle to upper third of the flank; and two to three narrow, shallow constrictions occur per whorl. In the largest specimen, from about $D = 70$ mm, with an unchanged whorl section, the primary ribs become somewhat stronger and more widely spaced, and the locus of furcation is fixed at the middle of the flanks; secondary ribs cross the venter unchanged and neither a ventral groove nor smoothing is observed; and there occur five shallow constrictions on the last preserved whorl.

One of the specimens (LPB 182, Fig. 11B) is more involute and finely ribbed, whereas another (LPB 181) is more evolute and coarsely ribbed. The most coarsely ribbed specimen (LPB 189), though incomplete, appears to be a microconch.

Remarks. The described variation may be accommodated into a pattern of covariation, such as could be interpreted by grouping the morphospecies *Paraulacosphinctes striolatissimus* (Steuer), *P. striolatus* (Steuer), and *P. transitorius* (Oppel in Steuer, 1921, pl. 15, fig. 6). The type specimens of *P. striolatissimus* (Steuer, 1921, pl. 14, figs. 5–7; here refigured in Fig. 9C and D) and *P. striolatus* (Steuer, 1921, pl. 14, figs. 8–10; here refigured in Fig. 9A and B) and the specimen of *P. transitorius* (Oppel in Steuer, 1921, pl. 15, fig. 6; here refigured in Fig. 9E and F) come from the same section and probably the same bed. They occur associated in several other localities of the Neuquén–Mendoza basin, such as in Arroyo del Yeso (cf. Leanza, 1945). These features indicate that they conform to variants of the same species. In this same species might be included '*Aulacosphinctes mangaensis*' Steuer (1921, pl. 13, figs. 7–8 [holotype by monotypy, here designated and refigured in Fig. 9G and H]) as the associated microconch; this is an ammonite with smaller final adult size and identical inner whorls but a coarsely ribbed and slightly uncoiled adult BC that occurs associated with the cited morphospecies at the type locality, and Arroyo del Yeso (Leanza, 1945, pl. 3, fig. 1), Mallín Redondo (Mendoza), and probably Cerro Lotena, Neuquén (unpublished material).

The present sample shows a pattern of covariation described by many authors who have related intraspecifically the macroconchs *Paraulacosphinctes transitorius* (Oppel) and *P. senex* (Oppel) and that can be observed in the original drawings by Oppel (in Zittel, 1868) for these species. The microconchs of these soft BC macroconchs seem to differ in the smaller adult size, the uncoiled BC, and the occurrence of lappets at the peristome. Most, if not all, of the specimens that Tavera (1985) included in *Andalusphinctes* Tavera and *Moravisphinctes* Tavera appear to be microconchs of *Paraulacosphinctes* and *Zittelia* Tavera (see Fig. 10A and B; cf. Cecca et al., 1989).

'*Reineckeia*' *striolata* Steuer and '*R.*' *striolatissima* Steuer have been directly compared with and related to *Paraulacosphintes senex* (Oppel) by Steuer (1921) and '*Aulacosphinctes*' *wanneri* Krantz with *P. transitorius* (Oppel) by Krantz (1928). The Andean morphospecies discussed conform to an assemblage that occurs in beds of equivalent stratigraphic position and are so close in morphology to the Tethyan morphotypes that conspecificity seems evident. However, a conservative taxonomy is adopted because (1) Tethyan forms have considerable vertical ranges (as appears to be the case for the Andean ones), (2) there are no occurrences of analogous forms safely recorded from either the Hispanic corridor (mid-Atlantic seaway/path) or Antarctica and Patagonia, and (3) the sexual dimorphism, if correctly adopted here, differs in the mode of expression of the microconchiate male.

Subfamily Torquatisphinctinae Tavera (1985)

The Torquatisphinctinae includes what appears to be an independently evolving lineage of the Indo-Malgach Province covered by the morphogenera: *Torquatisphinctes* Spath 1924, *Pachysphinctes* Dietrich 1925, and *Katroliceras* Spath 1924, all of which have type species from East Africa or Kutch, India (Callomon, pers. comm., 09/07/98). *Catutosphinctes* Leanza and Zeiss 1992 may be included as a local group close to *Katroliceras* and *Pachysphinctes*. The succession of the first three genera at Ler, Kutch, was recently reviewed by Krishna et al. (1996) and has been recognized as a closely related, homogeneous group by Enay (1972), Tavera (1985), Zeiss et al. (1996, p. 136) and Westermann (1996). Tavera (1985, p. 52) has suggested a possible origin of the subfamily in some 'conservative' Kimmeridgian Ataxioceratinae with an *Orthosphinctes*-like nucleus. These forms could be the Upper Kimmeridgian *Biplisphinctes* Olóriz, 1978 ('*Perisphinctes*' *cimbricus* Neumayr 1873 of the Beckeri zone, Upper Kimmeridgian), as suggested by Olóriz (1978) and Callomon (1993, p. 267). In addition to Torquatisphinctinae's occurrence at the Indo-Malgach Province, it seems to be represented at New Zealand (Westermann, 1996), Antarctica (Thomson, 1979; Riley et al., 1997), and the Austral basin of Patagonia in the form of *Torquatisphinctes* sp. [= *Aulacosphinctoides* sp. in Kraemer and Riccardi, 1997, fig. 4, 2a–2b) and some *Torquatisphinctes*-like specimens figured by Feruglio (1937, pl. 5, figs. 1–2).

In the Neuquén–Mendoza basin, the subfamily Torquatisphinctinae appears to be a well represented group through the Tithonian. A relatively continuous succession of species suggests that they could conform to a single lineage that is documented by the following occurrences:

(1) The poorly known Upper Kimmeridgian–Lower Tithonian *Torquatisphinctes* sp. or spp. (Leanza and Hugo, 1977);
(2) The homogeneous upper Lower Tithonian (*Mendozanus* Biozone) group of morphospecies '*Virgatosphinctes*' gr. *mendozanus* Burckhardt, *andesensis* (Douvillé), and *evolutus* Leanza. This probably monospecific group, carefully described by Leanza (1980), clearly belongs to *Torquatisphinctes* Spath, as defined subsequently; no consistent true virgatotome ribbing occurs at any of the mentioned forms of '*Virgatosphinctes*'—only irregular virgatitid-like trifurcates at constrictions like the dischizotomous ribbing typical of some Ataxioceratids;
(3) The Middle Tithonian *T. proximus* (Steuer) with two morphs in phyletic connection or transients (see below);
(4) The upper Middle Tithonian *Catutosphinctes rafaeli* Leanza and Zeiss 1992; and
(5) The Middle-lower Upper Tithonian *Pachysphinctes americanensis* Leanza [M] and '*Subdichotomoceras*'

araucanense Leanza [m], which appear to conform a sexual dimorphic pair.

Genus *Torquatisphinctes* Spath, 1924

Type species *Ammonites torquatus* Sowerby 1840

Following Enay (1972), Schairer and Barthel (1981) and Callomon (1993), the genus is here interpreted as a Lower–Middle Tithonian group of forms characterized by an evolute shell, a wide-depressed whorl section that becomes more or less compressed throughout the adult BC, strong and acute ribbing that is bifurcated at the upper third of flanks, and intercalated simple ribs and occasional virgatitid-like triplicates at constrictions throughout the ontogeny. Virgatotome secondaries typical of *Virgatosphinctes* are absent.

Torquatisphinctes proximus (Steuer)

See Figs. 1, 9I–L, 12A–B, and 13A–C, as well as Appendix A.

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* 1921 *Reineckeia proxima* Steuer: p. 61, pl. 8, figs. 7–9 [lectotype], *non* 10–11.

(*continued on next page*)

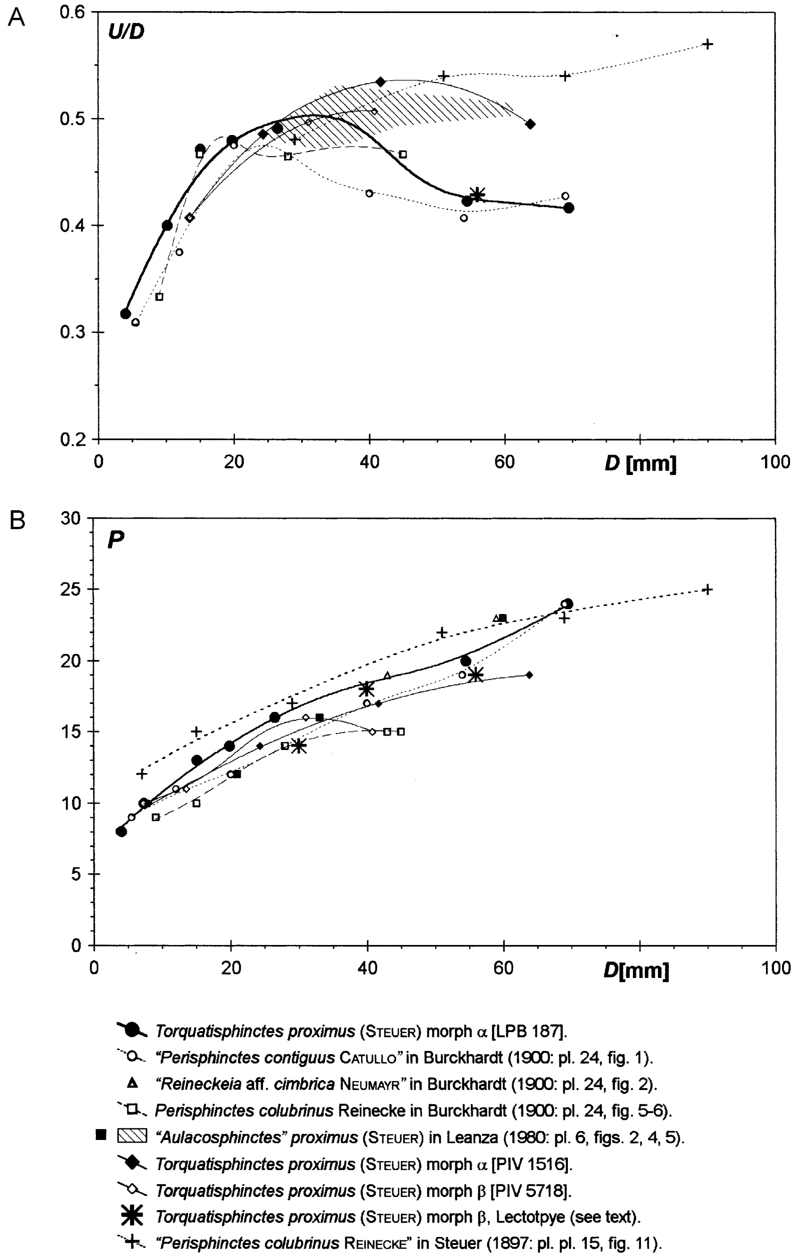

Fig. 12. *Torquatisphinctes proximus* (Steuer). Comparative biometric patterns of *U*/*D* (A) and *P* (B).

1921 *Perisphintes colubrinus* Reinecke: Steuer, p. 90, pl. 15, fig. 11.
1900 *P. contiguus* Catullo: Burckhardt, p. 45, pl. 24, fig. 1.
? 1900 *Reineckeia* aff. *cimbrica* Neumayr: Burckhardt, p. 40, pl. 24, fig. 2.
? 1900 *Perisphinctes colubrinus* Reinecke: Burckhardt, p. 44, pl. 24, figs. 5–6.
? 1900 *Perisphinctes colubrinus* (Reinecke): Burckhardt, p. 46, pl. 26, fig. 4.
? 1954 *V. prorsocostatus* n. sp.: Indans, p. 120, pl. 15, figs. 4–5.
? 1954 *Perisphinctes (Dichotomosphinctes?)* sp.: Indans, p. 124, pl. 20, fig. 3.
1980 *Aulacosphinctes proximus* (Steuer): Leanza, p. 44, pl. 6, figs. 2, 4–5.
1999 *Torquatisphinctes* cf. *proximus* (Steuer): Parent and Capello, p. 349.

Lectotype. The almost complete adult specimen from Arroyo Cieneguita[s] (Fig. 1), Mendoza, figured by Steuer (1897; trans. 1921, pl. 8, Figs. 7–8), is designated and refigured (Fig. 9I and J). Another syntype figured by Steuer (1897; trans. 1921, pl. 8, figs. 10–11) probably belongs to the dimorphic pair *Micracanthoceras* [M]/*Aulaconsphinctes* [m], but to determine whether this is correct, the inner whorls must be observed.

Material. One complete adult Ph with remains of the BC (LPB 187) and fragments of Phs from bed G13a, *Proximus* biozone (late Semiforme–Fallauxi zones, Middle Tithonian).

Description. Evolute, depressed, and strongly ribbed throughout the ontogeny. At $D = 3-4$ mm, the shell is very wide ($W/H_1 = 1.47$) and inflated with a small umbilicus ($U/D = 0.32$) and 8 strong, prosocline primary ribs that start at the umbilical shoulder. At $6 < D < 10$ mm, the shell becomes more widely umbilicated ($U/D = 0.45$), the whorl section reaches its greatest depression ($W/H_1 = 1.57$), and the primary ribs ($P = 11$) remain strong throughout the flanks and furcate at the ventro-lateral shoulder. At $10 < D < 30$ mm, the shell is the most widely umbilicate ($U/D \approx 0.48$) and moderately wide in the whorl section ($W/H_1 \approx 1.20$). There are about 14 primaries per half-whorl; in a pair, one bifurcates at the ventrol-lateral shoulder and the other remains undivided. The undivided primary ribs and secondaries cross the venter without any change in strength. They show only a very narrow interruption that is not extended to the last whorl of the Ph; moreover, it appears to be confined to about a half-whorl. The specimen reaches about 70 mm in diameter at the last adult septa. The last whorl is more compressed and involute than the preceding ones ($W/H_1 \approx 0.90, U/D = 0.42, H_2/H_1 = 0.74$). Primary ribs ($P = 20-24$) are strong; started at the umbilical seam, they cross the umbilical shoulder slightly curved backward and bifurcate at the middle of the flanks. There are two virgatitid-like triplicates associated with shallow constrictions. A short, badly preserved portion of the BC shows strong, acute, widely spaced primary ribs.

Discussion. *T. proximus* (Steuer) has been included in the himalayitid genus *Aulacosphinctes* Uhlig 1910 (type

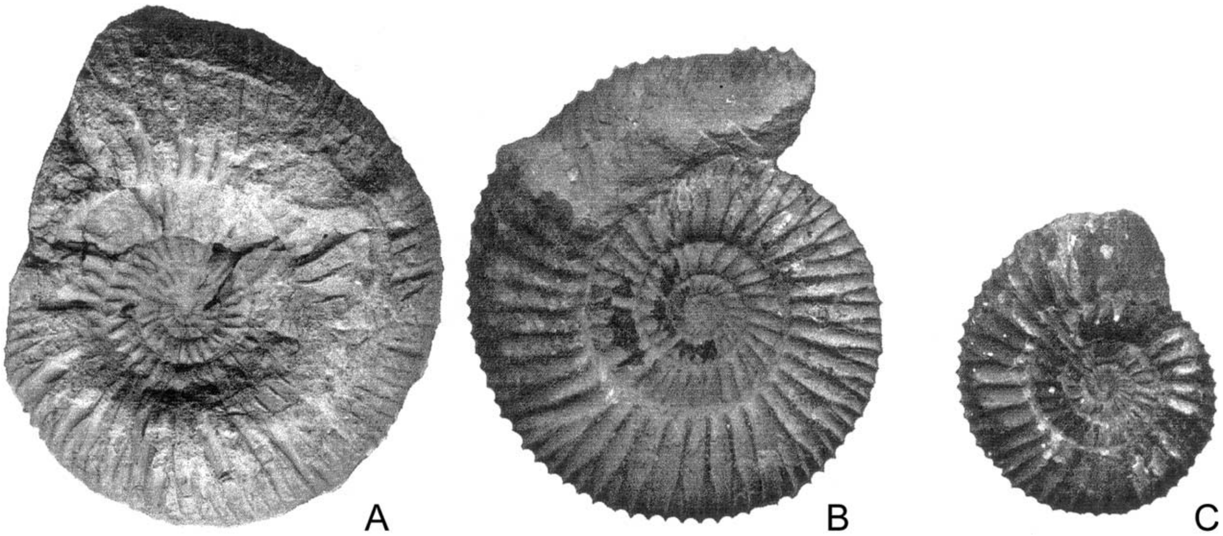

Fig. 13. *Torquatisphinctes proximus* (Steuer). A: Lateral view of an adult phragmocone of the morph α, Casa Pincheira, bed 13a. B: Lateral view of an adult phragmocone of the morph α, Cerro Lotena (PIV 1516). C: Lateral view of an adult phragmocone of the morph β, Cerro Lotena (PIV 5718).

species *Ammonites mörikeanus* Oppel 1863), which includes the microconchs of *Micracanthoceras* Spath (Donovan et al., 1981). The type species of *Aulacosphinctes* has a compressed shell with strong, distant, and widely biplicate primary ribs and a deeper and more persistent ventral groove or marked mid-ventral depression. In some specimens of *T. proximus* (Steuer), a narrow ventral groove or discontinuity of ventral ribbing occurs. Moreover, the virgatitid-like trifurcates at constrictions of *Torquatisphinctes*, absent in *Aulacosphinctes*, is a differential feature, as noted by Olóriz and Tintori (1991, p. 474). As indicated by Enay (in Verma and Westermann, 1973, p. 244), *Aulacosphinctes* has lateral tubercles on at least the inner whorls, a distinctive feature absent in *R. proxima* Steuer. A true *Aulacosphinctes* was found at Mallín Redondo, Mendoza, figured as *Aulacosphinctes* sp. indet. by Leanza (1945, pl. 3, figs. 7–8). This form is very close to the lectotype of *Ammonites köllickeri* Oppel as illustrated by Krantz (1928, pl. 3, fig. 1(a) and (b)). *Reineckeia proxima* Steuer closely fits with the characteristic features of *Torquatisphinctes* Spath and is morphologically and chronostratigraphically distant from *Aulacosphinctes*. Thus, and according to the stratigraphic range commonly admitted for this genus throughout the Indo-Malgach realm, the inclusion of the present species in *Torquatisphinctes* seems secure.

T. proximus covers a broad range of variation with two extreme morphotypes: (1) the morph β, compressed specimens such as the lectotype (Figs. 9I and J), and the specimen illustrated here in Fig. 13C from Cerro Lotena, Neuquén (Museo Olsacher, Zapala: PIV 5718) and (2) the morph α, larger adult-sized and inflated specimens such as the present specimen (Fig. 13A), the one illustrated in Fig. 13B from Cerro Lotena, Neuquén (Museo Olsacher, Zapala: PIV 1516), and *P. colubrinus* Reinecke (in Steuer, 1987, pl. 15, fig. 11; here refigured in Fig. 9K and L). Keidel (1925), Suero (1951), Leanza (1980) and Leanza and Hugo (1977), and new data suggest that these two morphotypes occur in different successive stratigraphic levels at Cerro Lotena and Arroyo Cieneguitas and that they could be transients of a single species, the oldest being morph α.

Torquatisphinctes gr. *mendozanus* (Burckhardt) differs at the level of the outer whorls and BC from *T. proximus*, the former being larger in adult size.

The specimen figured by Burckhardt (1900, pl. 24, fig. 1) as *Perisphinctes contiguus* Catullo strongly resembles the more inflated morphs of *T. proximus* (Steuer); '*P. colubrinus* Reinecke' (in Burckhardt, 1900, pl. 24, figs. 5–6), with identical inner whorls and a strong variocostation on the BC at a smaller adult size, could be the associated microconch.

The specimens illustrated as *Virgatosphinctes prorsocostatus* n. sp. and *Perisphinctes (Dichotomosphinctes?)* sp. by Indans (1954) closely match the morphology of *T. proximus* morph α.

The specimens of this species illustrated by Leanza (1980) come from a 21 m thick series of shales with nodules and concretions. There are no clear indications of the relative position of these specimens in this thick series, but the two morphotypes differentiated previously seem to be represented in Leanza's figures.

Of the Mexican faunas, *Torquatisphinctes* gr. *lauri–potosinus* (Aguileira)–*inversum* (Spath), as illustrated by Verma and Westermann (1973), closely resemble *T. proximus* (Steuer), and their ages appear to be equivalent (cf. Villaseñor, 2000 for an updated biostratigraphic analysis). The fauna from Sierra de Symón, Toboso, described by Burckhardt (1919–1921) includes many morphospecies, more or less resembling *T. proximus* (Steuer), but they conform to a group of forms likely of Darwini zone age (Callomon, 1993; Villaseñor, 2000), that is, somewhat older than the typical *T. proximus* (Steuer) of the Andes.

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Appendix A

Dimensions of the studied and refigured specimens. All measurements in mm, other references in the text

	[M/m]	Ph/BC	D	U	U/D	W	W/D	H_1	H_1/D	W/H_1	H_2	H_2/D	P	V	LBC (°)
Euvirgalithacoceras malarguense (Spath, 1931) [M&m]															
LPB 178	[M]	BC	165.00	76.98	0.46	–	–	48.90	0.30	–	42.73	0.26	20	97	365(^{e})
		Ph	123.00	54.77	0.44	–	–	38.30	0.31	–	–	–	23	93	
		Ph	92.00	38.98	0.42	18.80	0.20	29.60	0.32	0.64	–	–	36	–	
		Ph	67.15	29.55	0.44	–	–	–	–	–	–	–	37	–	
		Ph	10.56	4.00	0.38	–	–	–	–	–	–	–	14	–	
LPB 191	[M]	BC	73.55	28.00	0.38	17.00	0.23	23.57	0.32	0.72	–	–	32	–	–
		Ph	34.00	–	–	–	–	–	–	–	–	–	23	–	
LPB 185	[M]	BC?	49.00	16.80	0.34	14.00	0.29	–	–	–	–	–	24	–	–
		Ph	26.00	–	–	–	–	–	–	–	–	–	21	–	
LPB 180	[M]	Ph	44.00	16.50	0.37	–	–	15.50	0.35	–	–	–	23	42	–
		Ph	27.00	9.30	0.34	–	–	–	–	–	–	–	21	–	
LPB 407	[M]	Ph	5.00	–	–	–	–	–	–	–	–	–	15	–	–
LPB 188	[m]	BC	90.00	–	–	–	–	–	–	–	–	–	31	–	–
		Ph	56.00	30.00	0.54	–	–	–	–	–	–	–	24	–	
		Ph	46.00	20.60	0.45	16.00	0.35	15.00	0.33	1.07	–	–	24	–	
		Ph	34.00	14.00	0.41	–	–	–	–	–	–	–	20	–	
		Ph	17.00	–	–	–	–	–	–	–	–	–	17	–	
Choicensisphinctes choicensis (Burckhardt, 1903) [m]															
LPB 197	[m]	BC	146.00	65.00	0.45	45.10	0.31	45.99	0.32	0.98	–	–	12	–	360 (^{e})
		Ph	86.26	32.13	0.37	28.30	0.33	27.80	0.32	1.02	–	–	26	–	
		Ph	52.00	17.10	0.33	19.00	0.37	19.60	0.38	0.97	–	–	21	–	
		Ph	8.00	–	–	–	–	–	–	–	–	–	14	–	
		Ph	4.00	–	–	–	–	–	–	–	–	–	10	–	
Paraulacosphinctes striolatus (Steuer, 1897) [M&?m]															
LPB 184	[M]	Ph	81.41	32.07	0.39	28.00	0.34	27.00	0.33	1.04	23.00	0.28	–	–	–
		Ph	63.00	22.30	0.35	24.40	0.39	22.00	0.35	1.11	16.05	0.25	35	63	
		Ph	32.33	9.78	0.30	11.50	0.36	10.37	0.32	1.11	–	–	30	–	
		Ph	15.00	4.70	0.31	6.00	0.40	–	–	–	–	–	23	–	
		Ph	5.50	3.01	0.55	–	–	–	–	–	–	–	17	–	
		Ph	3.64	–	–	–	–	–	–	–	–	–	8	–	
LPB 182		Ph	40.00	13.00	0.33	11.90	0.30	14.50	0.36	0.82	–	–	–	–	
		Ph	30.00	7.60	0.25	11.00	0.37	–	–	–	–	–	–	–	
		Ph	11.80	3.00	0.25	5.00	0.42	4.90	0.42	1.02	–	–	35	–	
Lectotype (MGAU 499–45)	[M?]	Ph	49.00	16.00	0.33	17.60	0.36	18.00	0.37	–	15.00	0.31	37	–	–
R. striolatissima (MGAU 499–44)	[M?]	Ph	52.00	16.00	0.31	18.20	0.35	20.00	0.38	–	–	–	–	–	–
R. transitoria (MGAU 499–49)	[M?]	BC	56.00	23.00	0.41	17.00	0.30	19.00	0.34	0.89	–	–	25	48	–
R. mangaensis (MGAU 499–41)	[m?]	BC	65.00	35.00	0.54	19.00	0.29	17.00	0.26	1.12	–	–	25	36	
Torquatisphinctes proximus (Steuer, 1897) morph α															
LPB 187		Ph	69.53	28.97	0.42	22.05	0.32	22.13	0.32	1.00	–	–	24	50	
		Ph	54.50	23.06	0.42	18.20	0.33	20.25	0.37	0.90	19.00	0.35	20	42	
		Ph	26.50	13.00	0.49	9.80	0.37	8.20	0.31	1.20	–	–	16	–	
		Ph	19.80	9.49	0.48	7.19	0.36	5.98	0.30	1.20	4.70	0.24	14	–	
		Ph	15.09	7.11	0.47	6.00	0.40	4.95	0.33	1.21	–	–	13	–	
		Ph	10.24	4.61	0.45	4.70	0.46	3.00	0.29	1.57	–	–	–	–	
		Ph	7.34	3.21	0.44	3.61	0.49	–	–	–	–	–	11	–	
		Ph	4.00	1.27	0.32	2.50	0.63	1.70	0.43	1.47	1.39	0.35	8	–	
PIV1516 (Cerro Lotena)		BC(Dls)	63.80	31.60	0.50	20.80	0.33	20.40	0.32	1.02	–	–	19	40	

(*continued on next page*)

(*continued*)

	[M/m]	Ph/BC	*D*	*U*	*U/D*	*W*	*W/D*	H_1	H_1/D	W/H_1	H_2	H_2/D	*P*	*V*	LBC (°)
	Ph	41.70	22.30	0.53	16.00	0.38	13.80	0.33	1.16	–	–	17	36		
		Ph	24.30	11.80	0.49	–	–	–	–	–	–	–	14	–	
		Ph	13.50	5.50	0.41	–	–	–	–	–	–	–	11	–	
		Ph	8.00	–	–	–	–	–	–	–	–	–	10	–	
Per. colubrinus (MGAU 499–51)	[M]	BC	90.00	51.00	0.57	21.00	0.23	20.00	0.22	1.05	–	–	25	48	
		Ph	69.00	37.00	0.54	20.00	0.29	19.00	0.28	1.05	–	–	23	–	
		Ph	51.00	27.50	0.54	–	–	14.00	0.27	–	–	–	22	–	
		Ph	29.00	14.00	0.48	–	–	–	–	–	–	–	17	–	
		Ph	15.00	–	–	–	–	–	–	–	–	–	15	–	
		Ph	7.00	–	–	–	–	–	–	–	–	–	12	–	
Torquatisphinctes proximus (Steuer, 1897) morph β															
PIV5718 (Cerro Lotena)		BC(Dls)	40.80	20.70	0.51	11.50	0.28	12.00	0.29	0.96	–	–	15	32	
		Ph	31.00	15.40	0.50	10.00	0.32	9.00	0.29	1.11	–	–	16	29	
		Ph	13.50	5.50	0.41	–	–	–	–	–	–	–	11	–	
		Ph	7.20	–	–	–	–	–	–	–	–	–	10	–	
Lectotype (MGAU 499–30)		BC	57.00	25.00	0.44	15.00	0.26	18.00	0.32	0.83	–	–	19	33	
		Ph	40.00	–	–	–	–	–	–	–	–	–	18	–	
		Ph	30.00	–	–	–	–	–	–	–	–	–	14	–	

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