Upper Jurassic (Tithonian) ammonites from the lithographic limestones of the Zapala region, Neuquén Basin, Argentina

Arnold Zeiss & Héctor A. Leanza

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Abstract. This paper contains the taxonomic and biostratigraphic analysis of a new Tithonian ammonite fauna from the Neuquén Basin, Argentina. Most of the ammonites have been collected by the authors bed by bed in the lithographic limestone quarries of the Los Catutos region in the vicinity of Zapala city. Some additional material from Cerro Caicayén and Cerro Lotena has been contributed by the Olsacher Museum of Zapala.

The new subfamily Windhauseniceratinae has been established within the Ataxioceratidae Buckman, 1921; it consists of the two new tribes Windhauseniceratini (with the new species *Windhauseniceras stipanicici* sp. nov.) and Catutosphinctini (with two new genera and nine new species): *Mapuchesphinctes* gen. nov., with *M. garatei* sp. nov., (type species), *Parazapalia* gen. nov. with *P. hillebrandti* sp. nov. (type species) and *P. perezi* sp. nov., *Catutosphinctes callomoni* sp. nov., *C. westermanni* sp. nov., *Zapalia zapalensis* sp. nov., *Z. triplex* sp. nov., *Z. poultoni* sp. nov., and *Z. thomsoni* sp. nov. Within the Aspidoceratidae the new species *Aspidoceras quinchaoi* sp. nov. has been established.

The age of the described fauna is regarded as Late Middle Tithonian to Early Upper Tithonian. The fauna is encompassed in the upper part of the Proximus Zone (level x+a) and in the Internispinosum Zone (levels x, y, z, w), which in turn is divided in the Catutosphinctes rafaeli and the Zapalia fascipartita subzones. In the latter the horizons of *Aspidoceras quinchaoi* and *Djurjuriceras catutosense* have been recognized.

The most important result of this study is the refinement of the biostratigraphy of the Andean Middle and Upper Tithonian in the Neuquén Basin. The significance of the Internispinosum Zone for global correlation at the base of the Upper Tithonian is also discussed.

▪ ***Keywords:*** *Cephalopoda, Ammonoidea, Taxonomy, Biostratigraphy, Jurassic, Tithonian, Neuquén Basin, Argentina*

Zusammenfassung: In dieser Studie wird eine bisher fast unbekannte Ammonitenfauna des Grenzbereiches Mittel-/Ober-Tithonium der Provinz Neuquén, Argentinien, vorgestellt. Die Mehrzahl der untersuchten Ammoniten wurde von den Autoren in den Plattenkalk-Steinbrüchen des Gebietes ‚Los Catutos' in der Nähe der Stadt Zapala horizontiert gesammelt; zusätzlich werden auch einige Funde von den Lokalitäten ‚Cerro Caicayen' und ‚Cerro Lotena' behandelt.

Im taxonomischen Teil der Arbeit wird die Unterfamilie Windhauseniceratinae neu aufgestellt; sie gehört zur Familie Ataxioceratidae Buckman, 1921 und wird in die beiden Tribus Windhauseniceratini n. trib. und Catutosphinctini n. trib. gegliedert. Dem letztgenannten Tribus werden zwei neue Gattungen zugeordnet: *Mapuchesphinctes* n. gen. (Typusart: *M. garatei* sp. nov.) und *Parazapalia* n. gen. (Typusart: *P. hillebrandti* sp. nov.).

Insgesamt werden elf neue Arten beschrieben: *Aspidoceras quinchaoi* sp. nov., *Catutosphinctes callomoni* sp. nov., *C. westermanni* sp. nov., *Mapuchesphinctes garatei* sp. nov., *Parazapalia hillebrandti* sp. nov., *P. perezi* sp. nov., *Windhauseniceras stipanicici* sp. nov., *Zapalia poultoni* sp. nov., *Z. thomsoni* sp. nov., *Z. triplex* sp. nov. und *Z. zapalensis* sp. nov.

Das Alter der untersuchten Ammonitenfaunen reicht vom obersten Mittel- bis ins untere Ober-Tithonium, d.h. vom oberen Abschnitt der *Proximus*-Zone (level x+a) bis in die Internispinosum Zone (levels x, y, z und w). Die Internispinosum Zone wird in zwei Subzonen, *Catutosphinctes rafaeli* und *Zapalia fascipartita*, unterteilt. In letzterer werden die Faunenhorizontes *Aspidoceras quinchaoi* und *Djurjuriceras catutosense* ausgeschieden.

Damit ergibt sich eine wesentliche Verfeinerung der bisherigen biostratigraphischen Gliederung des andinen Mittel- und Obertithonium, jedenfalls im Bereich des Neuquén-Beckens. Auf die Bedeutung der Internispinosum-Zone für globale Korrelationen an der Basis des Ober-Tithonium wird abschließend hingewiesen.

▪ ***Schlüsselwörter:*** *Cephalopoda, Ammonoidea, Taxonomie, Biostratigraphie, Jura, Tithonium, Neuquén-Becken, Argentinien*

Resumen: En este trabajo se ofrece el estudio de una interesante fauna de ammonites del Tithoniano de la Cuenca Neuquina, Argentina. La mayoría de los ammonites han sido coleccionados personalmente por los autores capa por capa en los afloramientos de canteras de calizas litográficas de la comarca de Los Catutos, en las vecindades de la ciudad de Zapala, pero también se ilustra material adicional de los cerros Caicayén y Lotena.

Se erige la nueva subfamilia Windhauseniceratinae dentro de los Ataxioceratidae Buckman, 1921, y se la divide en las nuevas tribus Windhauseniceratini y Catutosphinctini. Se describen dos nuevos géneros y once nuevas especies, a saber: *Mapuchesphinctes* gen. nov. (especie tipo: *M. garatei* sp. nov.), *Parazapalia* gen. nov. (especie tipo: *P. hillebrandti* sp. nov.), *Windhauseniceras stipanicici* sp. nov., *Catutosphinctes callomoni* sp. nov., *C. westermanni* sp. nov., *Mapuchesphinctes garatei* sp. nov., *Zapalia zapalensis* sp. nov., *Z. triplex* sp. nov., *Z. poultoni* sp. nov., *Z. thomsoni* sp. nov. *Parazapalia hillebrandti* sp. nov., *P. perezi* sp. nov. y *Aspidoceras quinchaoi* sp. nov. La fauna estudiada se asigna al Tithoniano medio alto y al Tithoniano superior temprano. La misma está comprendida en la parte superior de la Zona de Proximus (horizonte x+a) y en la totalidad de la Zona de Internispinosum (horizontes x, y, z, w). Esta última se divide en la subzona de *Catutosphinctes rafaeli* y *Zapalia fascipartita*, en la cual se han reconocido a su vez los horizontes de *Aspidoceras quinchaoi* y *Djurjuriceras catutosense*.

Los más importantes resultados de este estudio contribuyen a un refinamiento de la bioestratigrafía en el Tithoniano Medio y Superior andino en la Cuenca Neuquina. Se discute también el significado de la Zona de Internispinosum en la base del Tithoniano Superior para fines de correlaciones globales.

▪ ***Keywords:*** *Cephalopoda, Ammonoidea, Taxonomía, Bioestratigrafía, Jurásico, Tithoniano, Cuenca Neuquina, Argentina*

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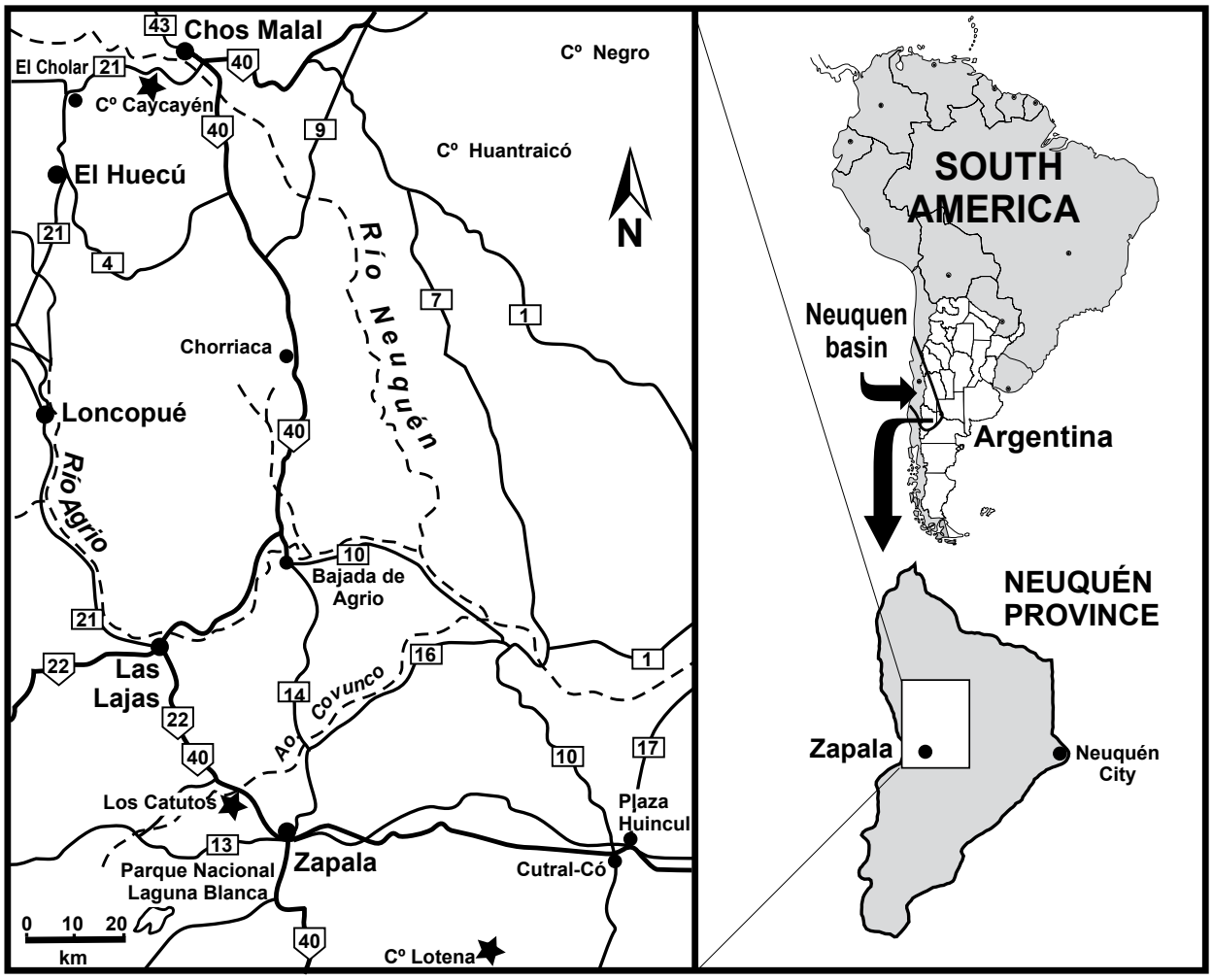
Preface

During the Second Field Meeting of the Circumpacific Jurassic Research Group held in Mendoza (Argentina), December 1983, an excursion took place to the Jurassic outcrops of the eastern foothills of the Andes in the provinces of Mendoza and Neuquén. At this opportunity also a visit was organized to the 'Museo Prof. Dr. Juan A. Olsacher' at Zapala (Neuquén province), which was then directed by Mr. José I.Garate-Zubillaga †. There, numerous fossils were exhibited which displayed in type and preservation an astonishing similarity to the fossils of the famous Solnhofen Lithographic limestones (or "Plattenkalke"). The fossils consisted mainly of ammonites, reptiles, and fishes and represented an hitherto completely unknown occurrence of Upper Jurassic „Plattenkalke", and the first occurrence of this facies type in the new world. Already at that time, the project of a joint German-Argentinian research work was discussed by the authors with Dr. Wolfgang Volkheimer (Buenos Aires). Because of the 'First International Symposium on Jurassic Stratigraphy' held in Erlangen (1984), the 'III International Field Meeting of the Circumpacific Jurassic Research Group' which took place in Japan (1985), and the preparations for these events the project had to be postponed. The 'IV Congreso Argentino de Paleontología y Bioestratigrafía' held in Mendoza (1986) allowed the senior author (A.Z.) a second visit to Argentina, offering him a favourable opportunity to renew contacts. As a first step, a record of the material in the 'Museo Prof. Dr. Juan A. Olsacher' was organized, and some days could be spent in the field to recognize the in situ occurrence of the fossils, mainly ammonites and fishes. At the same time the first bed-by-bed collection could be undertaken, and also the local litho- and biostratigraphic succession could be established. The preliminary results of these investigations were published by Cione et al. (1987). Thanks to a sabbatical semester granted to the senior author (A.Z.) in 1989/90, he could come to Argentina again. Together with the junior author (H.A.L.), fieldwork was continued under difficult circumstances at Los Catutos and surrounding areas (Text-fig. 1). At this opportunity, much additional material had been collected, revealing a new perisphinctid ammonite fauna. In addition, the whole material had been prepared, provisionally described and photographed under adventurous conditions in an old desolate factory with broken windows in Zapala, as the very fragile material did not allow any extensive transport. Leanza & Zeiss (1990, 1992, 1994) published first results of these investigations. Additional material from the famous, partially time-equivalent locality of Cerro Lotena, 70 km SE from Zapala, and Cerro Caycayén, 35 km SW from Chos Malal (Text-fig. 1) in the museum collection were also included in our studies.

Thanks to an Alexander von Humboldt Fellowship the junior author (H.A.L.) had an opportunity to visit Erlangen (August and part of September 1993); at this occasion, the whole manuscript was revised and prepared for publication. In the following years further additions and refinements of the text, inclusion of additional figures and compilation of a global biochronological correlation chart took place. Illness of the senior author prevented again and again the final completion of the manuscript.

Introduction

Initially, we expected the main purpose of our studies to be the comparison of the fauna from the Zapala Lithographic limestones with that of Solnhofen. However, it became soon evident that the knowledge of the taxa composing the two faunas was still too poor for a precise comparison. Therefore, we thought it necessary to concentrate, as a first step, on a precise study and documentation of the complete ammonite fauna from the Zapala region. Some taxonomic units were already been

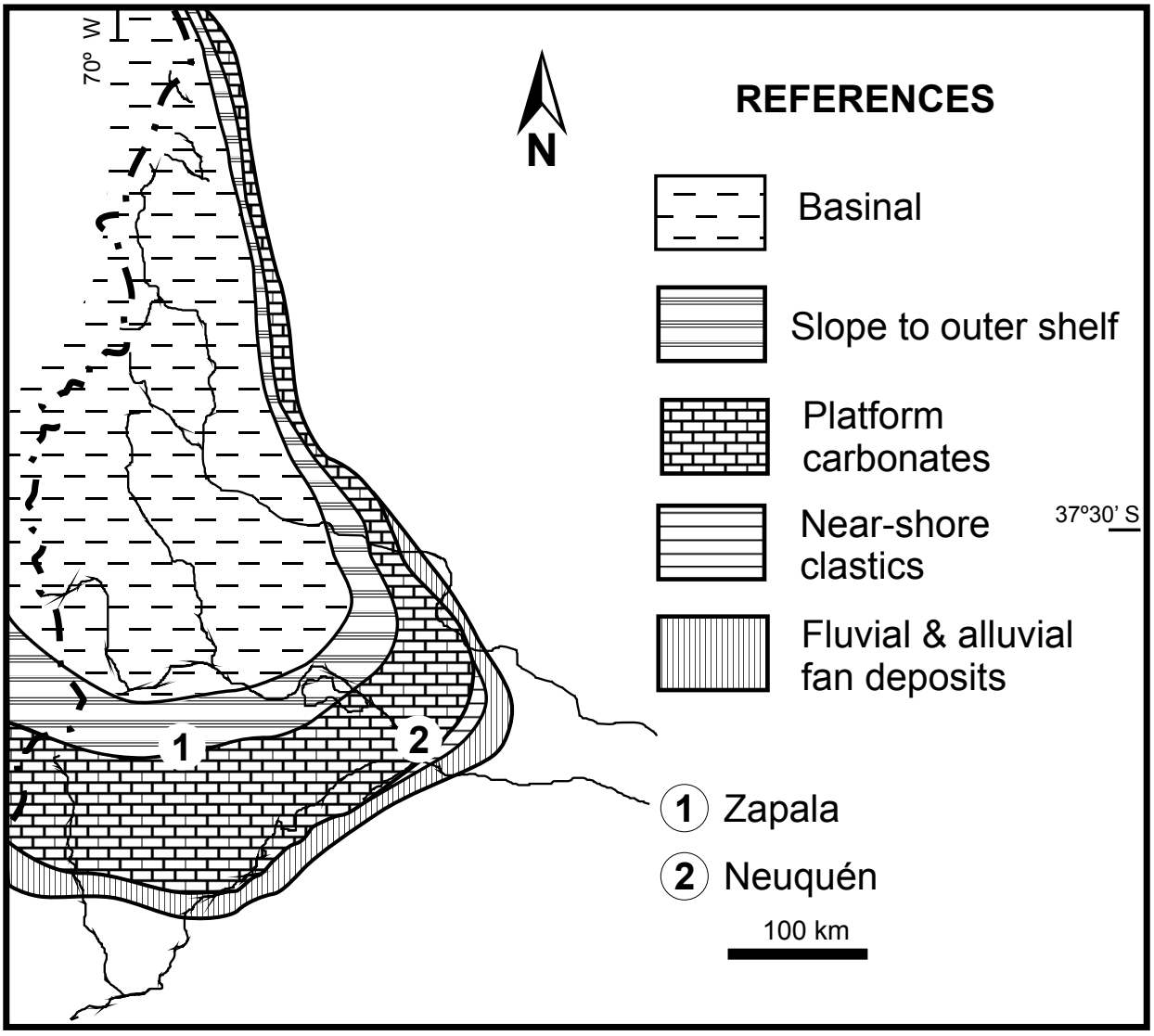


Text-Fig.1. Location map, showing fossil localities (*) at Cerro Caycayén, Los Catutos, and Cerro Lotena.

described or mentioned in earlier papers (Cione et al. 1987, Leanza & Zeiss 1990, 1992, 1994; Zeiss & Leanza 1999, 2008).

Contributions to the geology of the Los Catutos area (Text-fig. 1) were made by Lambert (1956), who recognized and mapped the Tithonian strata at a scale of 1:200.000, mentioning there for the first time the occurrence of "ammonites aplastados". Leanza (1973) described the Piedras Blancas section situated immediately north of route 22, referring it to the Picún Leufú Formation, consisting of 93 m of calcareous sandstones with a large number of bivalves and subordinate ammonites of Upper Tithonian/Lower Berriasian age. Leanza & Hugo (1977: 253) also gave a summary reference to the Los Catutos-Pichi Moncol section. However, it was not until 1987 that a first paper essentially devoted to the lithographic limestones of Los Catutos region was published (Cione et al. 1987), as a result of a joint German-Argentinian Research Project (see above). In that paper, a general report about the lithographic limestones and their fauna was given, illustrating for the first time some significant ammonites, fishes, and ichthyosaurs. Later in that year, Gasparini et al. (1987) published a pterosaur bone from the same locality. Gasparini (1988) described and illustrated the famous marine ichthyosaur *Ophtalmosaurus monocharactus* Appleby from the lithographic limestones of the Los Catutos region.

A complete report on the Upper Jurassic lithographic limestones of Argentina and their faunal content was presented by Leanza & Zeiss (1990), including a new geological map and cross-section, and proposing a new lithostratigraphic unit, 'Los Catutos Member' for the lithographic limestones within the Vaca Muerta Formation. Some sedimentological and palaeoecological aspects of the Argentinean lithographic limestones were discussed and they were compared with the Solnhofen Lithographic Limestone. In the same paper, the new ammonite genus *Zapalia* was established, and for the first time the genus *Djurjuriceras* was described from South America. The new species *Zapalia fascipartita* and *Djurjuriceras catutosense* were established, and the great number of aspidoceratids and aptychi mentioned. In addition, all known other fossil groups were described and figured (especially reptiles, fishes, crustaceans, algae and coccolithophorids). The same authors (Leanza & Zeiss 1992) published a preliminary report on the quantitative and qualitative composition of the ammonite fauna of the lithographic limestones of Los Catutos region, and established the new ammonite genus *Catutosphinctes*. The



Text-Fig.2. Upper Tithonian palaeogeographic map of the Neuquén Basin (slightly modified after LEGARRETA & ULIANA 1991).

Internispinosum Zone was subdivided from base to top into the Catutosphinctes rafaeli and Zapalia fascipartita subzones, the latter with the faunal horizons *Aspidoceras altum* (now *A. quinchaoi*), and *Djurjuriceras catutosense* (see LEANZA & ZEISS 1992: 1845). In the same paper, the subfamily 'Windhauseniceratinae' was informally introduced; it was considered as an Eastern Pacific offshoot of perisphinctids and as a parallel development to the subfamily Paraulacosphinctinae in Europe. The subfamily Windhauseniceratinae is formally established in this monograph. Later, a short review on the Zapala lithographic limestones with some notes on their microfacies and mineralogical composition, a plate with the most important fossils and a table with all known plant and animal fossils has been published by LEANZA & ZEISS (1994).

Geological setting

The Neuquén Basin lies within a region which is known as the southern part of the Central Andes (RAMOS 1988). South of 35°S latitude, the Neuquén Basin expands towards the eastern foreland forming a back-arc shelf domain known as the Neuquén Embayment. It is considered a Mesozoic rifted back-arc basin located on the western convergent margin of the South America Plate (ULIANA et al. 1989; VERGANI et al. 1985; LEANZA et al. 2000; LEGARRETA & ULIANA 1996, 1999; RAMOS 1988, 2009). The infill of the Neuquén Basin exceeds 7000 m of marine and continental sedimentary rocks (epiclastics, carbonates, evaporites and pyroclastics) which range in age from Late Triassic to Paleocene.

The area studied here belongs to the southern part of the Neuquén Basin (Text-fig. 1-2). The Jurassic/Cretaceous marine sedimentary rocks have been accommodated in the Mendoza Group (GROEBER 1946). The marine Tithonian-Berriasian interval is represented by widely exposed, organic-rich dark shales with calcareous nodules (Vaca Muerta Formation; WEAVER 1931), and micritic limestones and calcarenites with a lesser proportion of shales (Picún Leufú Formation; LEANZA 1973) which are well developed along the entire southeastern margin of the basin (carbonate shelf of LEGARRETA & ULIANA 1991) and were deposited in the context of a highstand systems tract (LEANZA & HUGO 1997; ARMELLA et al.

Age	Zones	Subzones	Horizons
Lower Berriasian	*Substeueroceras koeneni*	*„Sp.“ acutum*	
		Sch. longaeva	
Upper Tithonian		*„Mi.“ vetustum*	
		Hi. andinus	
	Corongoceras alternans	*„B.“ inaequicostata*	
		Mi. tapiai	
	Windhauseniceras internispinosum	*Z. fascipartita*	*D. catutosense*
			As. quinchoai
		Ca. rafaeli	
Middle Tithonian	*Aulacosphinctes proximus*	*Psh. steinmanni*	
	Pseudolissoceras zitteli	*P. pseudolithicum*	
Lower Tithonian	*Virgatosphinctes mendozanus*	*Ch. choicensis*	
		„L.“ malarguense	

Tab.1. Ammonite zones, subzones and horizons in the Andean Tithonian. *Ch.* = *Choicensisphinctes*, *P.* = *Pseudolissoceras*, *Psh.* = *Pseudhimalayites*, *Ca.* = *Catutosphinctes*, *Z.* = *Zapalia*, *As.* = *Aspidoceras*, *D.* = *Djurjuriceras*, *Mi.* = *Micracanthoceras*, *B.* = *Berriasella*, *Hi.* = *Himalayites*, *Sch.* = *Schaireria*, *Sp.* = *Spiticeras*, *„L.“* = *„Lithacoceras“*.

2007, 2008). The contact between the Vaca Muerta and the Picún Leufú formations is diachronous (Leanza 1973, 1981a; Leanza & Hugo 1977; Leanza et al. 1977) and progradational (Gulisano et al. 1984; Mitchum & Uliana 1985; Legarreta & Gulisano 1989), becoming younger towards the basin depocentre, where the Picun Leufú Formation is laterally replaced by the dark shales of the former unit.

A paleogeographic map of the Upper Tithonian of the Neuquén Basin slightly modified from Legarreta & Uliana (1991: 436, figs. 7A, B), Riccardi et al. (1992), and Gulisano & Gutiérrez Pleimling (1995) is presented in Text-fig. 2.

The Vaca Muerta Formation

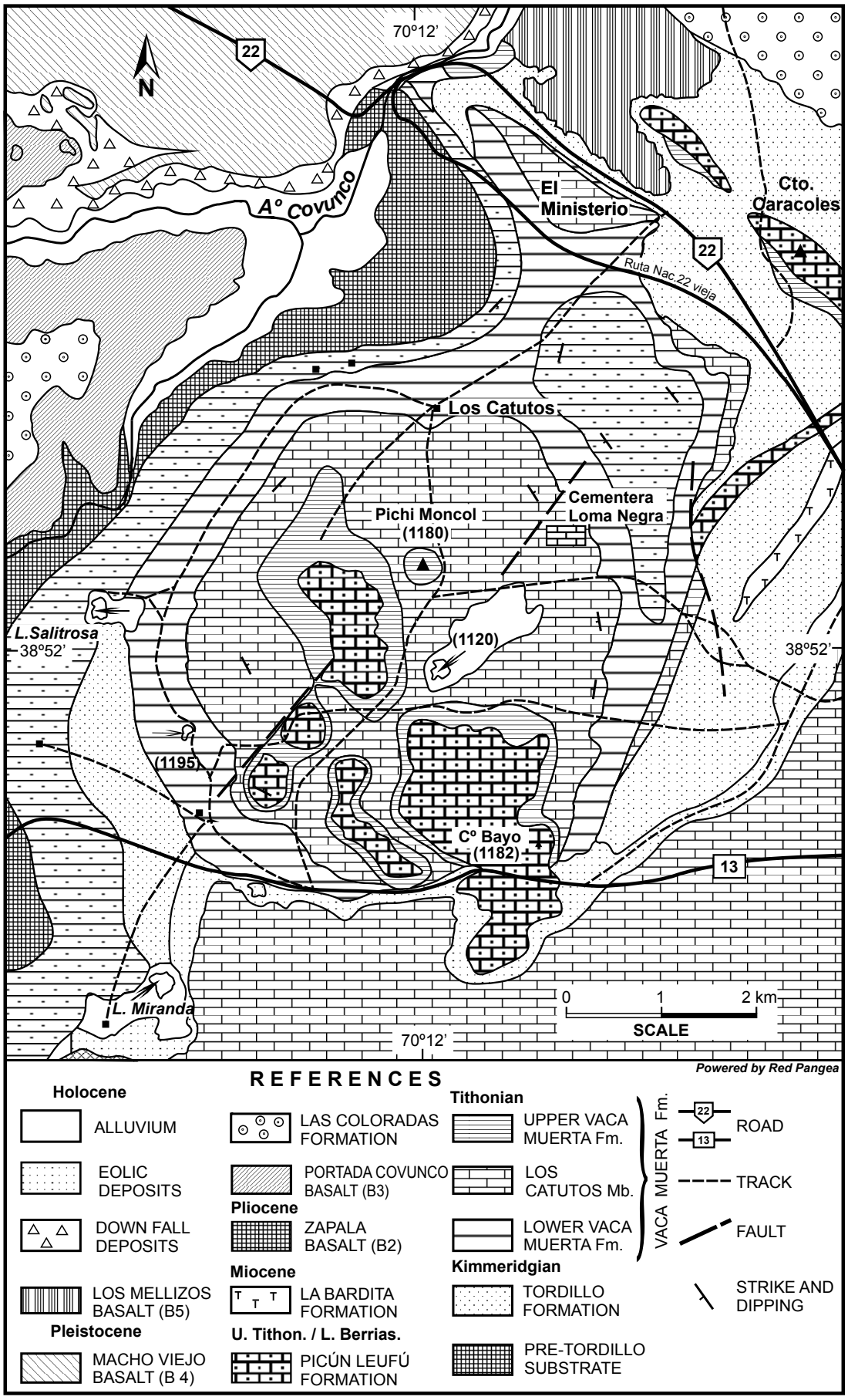
This unit was originally defined by Weaver (1931) to identify the succession of Tithonian strata composed of dark calcareous shales and characterized by the Mendozanus, Zitteli and Internispinosum zones. The type locality is situated at the western slope of the Vaca Muerta Range, in the central part of the Neuquén Province, where it is overlain by the Quintuco Formation. The base of this unit is notably uniform throughout the basin, with a transgressive surface at its base overlying eolian and fluvial sandstones (Quebrada del Sapo Formation; Digregorio 1972) in the southern region of the basin, or fluvial conglomerates and sandstones (Tordillo Formation, Groeber 1946) in the depocenter. It consists of bituminous black shales with common variably sized calcareous nodules and concretions, usually containing well preserved ammonites (Virgatosphictinae beds of Leanza 1980). The sediment and associated faunal content suggests shallow marine waters of moderate to warm temperature in an offshore environment. The upper limit of the Vaca Muerta Formation is determined by the onset of nearshore facies of the Carrín Curá Formation (Leanza et al. 1977) and Picún Leufú Formation (Leanza 1973), and the fluvial Bajada Colorada Formation (Roll in Fossa Mancini et al. 1937). As a result of the diachronous base of these units, the Vaca Muerta Formation includes younger strata towards the center of the basin. In southern Neuquén, the Vaca Muerta Formation embraces the upper Lower Tithonian and the lower Upper Tithonian; in central Neuquén, the whole Tithonian and the Lower Berriasian, and in northern Neuquén the Tithonian, the Berriasian and the Lower Valanginian (Leanza 1981a; Leanza et al. 2001).

The Tithonian ammonite zones, mostly from the Vaca Muerta Formation, used in this monograph, were established or emended by Weaver (1931), Leanza (1945, 1947), Leanza & Hugo (1977), Leanza (1981a, b), Leanza & Zeiss (1990, 1992, 1994), Riccardi (1984, 1988, 2008), Riccardi et al. (2000), and Zeiss & Leanza (2008). On the basis of these papers and previous information (Steuer 1897 [=1921]; Haupt 1907; Krantz 1926, 1928) the ammonite zones distinguished in the Tithonian of the Neuquén Basin are summarized in Table 1.

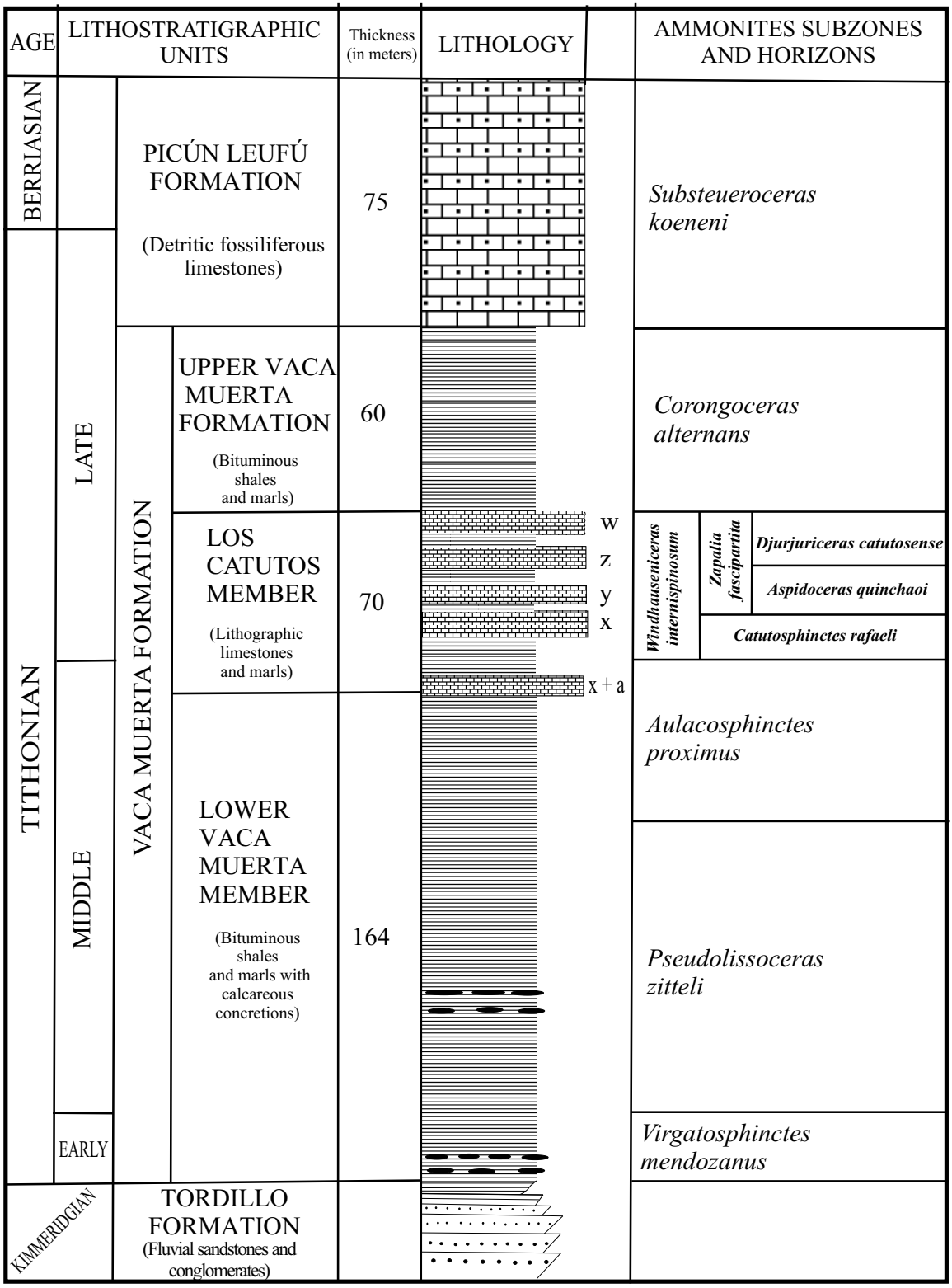
Los Catutos Member

The Tithonian lithographic limestones cropping out in the Zapala region were termed for the first time as Los Catutos Member by Leanza & Zeiss (1990). The type locality was established in the Los Catutos area (S 38°71‘ S – W 70°12‘), situated only 13 km northwest of Zapala city, Neuquén Province, western Central Argentina (Text-fig. 1).

The Los Catutos Member is developed within the Vaca Muerta shales (Text-figs. 3 and 4). Its limestones are thin-bedded (“Plattenkalke”) and mostly white to yellow-brownish in colour. Only in some lenticles the original blue-grey colour can be observed. The limestone beds are 10 to 15 cm in thickness and can be easily split which allows their use as slab stones. As a result of



Text-Fig.3. Regional geology of the Los Catutos area (slightly modified after LEANZA & ZEISS, 1990).



Text-Fig. 4. Generalized stratigraphic column of the Tithonian strata in the Los Catutos area.

a severe compaction, most of the ammonites preserved are flattened, although excellent imprints are commonly preserved.

While collecting the ammonites in the field, Leanza & Zeiss (1990) informally designated, from base to top, the following limestone horizons: x+a, x, y, z, and w (Text-fig. 4), which in turn are separated by shales and marls of light-brown colour. Northwards the lithographic limestones extend up to the Mallín Quemado region. As has been demonstrated by Leanza et al. (2001), the Los Catutos Member displays a sigmoidal clinoform with a progradational pattern in the direction of the depocenter of the basin. In the Los Catutos region, the member starts 164 m above the top of the Tordillo Formation, where-

as in the Mallín Quemado area or at the outcrops crossing the national route 22 in the direction to Las Lajas, it lies only 30 m above the top of the same unit. The Los Catutos Member can also be correlated with the bulk of limestones occurring at the southern end of the Cerro Lotena, where they have been recognized and illustrated in a section nearly a hundred years ago by Windhausen (1914: fig. 1).

Scasso & Concheyro (1999) and Scasso et al. (2002) also contributed with papers devoted to petrological and geochemical studies of the Los Catutos Member, interpreting the limestone-marl rhythmites of this member as result of palaeoclimatic changes caused by the orbital eccentricity of the Earth.

Geology of the Los Catutos region

The geology of this region has been summarized and updated in Text-fig. 3, following the papers by Leanza & Zeiss (1990) and Leanza et al. (2001). Along the Covunco creek the sediments below the Tordillo Formation consist of well-developed parts of the Cuyo Group (Los Molles, Lajas and Tábanos formations) and the Lotena Group (Lotena and La Manga formations). The Tordillo Formation is composed by reddish fluvial coarse conglomerates and sandstones.

The lower member of the Vaca Muerta Formation (164 m) overlies the Tordillo Formation and is composed by offshore bituminous shales and marls with calcareous concretions. They are followed by the lithographic limestones of the Los Catutos Member (70 m), which cover extensive parts of the region. They belong to a gently inclined structure being particularly well exposed at the El Ministerio quarry. The upper member of the Vaca Muerta Formation (60 m) crops out below the fossiliferous calcareous sandstones of the Picún Leufú Formation (75 m) at Cerrito Caracoles, east of national route 22 (Text-fig. 3).

Material and methods

Preservation of the material

The preservation of the ammonites of Los Catutos region strongly depends on the sedimentation and diagenesis of the rather thin-bedded limestones ("Plattenkalke"). As a result of severe compaction, most of the ammonites are more or less flattened, but excellent imprints are commonly preserved. This kind of preservation, which precludes reconstruction of whorl sections and/or observation of suture lines, is rather similar to that of the famous Tithonian "Solnhofener Plattenkalke" (= Solnhofen Formation; Zeiss 1977) and similar sediments in Southern Germany. Although the fossils from the Los Catutos area have been known for many years, their fragile and compressed nature apparently precluded their study until our first excursion in the area (see Cione et al. 1987).

The material in general is large in size and very fragile so that it cannot be transported for long distances. Therefore, all studies had to be executed in Zapala, where the local Museum Prof. Dr. Juan A. Olsacher provided a room in an old 'depositorio' for our studies. These were carried out under very difficult circumstances in this depositorio - an abandoned factory hall with broken windows, without electricity, and where the ammonites had to be cleaned daily because of the permanent wind, which distributed fine sand and dust in the hall during the night. The photographic work could be undertaken only, if enough sunlight was available during the middle of the day. As mentioned above, the ammonites are partly rather large to giant in size, and figuring them in natural size would exceed the size of the plates. Consequently, figures had to be reduced to different sizes, and are referred to the same linear scale (i.e., the bar in all figures of the plates represents 1 cm). The ammonites from Cerro Lotena and Cerro Caicayén display normal preservation.

	Macroconchs	Microconchs
Giant	>300	
Large	200-300	>150
Medium	100-200	150-50
Small	100-50	50-10
Very small	<50	<10

Adopted scale of shell sizes (in mm)

Abbreviations

D: Diameter; WH: Whorl height; WW: Whorl width; UW: Umbilical width; IW: Internal whorls; OW: Outer whorls; IR: Internal ribs; ER: External ribs; IT: Internal tubercles; ET: External tubercles; M: macroconch; m: microconch.

L: Length (for aptychi; after Trauth 1927); B: Width (for aptychi; after Trauth 1927).

Repositories

(A) Museo Prof. Dr. Juan A. Olsacher (MOZ), Paleontological collections (P): Ejercito Argentino y Monti, 8340 Zapala, Neuquén Province, Argentina.

(B) Servicio Geológico Minero Argentino (SGN), Av. Julio A. Roca 651, 1322 Buenos Aires, Argentina.

Taxonomy

Order Ammonoidea Zittel, 1884
Suborder Ammonitina Hyatt, 1889
Superfamily Perisphinctaceae Steinmann, 1890
Family Himalayitidae Spath, 1925
Subfamily Himalayitinae Spath, 1925
Genus *Aulacosphinctes* Uhlig, 1910

Type species. *Ammonites moerickeanus* Oppel, 1863.

Diagnosis. Shell of small to medium size; rather compressed. Ribs strong, distant, bifurcate, some simple. Ventral furrow well developed, deep and persistent, even on the body chamber. Microconchs with lappets at the aperture. No tubercles present at any stage of development (cf. Arkell et al. 1957; Olóriz 1978).

Remarks. Since Uhlig (1910), the species '*proximus*' has been attributed to his genus *Aulacosphinctes*. Recently, Parent (2001; 2003a) ascribed the species to *Torquatisphinctes* Spath. However, *Torquatisphinctes* is a characteristic genus from India where it is limited to the Upper Kimmeridgian (Krishna & Pathak 1993; Pandey 1993), while in Pakistan (Fatmi & Zeiss 1999), in eastern Africa and Madagascar (e.g., Zeiss 1983) it occurs also in the Middle Kimmeridgian. The genus displays large species with a distinct type of ornamentation not observable in the much younger forms from the Proximus Zone of Argentina. Recently, the species *Aulacosphinctes proximus* has been described from the uppermost Lower Tithonian [= upper Middle Tithonian] of Tibet by Yin & Enay (2004).

Distribution. Tithonian. Europe (Spain); Africa (Algeria, Somaliland, Madagascar); Asia (Kachchh, Attock, Himalaya); ?North America (California); South America (Perú, Chile, Argentina).

Aulacosphinctes proximus (Steuer, 1897)

Pl. 1, Figs. 1- 4, 6

1897 *Reineckeia proxima* nov. sp. – Steuer: 34, pl. 8, figs. 7-11.
1907 *Perisphinctes proximus* (Steuer) – Haupt: 192.
1910 *Aulacosphinctes proximus* (Steuer) – Uhlig: 347.
1911 *Aulacosphinctes proximus* (Steuer) – Steuer: 61, pl. 8, figs. 7-11.
1928 *Aulacosphinctes proximus* Steuer – Krantz: 41.
1931 ?*Aulacosphinctes proximus* (Steuer) – Weaver: 411, pl. 44, figs. 298-299.
1959 *Aulacosphinctes proximus* (Steuer) – Corvalan: 13, pl.5, figs. 20-22.
1980 *Aulacosphinctes proximus* (Steuer) – Leanza: 44, pl. 6, figs. a-b, 4a-b, 5a-b, text-fig. 10b.
2001 *Torquatisphinctes proximus* (Steuer, 1897) – Parent: 30, figs. 2, 8D-H; Table 1.l.
2003a *Torquatisphinctes proximus* (Steuer) – Parent: 159, figs. 9I-J, 12-13, ?fig. 9K-*L*.
2004 *Aulacosphinctes* cf. *proximus* (Steuer) – Yin & Enay: 670, 675, 682, fig. 3 (4).

Material. 15 specimens. Macroconchs (P 3741 MOZ, P 5214 MOZ, P 5216 MOZ, P 3745 MOZ, P 5222 MOZ). Microconchs (P 5209 MOZ, P 3744 MOZ, P 5219 MOZ, P 5210 MOZ, P 5220 MOZ, P 3742 MOZ, P 3746 MOZ, P 5217 MOZ, P 5221 MOZ).

Specimen	D	WH	UW	IR	ER
P 3741 MOZ [M]	80	23(0.29)	39(0.49)	31	51
P 5214 MOZ [M]	78	23(0.29)	35(0.49)	33	-
P 52l6 MOZ [M]	75	23(0.31)	41(0.55)	30	50
P 5222 MOZ [M]	76	25(0.33)	35(0.46)	37	~60
P 5209 MOZ [m]	57	16(0.28)	29(0.51)	22	33
P 3744 MOZ [m]	55	17(0.31)	25(0.45)	18	32
P 5219 MOZ [m]	59	19(0.32)	26(0.44)	24	39
P 5210 MOZ [m]	52	~14(0.17)	23(0.44)	20	35
P 5220 MOZ [m]	53	18(0.33)	25(0.45)	~21	-

Measurements (in mm; better preserved specimens only).

Description. Our material allowed to distinguish macro- and microconch dimorphs occurring together in the level x+a. Six specimens are referable to macroconchs, and nine to microconchs.

Macroconchs (Pl. 1, Figs. 4, 6) are small in size (D=75-80 mm), and evolute (UW=0.46-0.55); ribbing is usually bifurcate, but simple ribs may occur. Constrictions are also present. The point of bifurcation on internal whorls is situated at three-quarters of the whorl height, but on the body chamber it is observable at the middle of the whorl height. On the last whorl there are 30 to 37 primary ribs, and 50 to 60 secondaries. The ribs follow mostly a radial direction. Only on the body chamber, close to the aperture, the ribs exhibit a slightly adoral projection together with a gentle thickening.

Microconchs (Pl. 1, Figs. 1-3) are only slightly smaller in size (UW=0.44-0.51). In a general way, microconchs are more finely sculptured, and although ribs exhibit the same bifurcate pattern as the macroconchs, they are relatively less numerous. Six constrictions per whorl can also be observed. In the specimen P 5210 MOZ a small ear is present. The diagnostic ventral furrow can be recognised on a fragment figured on Pl. 1, Fig. 2.

Remarks. *Aulacosphinctes proximus* (Steuer) has been described in detail and revised by Leanza (1980). The similar *Aulacosphinctes mangaensis* (Steuer 1897: 33, pl. 13, figs. 7-8; refigured by Parent 2003a: fig. 9G-H) from the Cieneguitas creek in southern Mendoza, described by Leanza (1945: 21, pl. 3, figs. 1-2) also from the Sierra Azul region (Mendoza), differs from *A. proximus* (Steuer) in having a more evolute shell, which is ornamented by sharper and more numerous ribs with many single ones. *A. occultefurcatus* (Waagen 1875: 195, pl. 1, figs. 4a, b) from Kachchh, India, and *A. wanneri* Krantz (1928: 42, pl. 2, fig. 6a ,b) from Arroyo de la Manga, Mendoza, are closely related species. With regard to the forms from Madagascar, the material described here resembles *A. proximus* (Steuer) var. *angusta* Collignon (1960: pl. 172, fig. 731). *A. proximus* as figured by Weaver (1931: 411, pl. 44, figs. 298-299) does not display the interruption of the ribs on the venter, and therefore its attribution to

Aulacosphinctes is doubtful. *A. proximus* (Steuer) was also quoted from the Río Leñas valley, Chile, by Corvalan (1959). Leaving aside a possible case of homeomorphy, *A. proximus* also resembles *A. quadri* Olóriz (1978: 638, pl. 53, figs. 15a, b) from the 'Burckhardticeras' Zone of southern Spain. Concerning the assumption of Parent (2003a) that this species consists of two morphs or transients being phyletically connected seems at least possible between the Cieneguitas specimens, while those of Cerro Lotena are questionable as there is no indication of their stratigraphic levels and their morphology is too different.

Distribution. *A. proximus* (Steuer) is the index species of the ammonite zone, which occurs between the Zitteli and the Internispinosum Zone. Its age is regarded as upper part of the Middle Tithonian. The taxon is widespread in the outcrops of the Vaca Muerta Formation within the Neuquén and Mendoza basins, as well as in Central Chile (Leanza 1981b).

In the Zapala region, *Aulacosphinctes proximus* occurs in level x+a (El Ministerio quarry, Los Catutos Member, Vaca Muerta Formation), in association with *A.* aff. *proximus* and *Corongoceras* cf. *praecursor*.

Aulacosphinctes aff. *proximus* (Steuer, 1897)

Pl. 1, Fig. 5

Material. Two fragmentary specimens (P 5212 M0Z, P 3740 MOZ).

Specimen	D	WH	UW	R	ER
P 5212 MOZ	~75	~25(0,33)	~36(0,48)	~28	~38/4

Measurements (in mm).

Description. The specimens are only fragments, showing the inner whorls and the last half of the last whorl. Preservation of specimen P 5212 MOZ allows observation of the ventral region, where a sharp furrow is present, presumably up to the body chamber (Pl. 1, Fig. 5). The specimen is densely ribbed, and the point of bifurcation of ribs occurs slightly below the middle of the flank height. The angle of bifurcation is rather small. The suture line could not be detected.

Remarks. The described specimen fits well into the genus *Aulacosphinctes* Uhlig. Although it resembles *A. proximus* (Steuer), it clearly differs in being much more densely ribbed, and the angle of bifurcation is considerably smaller. *A.* aff. *proximus* resembles to a lesser degree also *A. berriaselliformis* Olóriz (1978: 641, pl. 53, figs. 16a, b) from the Betic Ranges of Southern Spain, but the specimen from Argentina appears to be more evolute and more densely ribbed.

Distribution. *A.* aff. *proximus* (Steuer) occurs in association with *A. proximus* (Steuer) and *Corongoceras* cf. *praecursor* Zeiss, in level x+a of the El Ministerio quarry (Los Catutos Member, Vaca Muerta Formation).

Genus *Corongoceras* Spath, 1925

Type species. *Hoplites koellickeri* Haupt, 1907 [= *C. lotenoense*, see Spath, 1925: 144], non Oppel, 1863.

Diagnosis. On the inner whorls ribs bifurcate, forming high lateral swellings and small ventral tubercles bordering a smooth, concave, ventral furrow. Outer whorls display strong, distant bifurcate ribs with a lateral and ventral row of tubercles; some secondaries are looped or zig-zag-like. Ventral and lateral tubercles may be very spiny in some species (Arkell et al. 1957; Leanza 1980).

Remarks. Although Tavera (1985) and Benzaggagh & Atrops (1997) considered *Corongoceras* as a subgenus of *Micracanthoceras* Spath, this opinion is not maintained here, as *Corongoceras* displays sufficient characteristic features allowing an easy distinction from the latter genus.

Distribution. Since Spath (1925) established the genus *Corongoceras*, it has been found on several continents (Helmstaedt 1969; Biró-Bagoczky 1978; Leanza 1980; Nikolov 1982; Tavera, 1985; Zeiss 2001), and has become an excellent marker fossil for the lower part of the Upper Tithonian of Europe (Spain, Austria), South and Central America (Argentina, Chile, Peru, Cuba, Mexico), Antarctica (Antarctic Peninsula), Africa (Algeria, Madagascar), and Asia (Nepal, India, Tibet, Japan).

Corongoceras cf. *praecursor* Zeiss, 2001

Pl. 1, Figs. 7-9, 11-13

cf. 2001 *Corongoceras praecursor* sp. nov. – Zeiss: 63, pl. 13, figs. 2-3.

Material. Six specimens (P 5213 MOZ, P 5260 MOZ, P 5218 M0Z, P 5226 MOZ, P 5211 MOZ, P 3739 MOZ).

Specimen	D	WH	UW	IR	ER
P 5213 MOZ	25	9(0.36)	11(0.44)	~12	~20
P 5218 MOZ	40	11(0.28)	17(0.43)	16	24
P 5211 MOZ	33	11(0.33)	14(0.42)	13	24
P 3739 MOZ	50	16(0.32)	22(0.44)	16	22

Measurements (in mm).

Description. Shells of very small size (D=25-50 mm). Not very evolute (UW=0.42-0.44). Ribbing not dense. Inner whorls with simple and bifurcate ribs with a small node at the point of branching, in coincidence with the line of coiling. Outer whorl developing lateral and ventral bead-like nodes, even on simple or bifurcate ribs. The angle of bifurcation is relatively wide. Four to five constrictions are also developed on the last whorl. The aperture is simple, forming a strongly attenuated sigma bounded by a prominent rib (Pl. 1, Figs. 9, 11).

The studied material is rather compressed, but it can be compared with *Corongoceras praecursor* Zeiss (2001), an early species of the genus from Austria, quite closely related to *C. lotenoense* Spath (1925), which has been found in the Vaca Muerta Formation.

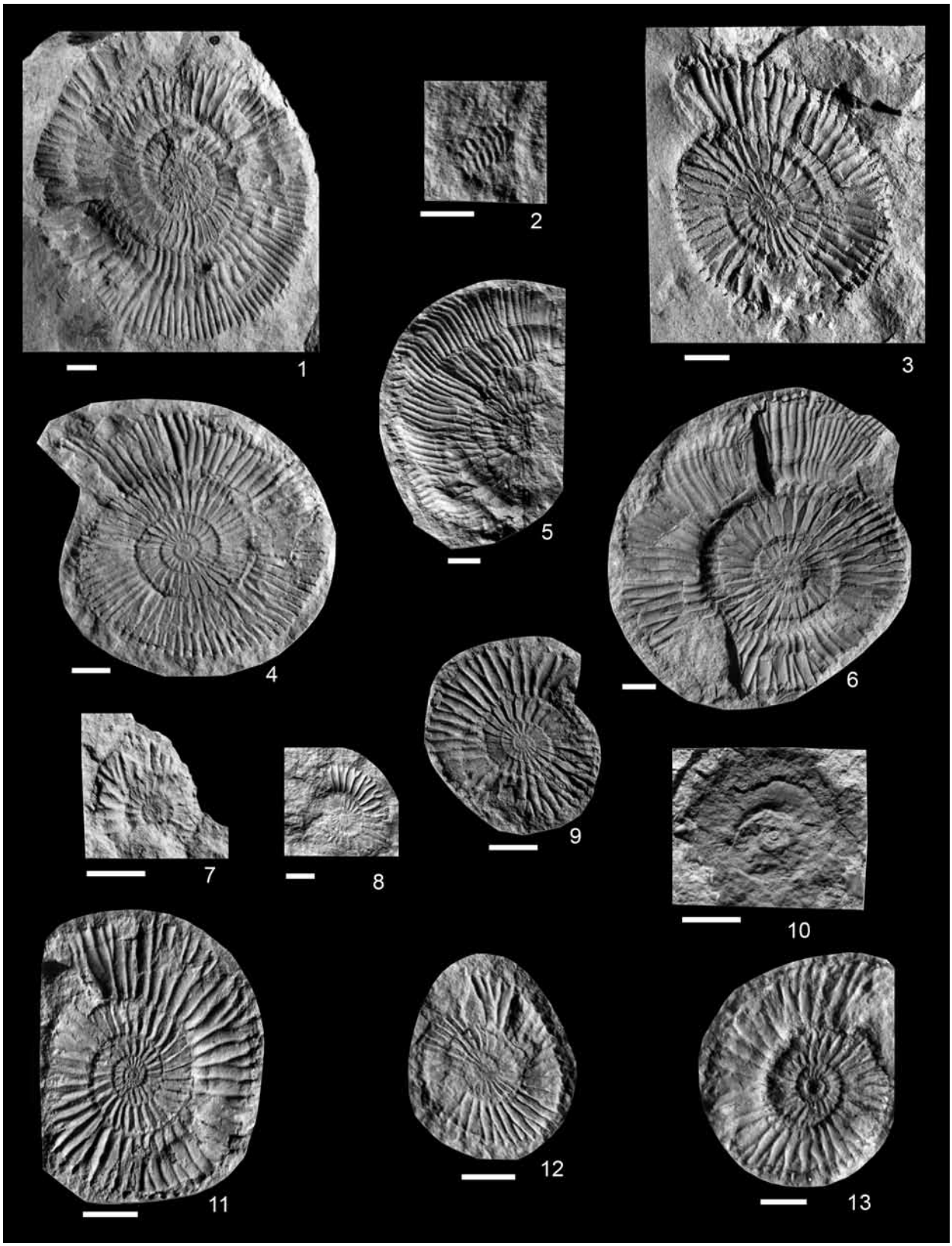


Plate 1. *Aulacosphinctes*, *Corongoceras*, and Oppeliidae

Figs. 1-4, 6. *Aulacosphinctes proximus* (Steuer) from Level x+a, Los Catutos Member, El Ministerio quarry. 1. Hypotype P 5209 MOZ [mi]. 2. Hypotype P 5217 MOZ [mi], ventral view. 3. Hypotype P 3744 MOZ [mi]. 4. Hypotype P 3741 MOZ [Ma]. 6. Hypotype P 5222 MOZ [Ma]. Fig. 5. *Aulacosphinctes* aff. *proximus* (Steuer). P 5212 MOZ. Level x+a, Los Catutos Member, El Ministerio quarry. Figs. 7-9, 11-13. *Corongoceras* cf. *praecursor* Zeiss from Level x+a, Los Catutos Member, El Ministerio quarry. 7. Hypotype P 5213 MOZ. 8. Hypotype P 5260 MOZ. 9. Hypotype P 5218 MOZ. 11. Hypotype P 5226 MOZ. 12. Hypotype P 5211 MOZ. 13. Hypotype P 3739 MOZ. Fig.10. Oppeliidae indet. P 3782 MOZ. Level y, Los Catutos Member, El Ministerio quarry. In all figures the bar corresponds to 10 mm.

Remarks. *Corongoceras* cf. *praecursor* is a guide fossil of the Internispinosum Zone at Cerro Lotena (see Leanza 1980). "*Reineckeia koellickeri*" as described and figured by Steuer (1897: 31, pl. 8, figs. 5, 6) was collected by Bodenbender (1892) in the Loncoche creek area, Mendoza, Argentina; it belongs undoubtedly to the genus *Corongoceras*, but differs from *Corongoceras lotenoense* in having a more disordered ribbing style, as well as a larger umbilicus. *Corongoceras lotenoense* var. *fortior* Collignon (1960: pl. 167, fig. 687) from Madagascar apparently does not belong to the species *lotenoense*, as it displays greater involution, and less divergent secondary ribs. Although Tavera (1985) and Benzaggagh & Atrops (1997) considered *Corongoceras* as a subgenus of *Micracanthoceras* Spath, this opinion is not maintained here, as *Corongoceras* displays characteristic features allowing an easy distinction from the latter genus.

Distribution. In the Los Catutos region, *C.* cf. *praecursor* Zeiss has been collected together with *A. proximus* (Steuer) and *A.* aff. *proximus* (Steuer) from level x+a (El Ministerio quarry, Los Catutos Member, Vaca Muerta Formation). The related, but younger *C. lotenoense* Spath is very common in other parts of the Andean region (Chile, Argentina).

Family Ataxioceratidae Buckman, 1921
Subfamily Windhauseniceratinae nov.

The new subfamily was informally mentioned for the first time in Leanza & Zeiss (1992). This new subfamily developed in the Proximus and Internispinosum zones, when new ataxioceratids immigrated into the Andean basins of Argentina and Chile. Arkell et al. (1957) included the genus *Windhauseniceras* Leanza (1945) in the subfamily Himalayitinae Spath (1925); but based on our research *Windhauseniceras* is related to a number of perisphinctid genera, which have a common origin in forms described by Leanza (1980: pl. 8, fig. 5) as '*Subdichotomoceras*' sp. It can be demonstrated that the subfamily consists of two main branches, the first one including *Windhauseniceras internispinosum* (Krantz, 1926),'*Subdichotomoceras*' windhauseni (Weaver, 1931), a possible microconch of *Windhauseniceras*, and *Hemispiticeras steinmanni* (Steuer, 1897), the latter most probably a giant *Windhauseniceras*. The second branch consists of forms which have been described on the one hand by Leanza (1980) as '*Parapallasiceras*' and '*Aulacosphinctoides*', and on the other hand by the present authors as *Mapuchesphinctes*, *Catutosphinctes*, *Zapalia*, and *Parazapalia*. The first branch is characterized by more or less coronate inner whorls and a rather simple ornamentation on outer whorls. The second branch displays commonly only small nodes at the branching points of bifurcate ribs on the inner whorls; the outer whorls exhibit a great variety of ornamental sculpture. *Djurjuriceras catutosense* may well belong to this second branch, too.

As the holotype of *Subdichotomoceras* (type species: *Subdichotomoceras lamplughi* Spath, 1925) comes from the Upper Kimmeridgian (Autissiodorensis Zone) of southern England, the South American species from the uppermost Middle Tithonian to the lowermost Upper Tithonian can be considered to belong to another homeomorph group. The taxonomical problems connected to this statement are beyond the scope of this paper, and therefore are not discussed here in more detail.

The genus *Djurjuriceras* was originally included in the family Perisphinctidae by Roman (1936), and subsequently in the subfamily Virgatosphinctinae by Arkell et al. (1957). Later Tavera (1985) placed it in the family Himalayitidae. In our opinion, the subfamily Windhauseniceratinae is a descendent of the subfamily Virgatosphinctinae and is therefore included in the family Ataxioceratidae (see Callomon in Donovan et al. 1981: 150), but not in the Himalayitidae. This view is supported by the style of ornamentation, which characterizes mainly the sculpture of the outer whorls of related genera such as *Catutosphinctes*, *Zapalia*, and *Parazapalia*. At the same time when this eastern Pacific offshoot of ataxioceratids accommodated in the Windhauseniceratinae was evolving, a parallel development can be recognized in the Tethyan region of Europe: the subfamily Paraulacosphinctinae Tavera (1985).

The subfamilies Windhauseniceratinae and Paraulacosphinctinae together with the subfamily Pseudosubplanitinae represent the last ataxioceratids in the geological record of the Tethyan and Indopacific regions. The subfamily Windhauseniceratinae can be divided into two tribes corresponding to the two already mentioned branches:

1. Tribus Windhauseniceratini nov. (type genus: *Windhauseniceras* Leanza, 1945), and 2. Tribus Catutosphinctini nov. (type genus: *Catutosphinctes* Leanza & Zeiss, 1992). In the following paragraphs a compilation of the members of the subfamily Windhauseniceratinae is provided (see also Table 2).

1. Tribus Windhauseniceratini nov. – *Windhauseniceras internispinosum* (Krantz, 1926) [including ‚*Subdichotomoceras*' *windhauseni* (Weaver, 1931)], *W. humphreyi* Leanza, 1949, *W. stipanicici* sp. nov., *Hemispiticeras steinmanni* (Steuer, 1897), and *H.* aff. *steinmanni* (Steuer, 1897 in Leanza 1980).

2. Tribus Catutosphinctini nov. – *Catutosphinctes rafaeli* Leanza & Zeiss, 1992, *C. americanensis* (Leanza, 1980), *C. westermanni* sp. nov., *C. callomoni* sp. nov., *Djurjuriceras catutosense* Leanza & Zeiss, 1990, *Zapalia fascipartita* Leanza & Zeiss, 1990, *Z. zapalensis* sp. nov., *Z. triplex* sp. nov., *Z. poultoni* sp. nov., *Z. thomsoni* sp. nov., *Parazapalia hillebrandti* sp. nov., *P. perezi* sp. nov., and *Mapuchesphinctes garatei* sp. nov. The following specimens described and figured by Leanza (1980) apparently belong also to this tribe: "*Parapallasiceras* aff. *P. pseudocolubrinoides* Olóriz, 1978, *Parapallasiceras* aff. *recticosta* Olóriz, 1978, *Parapallasiceras* sp. indet., *Aulacosphinctoides* aff. *hundesianus* (Uhlig, 1910)", and "*Subdichotomoceras* sp. juv. indet.", which obviously represents the most ancestral form of this tribe; '*Subdichotomoceras*' *araucanense* Leanza constitutes an independent side branch. These South American representatives of European and Indian genera

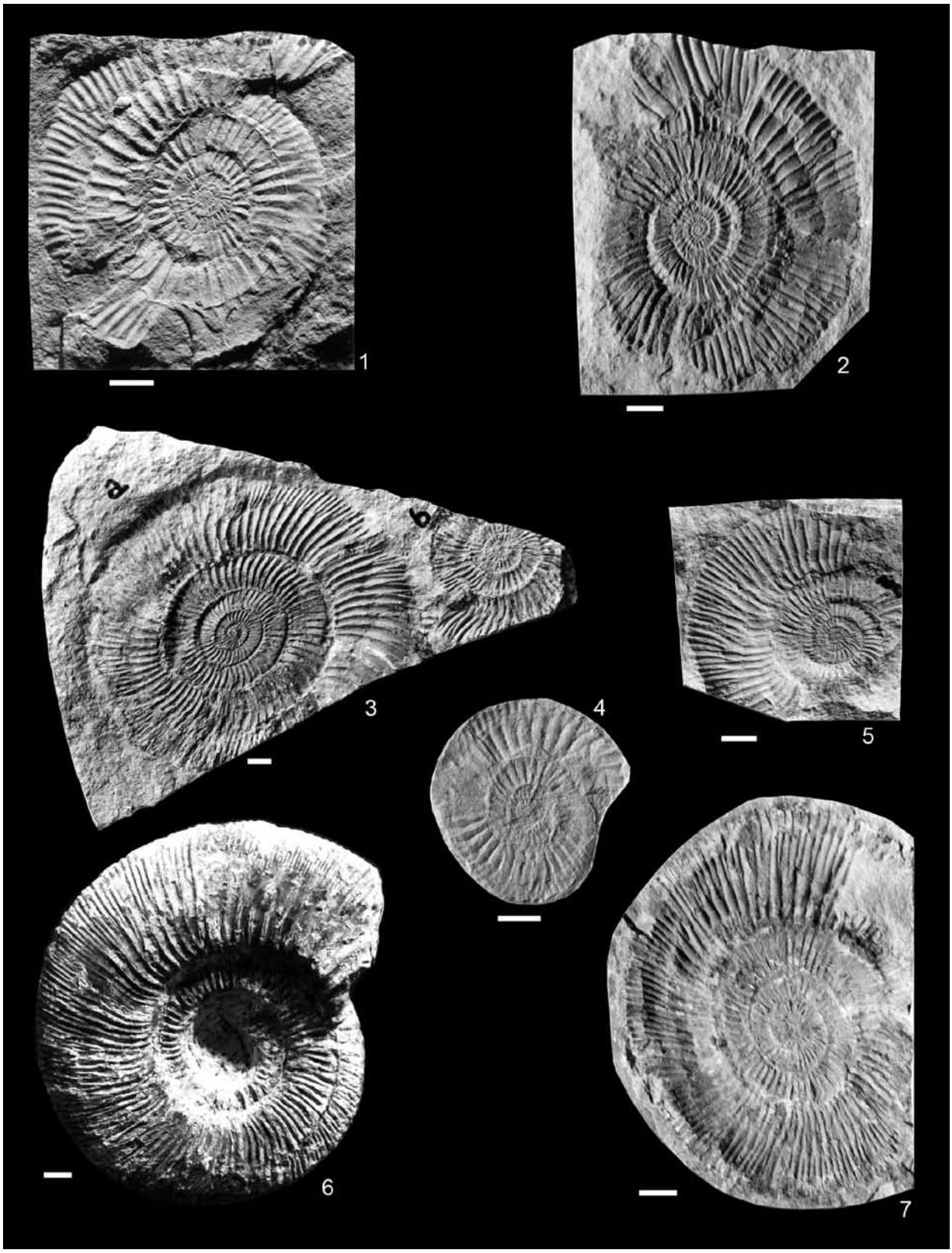


Plate 2. *Windhauseniceras*

Figs. 1-2, 4-5. *Windhauseniceras internispinosum* (Krantz) from the Los Catutos Member. 1. Hypotype 5152 MOZ. Level w, Pichi Moncol quarry. 2. Hypotype 3821 MOZ. Level w, El Ministerio quarry. 4. Hypotype 3826 MOZ. Level w, El Ministerio quarry. 5. Hypotype 3761 MOZ. Level y, El Ministerio quarry.

Figs. 3, 6-7. *Windhauseniceras stipanicici* sp. nov. 3. Paratypes P 5225 MOZ [Ma] and P 5225b MOZ [mi ?]. Level w, Los Catutos Member. El Pozo quarry. 6. Holotype P 1159 MOZ [Ma]. Vaca Muerta Formation. Cerro Lotena. 7. Paratype P 5228 MOZ [Ma]. Level w, Los Catutos Member. El Pozo quarry. In all figures the bar corresponds to 10 mm.

are probably homeomorph developments. Their exact taxonomic position requires further study. Table 2 contains a key to differentiate genera and species of the subfamily Windhauseniceratinae nov..

Tribus Windhauseniceratini nov.
Genus *Windhauseniceras* A. F. Leanza, 1945

Type species. *Perisphinctes internispinosus* Krantz, 1926.

Diagnosis. Inner whorls with strong, distant, bi- and trifurcate ribs and a row of lateral tubercles at the points of branching. Ribbing not interrupted or tuberculate on venter, which is somewhat flattened. On the outer whorl the cross-section becomes externally rounded and the ribs loose their tubercles and revert to a typical *Perisphinctes*-style of ornamentation (Krantz 1926; Leanza 1945; Arkell et al. 1957).

Distribution. Lowermost Upper Tithonian of South America (Argentina, Chile, Colombia).

Windhauseniceras internispinosum (Krantz, 1926)

Pl. 2, Figs. 1-2, 4-5

1926 *Perisphinctes internispinosum* – Krantz: 453, pl. 14, figs. 1-2; pl. 15, figs. 5-6 (= 1928: 39, pl. 2, figs. 3a-b, 4a-b).
1945 *Windhauseniceras* cf. *internispinosum* (Krantz) – Leanza: 23, pl. 21, fig. 6. [m].
1959 *Windhauseniceras internispinosum* (Krantz) – Corvalán: 16, pl. 4, figs. 16, 17.
1980 *Windhauseniceras internispinosum* (Krantz) – Leanza: 43, pl. 8, figs. 4a-b; pl. 9, figs. 1a-b, text fig. 10d.
1981b *Windhauseniceras internispinosum* (Krantz) – Leanza: pl. 2, figs. 7-8.
2003b *Windhauseniceras internispinosum* (Krantz 1926) – Parent: 354, figs.1-4, tab.1.
2007 *Windhauseniceras internispinosum* (Krantz 1926) – Parent et al.: 20, figs. 9-10.
2008 *Windhauseniceras internispinosum* (Krantz 1926) – Zeiss & Leanza: 9, figs. 4-6 [m].

Material. Eight specimens. El Ministerio quarry, level y (P 3761 MOZ, P 3769 MOZ, P 5208 MOZ), level w (P 3821 MOZ, P 3826 MOZ). Pichi Moncol quarry, level w (P 5152 MOZ). El Pozo quarry, level y (5257 MOZ) and level w (P 5231 MOZ).

Specimen	D	WH	UW	IR	ER
P 5152 MOZ	74	25(0.34)	27(0.37)	22	44
P 3821 MOZ	100	32(0.32)	45(0.45)	26	56
P 5208 MOZ	90	28(0.31)	42(0.46)	30	56
P 3761 MOZ	~100	33(0.33)	46(0.46)	30	55

Measurements (in mm, better preserved specimens only).

Description. Shells of small to medium size (D=74-100 mm), not very evolute (UW=0.37-0.45). Inner whorls ornamented with radial, rather strong ribs. On the penultimate whorl, at about 1/2 of the whorl height, they display a small node, radially enlarged, spiny in specimens that are not flattened. From this node bi- or triplicate secondary ribs split off, which are less prominent than the primary ribs (Pl. 2, Fig. 1). The nodes can be observed immediately below the line of coiling. The ornamentation of the outer whorl is characterized by very regular recticostate or somewhat prorsicostate simple or bifurcate ribs. The branching points occur at the middle of the whorl height but without forming nodes, and the secondary ribs have the same thickness as the primaries. Simple intercalatory ribs extending from the outer marginal periphery to different heights on the flank are also present. As a result, the better preserved specimens exhibit 22 to 26 internal ribs, while 44 to 56 external ribs can be counted. The aperture is simple, describing a somewhat sigmoidal curve. The specimen figured on Pl. 2, Fig. 4 consists only of internal whorls. Superficially it resembles *Corongoceras* Spath, as the distinct external whorls are missing.

Remarks. On the type specimen of *Windhauseniceras* (Krantz 1926: pl. 14, figs. 1-2, Parent 2003b: Fig. 1) the body chamber is only partly preserved. Therefore, no exact comparison can be made with the complete macroconchs of this genus. Such a complete macroconch has been figured by Leanza (1980: pl. 9, fig. 1a-b). A complete microconch has been published by Zeiss & Leanza (2008). *Windhauseniceras* cf. *internispinosum* (Krantz) as illustrated by Leanza (1945: pl. 21, fig. 6) from the Sierra Azul region, southern Mendoza, can be regarded also as a microconch specimen of *Windhauseniceras*.

Distribution. *Windhauseniceras internispinosum* (Krantz) was collected from the Los Catutos Member, Vaca Muerta Formation, at level w (El Ministerio and Pichi Moncol quarries), and levels y and w (El Pozo quarry). It occurs also in Chile (Corvalán 1959) and Colombia (Bürgl 1960).

Windhauseniceras stipanicici sp. nov.

Pl. 2, Figs. 3a-b, 6-7

Holotype. Specimen P 1159 MOZ, a well-preserved phragmocone, figured on Pl. 2, Fig. 6.

Further Material. Four specimens (S.G.*N*. 8949; Windhausen collection) from Cerro Lotena. El Pozo quarry, level w (P 5225a MOZ, P 5225b MOZ, P 5228 MOZ.)

Stratum typicum. Vaca Muerta Formation, Mendoza Group.

Locus typicus. Cerro Lotena, Zapala Department, Neuquén Province, Argentina.

Derivatio nominis. In honour of Dr. Pedro N. Stipanicic† (Buenos Aires), who made important contributions to the Jurassic geology and paleontology of Argentina.

Specimen	D	WH	WW	UW	IR	ER
Holotype	200	70 (0.35)	46 (0.23)	81 (0.40)	47	96
SGN 8949	140	54 (0.38)	43 (0.30)	58 (0.41)	45	84
P 5228 MOZ	160	50 (0.31)	-	74 (0.46)	41	82
P 5225a MOZ	133	35 (0.26)	-	61 (0.45)	40	~80
P 5225b MOZ	65	20 (0.31)	-	30 (0.46)	20	-

Measurements (in mm, better preserved specimens only).

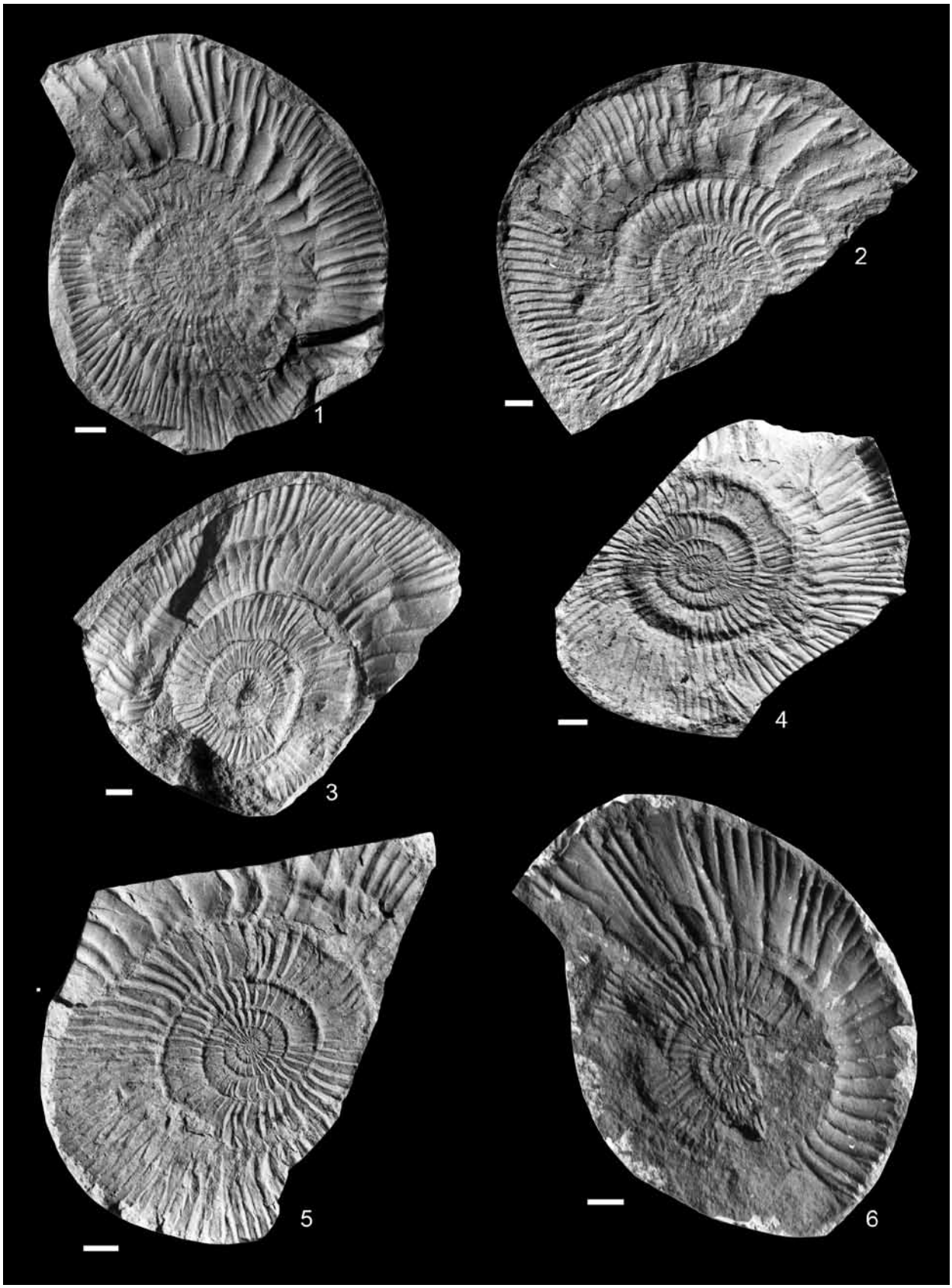


Plate 3. *Catutosphinctes*

Figs. 1-6. *Catutosphinctes rafaeli* Leanza & Zeiss from Level x, Los Catutos Member. El Ministerio quarry. 1. Holotype P 5189 MOZ [Ma], Morphotype A. 2. Paratype P 5190 MOZ [Ma], Morphotype A. 3. Paratype P 3770 MOZ [Ma], Morphotype D. 4. Paratype P 5202 MOZ [Ma], Morphotype A. 5. Paratype P 3768 MOZ. [Ma], Morphotype B. 6. Paratype P 5204 MOZ. [Ma], Morphotype B. In all figures the bar corresponds to 10 mm.

Genera and species	Size	Inner whorl ribbing	Outer whorl ribbing
W. internispinosum	Small to medium	Spaced, with a spine at splitting point	Simple and bifurcate, no spines
W. stipanicici	Medium to large	Dense with a spine at splitting point	Very dense, bi- and trifurcate
W. humphreyi	Medium	Widely spaced	Virgatotomous
H. steinmanni	Large	Widely spaced, with a spine at splitting point	Mostly bifurcate, with a spine at splitting point
C. rafaeli (Ma)	Small to medium	Spaced	4 stages, mostly bi- and trifurcate
C. rafaeli (mi)	Small	Dense	Mostly bifurcate, stage 3 and 4 missing
C. callomoni	Large	Dense	Regulary ribbed, but stage 3 trifurcate
C. westermanni	Medium	Spaced	Very strong, mostly bifurcate, collar ribs
C. americanensis	Large	Dense	Mostly trifurcate, long stage 4
D. catutosense	Medium	Dense	Regulary bifurcate, last quarter of outer whorl with distant collar ribs
M. garatei	Giant	Spaced	Very strong, regulary bifurcate
Z. fascipartita	Large to giant	Widely spaced	Tri- and fascipartite
Z. zapalensis	Medium to large	Dense	Boundles with up to 5 ribs
Z. triplex	Giant to medium	Coarse	Trifurcate and polygyrate ribs
Z. poultoni	Medium	Widely spaced	Bifurcate, strongly projected, very low splitting point
Z. thomsoni	Large	Very dense	Tri- to quadrifurcate, then bifurcate on outer half of last whorl
P. hillebrandti	Medium	Dense	Bi- and trifurcate, lappets spoonlike
P. perezi	Small	Dense	Trifurcate

Tab.2. Key to differentiate genera and species of the Subfamily Windhauseniceratinae nov.: *W.* = *Windhauseniceras*, *H.* = *Hemispiticeras*, *C.* = *Catutosphinctes*, *D.* = *Djurjuriceras*, *M.* = *Mapuchesphinctes*, *Z.* = *Zapalia*, *P.* = *Parazapalia*.

Diagnosis. Medium to large size, evolute. Inner whorls with dense, prominent, single ribs terminating with spines just below the line of coiling. Outer whorl densely ribbed, with bi- and tripartite branching. Intercalatories and constrictions present.

Description. Shell of medium to large size (D=140-200 mm), evolute (UW=0.40-0.41). Whorl section oval-subtrapezoidal. Maximum whorl width at the umbilical borders. Ribs on the inner whorls prominent, simple and very narrowly spaced, terminating with a spine just below the line of coiling. In the holotype these ribs are not well preserved. It is assumed that the spines constitute a branching point, but secondaries are not observable. The holotype is a phragmocone, and the body chamber, which probably would occupy 3/4 of the last whorl, is no longer present. On the outer whorl ribs are densely arranged. They are mostly bifurcate, some trifurcate; the angle of furcation is very narrow. The branching point is situated at the middle of the whorl height. Some intercalatory ribs are also present. Four constrictions have been observed on the last whorl.

The dense ribbing, which is a diagnostic feature of this species, consists of nearly 100 ribs on the ventral region of the outer whorl. The specimen figured on Pl. 2, Fig.3a appears to have a shorter whorl height (WH=0.26), but this is probably due to the fact that the imprint is not fully preserved. The specimen figured on Pl. 2, Fig. 3b, might well constitute a microconch of this species.

Remarks. This new species of *Windhauseniceras* can be easily differentiated from *W. internispinosum* (KRANTZ, 1926: pl. 14, figs. 1-2, pl. 15, figs. 5-6; LEANZA 1980: pl. 8, fig. 4a-b, pl. 9, fig. 1a-b) from Cerro Lotena by its much more densely ribbed shell, in which the angle of the secondary ribs is extremely narrow. *W. humphreyi* LEANZA (1949: 240, pl. 1, figs. 1-2) from the Tithonian of arroyo Los Molles, Neuquén, Argentina, differs from *W. stipanicici* sp. nov. by its virgatotome-branching ribs on the outer whorl, a feature which is not present in our new species.

Distribution. The holotype of *Windhauseniceras stipanicici* sp. nov. was collected by J. I. Garate Zubillaga† from an unknown level of the Vaca Muerta Formation at Cerro Lotena, Neuquén Province. It probably belongs to the interval between beds 16 to 22 of the Cerro Lotena section published by LEANZA (1980: 9). In the region of Los Catutos *W. stipanicici* sp. nov. was collected from level w at El Pozo quarry.

Tribus Catutosphinctini nov.

Genus *Catutosphinctes* LEANZA & ZEISS, 1992

Type species. *Catutosphinctes rafaeli* LEANZA & ZEISS, 1992.

Diagnosis. Dimorphic genus of medium size, evolute. Macroconchs with four stages of ribbing during ontogenetic development: Stage 1 with single and bifurcate ribs on the inner whorls. On outer whorl transition to stage 2 occurs: bifurcate ribs alternate with trifurcate and intercalatory ribs, followed by a constriction, then stage 3 follows with distant primaries and secondaries, either bi- or trifurcate, often irregularly splitting. After another constriction stage 4 starts with distant bifurcate, projected or

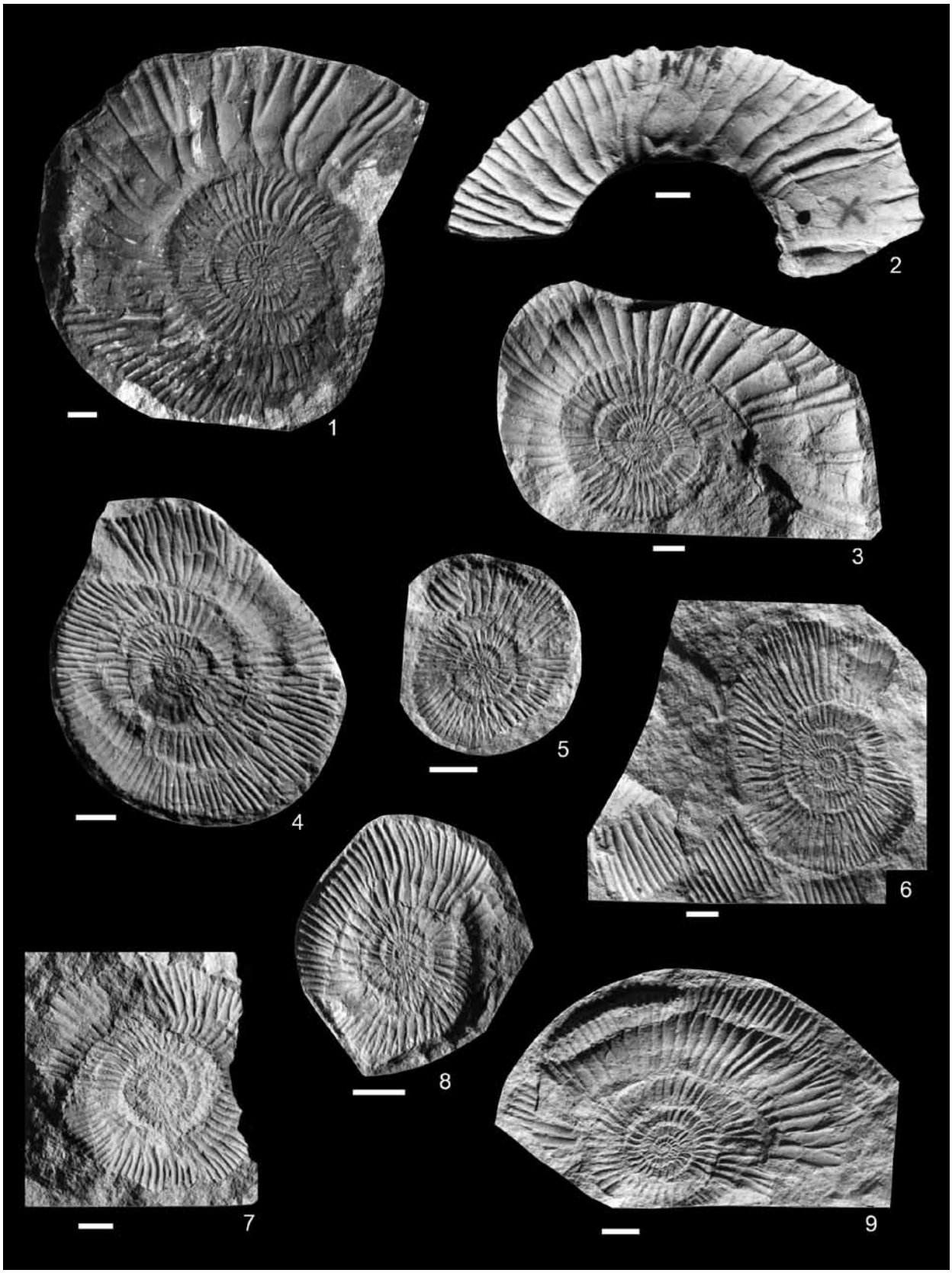


Plate 4. *Catutosphinctes*

Figs. 1-9. *Catutosphinctes rafaeli* Leanza & Zeiss from Level x, Los Catutos Member, El Ministerio quarry. 1. Paratype P 5192 MOZ [Ma], Morphotype A. 2. Paratype P 3773 MOZ [Ma], Morphotype B, Body chamber. 3. Paratype P 5191 MOZ [Ma], Morphotype C. 4. Paratype P 3766 MOZ [mi], Morphotype A. 5. Paratype P 3765 MOZ [mi], Morphotype A. Fig. 6. Paratype P 3747 MOZ [mi], Morphotype A. 7. Paratype P 5199 MOZ [mi], Morphotype B. 8. Paratype P 3759 MOZ [mi], Morphotype B. 9. Paratype P 5206 MOZ [mi], Morphotype B.In all figures the bar corresponds to 10 mm.

irregularly arranged, prominent ribs; intercalatories may be present. Microconchs are smaller, mainly bifurcate, but single or trifurcate ribs may be present; stages three and four are not developed.

Remarks. The Andean genus *Catutosphinctes* shows some resemblance to *Djurjuriceras* Roman, 1936 (type species: *D. djurjurense* Roman, 1936: 17, pl. 2, fig. 5, pl. 3, fig. 4), especially to the morphotype C of the type species. The difference is apparently that in true *Djurjuriceras* the ribbing stages 2 and 3 are not represented. Other, somewhat similar forms have been found in the upper Lower Tithonian of the Franconian Jura (Germany), such as *Usseliceras obscurum* Zeiss (1968: 56, pl. 5, figs. 1-2; pl. 6, fig. 4), but this species is more densely ribbed and has tubercles at the umbilical margin, and *Dorsoplanitoides bavaricus* Zeiss (1968: 15, pl. 15, figs. 1-3; pl. 16, figs. 1-2), which has similar outer whorls, but also displays tubercles at the umbilical margins and shows complicate rib branching on the inner part of the last whorl.

The inner whorls of *Windhauseniceras internispinosum* (Krantz, 1926) are somewhat reminiscent to the inner whorls of the genus *Catutosphinctes*, but the former displays an entirely different style of ornamentation on the last whorl (cf. Krantz 1928: pl. 2, fig. 3a-b; Parent et al. 2007: figs. 9-10). A complete macroconch has been figured by Leanza (1980: pl. 9, fig. 1a-b). Furthermore, species such as *W. stipanicici* sp. nov. or *W. humphreyi* Leanza (1949: 240, pl. 1, figs. 1-2) demonstrate that their outer whorls are very regularly ribbed, and therefore they are different from *Catutosphinctes*.

Four species of the Andean genus *Catutosphinctes* are known: *C. rafaeli* Leanza & Zeiss, 1992 and *C. westermanni* sp. nov. from the Los Catutos region, and *C. callomoni* sp. nov. and C *americanensis* (Leanza, 1980) from the Cerro Lotena area. The latter species was originally described as *Pachysphinctes americanensis* by Leanza (1980: 41, pl. 7, fig.1a-d). Later on, it was transferred to the genus *Catutosphinctes* by Leanza & Zeiss (1992: 1847).

Distribution. Cerro Lotena and Los Catutos, Neuquén, Argentina. Vaca Muerta Formation, lowermost Upper Tithonian.

Catutosphinctes rafaeli Leanza & Zeiss, 1992

Pl. 3, Figs. 1-6, Pl. 4, Figs. 1-9, Pl. 5, Figs. 1-4, 6

1992 *Catutosphinctes rafaeli* sp. nov. – Leanza & Zeiss: 1848, fig. 3 [M].
2007 *Catutosphinctes rafaeli* Leanza & Zeiss – Parent & Cocca: fig. 3A-*G*.

Material. 54 specimens, of which 30 are macroconchs [M], and 24 are microconchs [m]; both are classified into four morphotypes: A, B, C, and *D*.

Macroconchs [M]: Morphotype A (P 5189 MOZ Holotype; P 5190 MOZ, P 5202 MOZ, P 5192 MOZ, P 3755 MOZ, P 5200 MOZ, P 5198 MOZ, P 5258 MOZ); Morphotype B (P 3756 MOZ, P 3768 MOZ, P 3776 MOZ, P 5207 MOZ, P 5204 MOZ, P 3778 MOZ, P 3780 MOZ, P 3775 MOZ, P 3773 MOZ, P 3777 MOZ, P 3781 MOZ, P 3774 MOZ, P 5223 MOZ, P 5176b MOZ); Morphotype C (P 5191 MOZ, P 5196 MOZ); Morphotype D (P 3751 MOZ, P 5201 MOZ, P 5197 MOZ, P 3758 MOZ, P 3770 MOZ, P 5194 MOZ).

Microconchs [m]: Morphotype A (P 3747 MOZ, P 3765 MOZ, P 3766 MOZ); Morphotype B (P 3749 MOZ, P 3759 MOZ, P 3762 MOZ, P 3764 MOZ, P 3767 MOZ, P 3772 M.O.Z, P 5176a MOZ, P 5195 MOZ, P 5199 MOZ, P 5203 MOZ, P 5206 MOZ, P 5224 MOZ); Morphotype C (P 3748 M.O.Z, P 3752 MOZ, P 3771 MOZ, P 3779 MOZ, P 5193 MOZ); Morphotype D (P 3750 MOZ, P 3757 MOZ, P 3763 MOZ, P 5205 MOZ).

Specimen	D	WH	UW	IR	ER
P 5189 MOZ [M] – Holotype	150	45(0.30)	68(0.45)	20	45
P 5192 MOZ [M] - Morph. A	140	46(0.33)	39(0.49)	29	50
P 5202 MOZ [M] - Morph. A	125	40(0.32)	50(0.40)	31	53
P 5190 MOZ [M] - Morph. A	128	37(0.29)	62(0.48)	26	54
P 5204 MOZ [M] - Morph. B	120	42(0.35)	47(0.39)	23	~45
P 5191 MOZ [M] - Morph. C	145	50(0.35)	68(0.47)	29	56
P 3770 MOZ [M] - Morph. D	125	40(0.32)	68(0.40)	36	60
P 3758 MOZ [M] - Morph. D	128	40(0.31)	60(0.47)	24	75
P 3766 MOZ [m] - Morph. A	77	20(0.26)	35(0.45)	31	55
P 3765 MOZ [m] - Morph. A	38	12(0.32)	16(0.42)	22	38
P 3747 MOZ [m] - Morph. A	75	24(0.32)	32(0.43)	33	65
P 5199 MOZ [m] - Morph. B	55	18(0.33)	26(0.47)	28	-
P 3759 MOZ [m] - Morph. B	52	17(0.33)	22(0.42)	28	~52
P 5206 MOZ [m] - Morph. B	85	25(0.29)	43(0.51)	28	53
P 5193 MOZ [m] - Morph. C	75	22(0.29)	35(0.47)	25	41
P 3748 MOZ [m] - Morph. C	65	22(0.34)	27(0.42)	22	44
P 5205 MOZ [m] - Morph. D	95	30(0.32)	40(0.42)	24	52
P 3750 MOZ [m] - Morph. D	~50	~16(0.16)	~23(0.46)	~22	~18
P 3757 MOZ [m] - Morph. D	~95	~28(0.29)	~50(0.53)	-	-

Measurements (in mm, better preserved specimens only).

Description. Macroconchs.- While the inner whorls of the macroconchs show only some differences in the density of the ribbing, the outer whorls display a clear differentiation, which allows to establish four morphotypes.

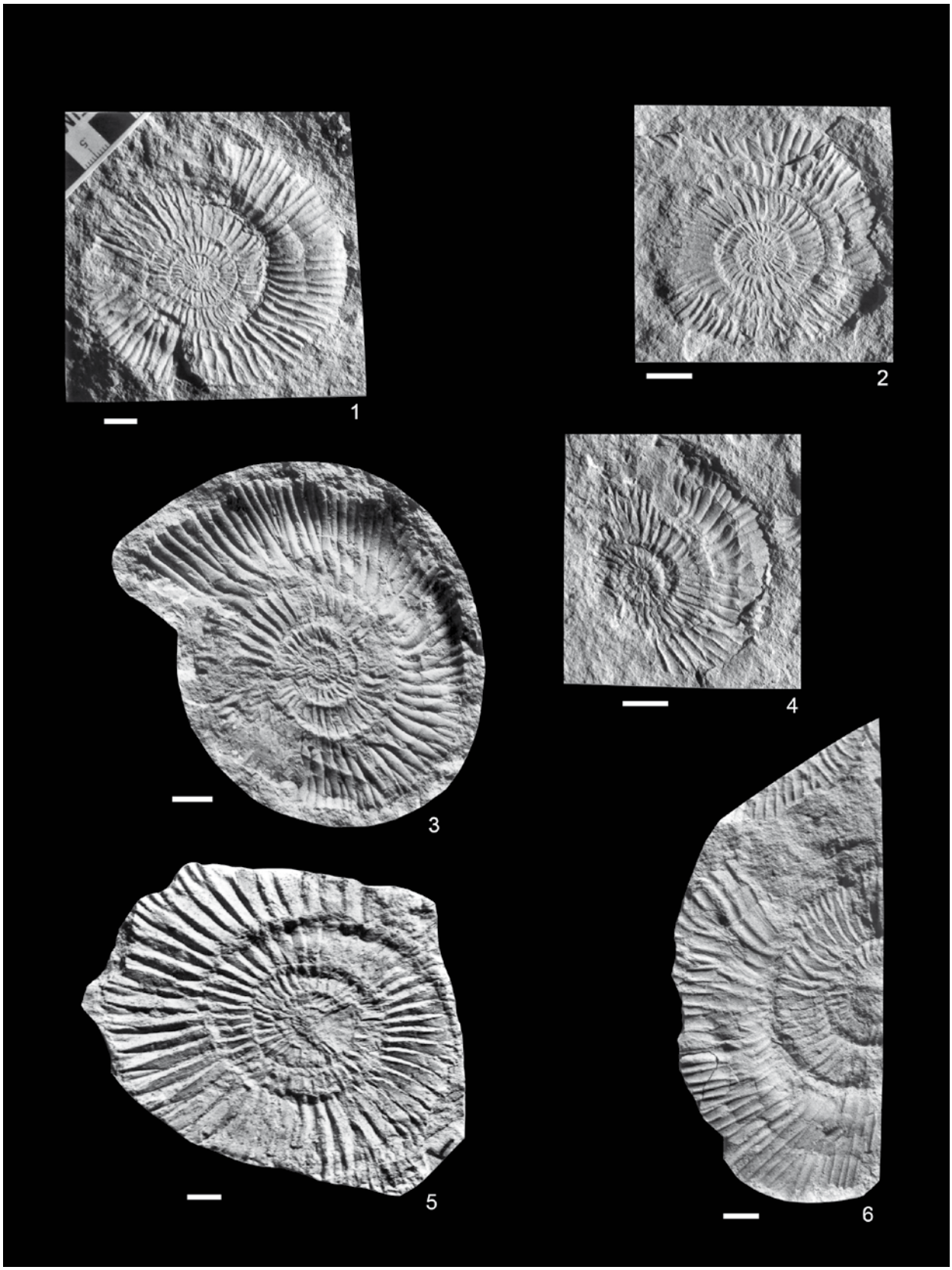


Plate 5. *Catutosphinctes*

Figs. 1-4, 6. *Catutosphinctes rafaeli* Leanza & Zeiss from Level x, Los Catutos Member, El Ministerio quarry. 1. Paratype P 5193 MOZ [mi], Morphotype C. 2. Paratype P 3748 MOZ [mi], Morphotype C. 3. Paratype P 5205 MOZ [mi], Morphotype D. 4. Paratype P 3750 MOZ [mi], Morphotype D. 6. Paratype P 3757 MOZ [mi], Morphotype D.

Fig. 5. *Catutosphinctes westermanni* sp. nov. Paratype P 3812 MOZ, internal whorls. Level y, Los Catutos Member, El Ministerio quarry.In all figures the bar corresponds to 10 mm.

Morphotype A, to which the holotype belongs, shows inner whorls with a sculpture like in *Windhauseniceras*. There are sharp, radial internal ribs, which on the point of branching form a slight swelling (stage 1). On the outer whorls these swellings cannot be observed any more; here the ribs bifurcate at the middle of the whorl height. Apart from the mostly bifurcating ribs, there are also trifurcate and simple ribs (stage 2). In most cases after a constriction stage 3 follows, with internal ribs somewhat thickened and with larger interspaces. The arrangement of bi- and trifurcate ribs becomes irregular and often intercalatory ribs are present. After a further constriction, which is bordered by prominent ribs, stage 4 follows with coarsely bifurcate ribs, which split up at 1/3 of the whorl height. Intercalatory ribs and further constrictions may occur. They are often inclined forward and sinuous. The length of this stage differs. The aperture is simple, it is well preserved on the specimen figured on Pl. 4, Fig. 1. The length of the body chamber should be approximately 3/4 of the last whorl. The suture lines are not recognizable.

In a modification (Morphotype B) from the above described forms the ribbing of stages 3 and 4 displays a more irregular pattern (Pl. 3, Figs. 5-6). The specimen figured on Pl. 4, Fig. 3 shows a further modification (Morphotype C): In stage 3 no trifurcate ribs are developed, and in stage 4 only pairs of prominent collar-like ribs are present with large interspaces between them. These features resemble those of the genus *Djurjuriceras* ROMAN, 1936. However, the style of ribbing before stage 4 in *Catutosphinctes rafaeli* differs considerably from the ribbing style of the inner whorls of that genus.

A further group (Morphotype D) differs by its denser ribbing, especially of the secondaries, the more regular arrangement of ribs in stage 3, and the loss or strong reduction of stage 4 (Pl. 3, Fig. 3).

Microconchs.- Based on the differences in density and style of ribbing, four morphotypes of microconchs have been distinguished, although assigning them to distinct macroconch morphotypes is rather difficult. The first group of microconchs (Morphotype A) contains species with densely ribbed inner whorls. The ribs are fine, sharp, bifurcate, or single. The point of bifurcation of the inner whorls is located at 3/4 of the whorl height, and on the outer whorl at 1/2 or 2/3 of the whorl height. Constrictions are only weakly developed at the end of the last whorl (Pl. 4, Fig. 4), and inclined forward. In the specimen figured on Pl. 4, Fig. 5 one can recognize the beginning of a small lappet. The number of secondary ribs is mostly rather large.

Morphotype B has fewer primary ribs, although the number of secondaries is similar to the first group. In addition, 3-4 constrictions are seen, enclosed by sigmoidal collar-like ribs. At the end of the last whorl the ribs bifurcate with one intercalatory; the ribs are radial or somewhat prorsiradiate, showing a small swelling at the bifurcation point, just below the line of coiling (Pl. 4, Fig. 9). These swellings are hardly recognizable. Morphotype C is characterized by very evolute shells, which are ornamented by a small number of secondary ribs (see measurements); the ribs are bifurcate or single, strong and spaced, rectiradiate or prorsiradiate. The point of branching is high on inner whorls, and on outer whorls is situated at the middle of the whorl height. There are 3-4 sigmoidal constrictions enclosed by prominent ribs. Morphotype D shows similar dimensions as Morphotype *C*. On the last half whorl the sculpture displays many irregularities (see specimen figured on Pl. 5, Fig. 6); these occur especially at constrictions (Pl. 5, Fig. 3). Besides single and bifurcate ribs, also trifurcate ones occur in this group. The point of branching can be somewhat thickened on inner whorls, and is situated at 2/3 to 3/4 of the height on inner whorls, and 1/2 of the whorl height on outer whorls. Very evolute shells may have strong ribs at the end of the body chamber (Pl. 5, Fig. 6). Four sigmoidal constrictions can be observed on the last half whorl.

Remarks. Most remarkable of this highly variable species is the pronounced bifurcation point on the inner whorls of the macroconchs, which resemble somewhat the inner whorls of *Windhauseniceras*, *Corongoceras*, and related genera as figured by LEANZA (1980) from Cerro Lotena, as well as those of *Paraulacosphinctes* and *Oloriziceras* in Europe (cf. TAVERA 1985; ZEISS & BACHMAYER 1989; ZEISS 2001). The pairs of collar ribs of morphotype C are reminiscent of those of *Djurjuriceras* ROMAN, 1936.

Distribution. *Catutosphinctes rafaeli* LEANZA & ZEISS occurs in level x, El Ministerio quarry; lower part of Los Catutos Member, Vaca Muerta Formation, Neuquén Province.

Catutosphinctes callomoni sp. nov.

Pl. 7, Figs. 8-9

Holotype. Specimen P 3443 MOZ, figured on Pl. 7, Figs. 8-9.

Stratum typicum. Vaca Muerta Formation, Mendoza Group.

Locus typicus. Cerro Lotena, Zapala Department, Neuquén Province.

Derivatio nominis. In honour of Prof. Dr. John H. Callomon (London).

Specimen	D	WH	WW	UW	IR	ER
P 3443 MOZ, holotype	158	42(0.27)	47(0.30)	79(0.50)	?	?

Measurements (in mm).

Diagnosis. The most regularly ribbed species of the genus *Catutosphinctes*. It displays a characteristic style of ribbing in all four ontogenetic stagest. Stage 3 is clearly trifurcate. Stage 4 is well developed, mostly bifurcate, and can be divided into three substages.

Description. Shell of medium size (D=158 mm), evolute (UW=0.50). Whorl section sub-quadrate, somewhat wider than high, with rounded convergent flanks, and rounded venter. Umbilical wall steep, almost vertical. Umbilical border rounded. Ribs begin on the umbilical wall, thicken on the umbilical edge, and become sharp

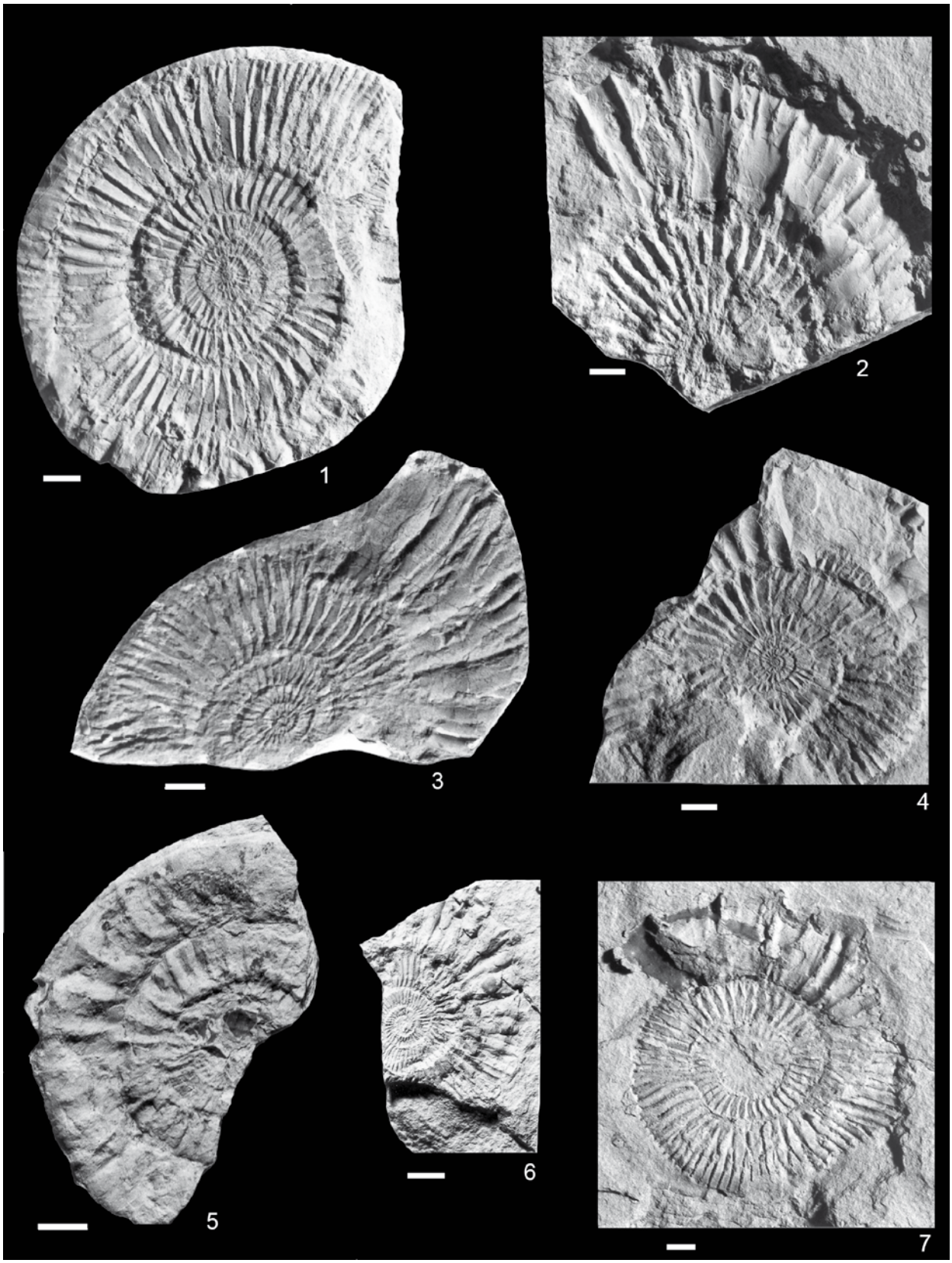


Plate 6. *Catutosphinctes, Djurjuriceras,* and *Simoceratidae*

Figs. 1-4. *Catutosphinctes westermanni* sp. nov. from the Los Catutos Member, Pichi Moncol quarry. 1. Paratype P 3808 MOZ, internal whorls. Level y. 2. Holotype P 3810 MOZ. Level y. 3. Paratype P 3807 MOZ. Level y. 4. Paratype P 5151 MOZ. Level w. Fig. 5. Simoceratidae indet. P 3832 MOZ. Level w, Los Catutos Member, El Ministerio quarry.

Figs. 6-7. *Djurjuriceras catutosense* Leanza & Zeiss from Level w, Los Catutos Member, Pichi Moncol quarry.6. Paratype P 5230 MOZ. 7. Reproduction of the holotype P 3827 MOZ (Leanza & Zeiss 1990: pl. 36, fig. 6). In all figures the bar corresponds to 10 mm.

and prominent on the flanks. Four stages of ribbing are recognized. Stage 1 is represented on the inner whorls by dense, presumably bifurcate, ribs. Stage 2 begins at the first constriction of the last whorl and is characterized by six trifurcate, and one bifurcate branching ribs. Stage 3 begins at D=120 mm, where another constriction occurs, followed by trifurcate rib bundles, between which some intercalatory outer ribs are present. Stage 4 occupies the outer half of the last whorl (i.e. the body-chamber); it is possible to divide it into three substages. Substage 4a begins with a constriction and collar-like rib, which is present at D=125 mm, and is characterized by regular and prominent, bifurcate ribs with wide interspaces; some intercalatories are also present. Substage 4b begins at D=153 mm with a constriction followed by three normally developed, prominent, bifurcate ribs; no intercalatories occur. Substage 4c starts at the last constriction (with collar-like rib) at D=165 mm: only two single, prominent, and distant ribs are observable on the last 40 mm of the whorl. Suture lines could not be detected.

Remarks. The described ammonite constitutes the most regularly ribbed species of the genus *Catutosphinctes*. A clearly trifurcate branching of ribs is present on stage 2, and an early beginning of bifurcate branching on stage 4, which can be divided into three substages. All other known species of *Catutosphinctes* are different, showing more irregularities in the ribbing pattern, and only a short bifurcate stage 4. *Catutosphinctes americanensis* (Leanza, 1980: 41, pl. 7, fig. 1a-e) from the Tithonian of Cerro Lotena is a very close species, but it does not display a clear trifurcate stage 2, and shows a much longer substage 4a, with presence of intercalatories, and lacks substage 4b with well-developed bifurcate ribs. Moreover, in a general way, ribs are also slightly more projected in *C. callomoni* sp. nov. than in *C. americanensis* (Leanza).

Distribution. *Catutosphinctes callomoni* sp. nov. was collected by J. I. Garate-Zubillaga† from an unknown level of the Vaca Muerta Formation at Cerro Lotena, Zapala Department, Neuquén Province. It probably comes from a layer between beds 16 and 22 of the Cerro Lotena section published by Leanza (1980: 9).

Catutosphinctes westermanni sp. nov.
Pl. 5, Fig. 5, Pl. 6, Figs. 1-4

Holotype. Specimen P 3810 MOZ, (level y, Pichi Moncol quarry) figured on Pl. 6, Fig. 2. Although the shell of this specimen is not completely preserved and it is not possible to establish its morphometric parameters, it was chosen as the holotype, as it displays the characteristic features of the species fairly well.

Additional material. Five specimens, all from the Pichi Moncol quarry, level y (P 3807 MOZ, P 3808 MOZ, P 5138 MOZ, P 3812 MOZ) and level w (P 5151 MOZ).

Locus typicus. Pichi Moncol quarry, Los Catutos region, Zapala Department, Neuquén Province.

Stratum typicum. Level y, Los Catutos Member, Vaca Muerta Formation, Mendoza Group.

Derivatio nominis. In honour of Prof. Dr. Gerd E. G. Westermann (Hamilton, Canada).

Specimen	D	WH	UW	IR	ER
P 3807 MOZ	~130	~45(0,34)	~55(0,42)	~18	-

Measurements (in mm, better preserved specimen only).

Diagnosis. A species of *Catutosphinctes* with very coarse ribs.

Description. The shells are not well preserved, but they constitute a distinct recognizable group within the genus; therefore they are described as a distinct species. Shell of medium size (D~130 mm), rather evolute (UW~0,42). Cross-section probably oval. Umbilical margin rounded, umbilical wall slightly inclined. The four ontogenetic stages of ribbing are recognized. Stage 1 is characterized by rather coarse ribs, displaying bifurcate branching at around 2/3 of whorl height. Stage 2 consists also of coarse ribs, but shows some triplicate ribs, too. Stage 3 is characterized by strong primary ribs with large interspaces, by bipartite secondary and one or two intercalatory ribs; the point of bifurcation may be pronounced. Stage 4 can be recognized by distant single ribs. It is separated from stage 3 by a constriction, which is bounded by strong collar ribs.

Remarks. *Catutosphinctes westermanni* sp. nov. differs from *C. rafaeli* Leanza & Zeiss by stronger and less numerous ribs on inner whorls and much stronger ribs on outer whorls. *C. callomoni* sp. nov. is a closely allied species, but differs from *C. westermanni* sp. nov. in having much more regular ribbing along its ontogenetic development, and a weaker ornamentation. *C. westermanni* sp. nov. may be considered ancestral to *Djurjuriceras catutosense* of level w, which does not display stages 2 and 3. Stage 1 is very similar, but shows constrictions combined with irregularities; stage 4 has the same paired collar ribs.

Distribution. Levels y and w, Pichi Moncol quarry, Los Catutos Member, Vaca Muerta Formation; Zapala district, Neuquén Province.

Genus *Djurjuriceras* Roman, 1936, emend. Olóriz, 1978

Type species. *Djurjuriceras* djurjurense Roman, 1936.

Diagnosis. Shell rather evolute. Inner and middle whorls with fine and dense biplicate ribs, which cross the venter without interruption. Outer whorls, probably identical with the body chamber, become strong and distant. Ribs are usually bifurcate and/or simple, but collar-like ribs and deep constrictions may also be present (Roman 1936, Olóriz 1978; Leanza & Zeiss 1990).

Distribution. South America (Argentina), Europe (Spain), Africa (Algeria).

Plate 7. *Mapuchesphinctes* gen. nov. and *Catutosphinctes*

Figs. 1-7. *Mapuchesphinctes garatei* sp. nov. from the Vaca Muerta Formation. 1. Holotype P 0900 MOZ [Ma], lateral view. Cerro Lotena. 2. Holotype P 0900 MOZ [Ma], ventral view. Cerro Lotena. 3. Holotype P 0900 MOZ [Ma], lateral view of the other side. Cerro Lotena. 4. Paratype P 3651 MOZ [Ma], anterior view. Cerro Caicayén. 5. Paratype P 3651 MOZ [Ma], lateral view. Cerro Caicayén. 6. Paratype P 3651 MOZ [Ma], ventral view. Cerro Caicayén. 7. Paratype P 3455 MOZ [mi], lateral view. Cerro Lotena. Figs. 8-9. *Catutosphinctes callomoni* sp. nov. from the Vaca Muerta Formation, Cerro Lotena 8. Holotype P 3443 MOZ, anterior view. 9. Holotype P 3443 MOZ, lateral view. In all figures the bar corresponds to 10 mm.

Djurjuriceras catutosense LEANZA & ZEISS, 1990

Pl. 6, Figs. 6, 7

1987 *Djurjuriceras* (?) aff. *americanense* (LEANZA) – CIONE et al.: fig. 6.
1990 *Djurjuriceras catutosense* sp. nov. – LEANZA & ZEISS: 176, pl. 36, fig. 6.

Material. Two specimens: P 3827 MOZ, which represents the holotype (here refigured), and P 5230 MOZ, a somewhat damaged specimen.

Specimen	D	WH	UW	IR	ER
P 3827 MOZ, holotype	140	40(0.36)	66(0.21)	21	32

Measurements (in mm, better preserved specimen only).

Description. Shell of medium size (D=140 mm), rather evolute. Ribbing on the inner whorls regular-bifurcate, as in a perisphinctid, but the last quarter of the outer whorl displays simple, distant and elevated ribs, some of them paired and collar-like. Deep radial constrictions are intercalated. The aperture of the body chamber is simple, somewhat resembling an attenuated sigma. The prominent paired ribs show that the specimen is a full-grown macroconch.

Remarks. *Djurjuriceras catutosense* LEANZA & ZEISS, 1990 differs from *D.* sp. gr. *ponti* (FALLOT & TERMIER) from southern Spain (OLÓRIZ 1978: 645, pl. 53, figs. 1-3) by its larger size, rectiradiate ribbing and much later beginning of the coarse ribs. *D. armonicum* OLÓRIZ (1978: 647, pl. 53, fig. 4), and *D. anularium* OLÓRIZ (1978: 648, pl. 53, fig. 5) from the same region are both somewhat larger in size; the ribs are coarser and distant (consequently the interspaces increase) and begin much earlier than in the South American species. In *D. djurjurense* ROMAN (1936: 17, pl. 2, fig. 5; pl. 3, fig. 4) the ribs on the inner whorls are prorsicostate and somewhat sigmoidal on the last whorl, and the prominent ribs of the terminal growth stage are usually arranged in pairs with large interspaces between them.

The genus *Catutosphinctes* LEANZA & ZEISS, 1992 shows close affinities to *Djurjuriceras catutosense* LEANZA & ZEISS, 1990, but differs by the presence of trifurcate ribs, by coarsening of the ribs, which are more projected on the last whorl, and by somewhat more evolute coiling.

Distribution. *Djurjuriceras catutosense* LEANZA & ZEISS, 1990 was collected at level w of the El Ministerio quarry, Los Catutos Member, Vaca Muerta Formation, Zapala district, Neuquén Province.

Genus *Mapuchesphinctes* gen. nov.

Type species. *Mapuchesphinctes garatei* sp. nov.

Derivatio nominis. After the native tribe "Mapuches", who since many centuries inhabits the Neuquén province.

Diagnosis. Giant shells with very strong, regularly spaced, primary ribs which bifurcate, very occasionally trifurcate; secondaries projected. Distant simple ribs occur at the end of the last whorl. Length of body chamber amounts to one whorl. Dimorphic.

Description. Same as for type species (see below).

Remarks. *Mapuchesphinctes* gen. nov. is monospecific. It is probably allied with *Catutosphinctes* LEANZA & ZEISS (1992), but this genus exhibits, during its ontogenetic development, different ribbing styles - including trifurcate and polygyrate branching -, which are easily recognizable. Such ribbing styles are not or only extremely seldom present in *Mapuchesphinctes*. *Zapalia* LEANZA & ZEISS, 1990 displays inner whorls more densely ribbed; outer whorls show multiple-branching ribs, including trifurcate, polygyrate and/or fascipartite ones.

Mapuchesphinctes is rather similar to the genus *Hegovisphinctes* ZEISS et al., 1996 from the Lower Tithonian Hybonotum Zone of southern Germany. It is questionable whether the latter could have migrated to the Neuquén Basin until the early Upper Tithonian. We consider, it displays more probable a heterochronous homeomorph development in South America.

Distribution. Lowermost Upper Tithonian. Middle part of Vaca Muerta Formation, Neuquén Basin.

Mapuchesphinctes garatei sp. nov.

Pl. 8, Figs. 1-2

Holotype. P 0900 MOZ [M], a very well preserved giant ammonite from Cerro Lotena, figured on Pl. 7, Figs. 1-3.

Further Material. Nine specimens from Cerro Caicayén (P 3651 MOZ), Cerro Lotena (P 3455 MOZ), additional material from El Ministerio quarry, level y (P 3796 MOZ, P 5132 MOZ) the Pichi Moncol quarry, level y (P 5150 MOZ) and level w (P 5135 MOZ, P 5144 MOZ, P 5148 MOZ, P 5149 MOZ).

Locus typicus. Cerro Lotena, Zapala Department, Neuquén Province.

Stratum typicum. Vaca Muerta Formation (WEAVER 1931), Mendoza Group (GROEBER 1946).

Derivatio nominis. In honour of Mr. José I. GARATE ZUBILLAGA† (Zapala, Argentina), former Director of the Museum Juan Olsacher, where the studied specimens are housed.

Specimen	D	WH	WW	UW	IR	ER
P 0900 MOZ Ht [M]	980	110 (0.29)	105 (0.28)	172 (0.45)	13	21
P 3651 MOZ [M]	190	57 (0.25)	70 (0.37)	90 (0.47)	12	23
P 5144 MOZ [M]	350	95 (0.27)	-	144 (0.41)	~18	?
P 3455 MOZ [m]	125	38 (0.30)	35 (0.28)	65 (0.52)	13	18

Measurements (in mm, better preserved specimens only).

Diagnosis. As for genus.

Plate 8. *Mapuchesphinctes* gen. nov. and *Zapalia*

Figs. 1-2. *Mapuchesphinctes garatei* sp. nov. 1. Paratype P 5144 MOZ. Level w, Los Catutos Member, Pichi Moncol quarry. 2. Paratype P 3796 MOZ. Level y, Los Catutos Member, El Ministerio quarry.

Figs. 3-5. *Zapalia poultoni* sp. nov. from Level w, Los Catutos Member, El Ministerio quarry. 3. Paratype P 5162 MOZ. 4. Paratype P 3830 MOZ. Level w. 5. Paratype P 5187 MOZ. Level w. In all figures the bar corresponds to 10 mm.

Description. Macroconchs.- The species consists of large to giant shells up to 380 mm in diameter, which are rather evolute (UW=0.41-0.52). Cross-section of inner whorls subquadrate, becoming elliptical on the outer whorl. Umbilical wall vertical, umbilical borders rounded. Ornamentation of shell characterized by very strong bifurcate ribs; only on the penultimate whorl they are occasionally trifurcate. The anterior branch of the bifurcate ribs is projected, whereas the posterior branch follows a nearly radial direction. The innermost whorls are more densely ribbed than the outer whorls (Pl. 7, Fig. 1).

Microconchs.- The specimen P 3455 MOZ (Pl. 7, Fig. 7) is interpreted as a microconch. It reaches a diameter of 125 mm, and the ribbing style remains very similar to the macroconch. There is one triplicate rib at the beginning of the last whorl which already belongs to the body chamber. There is one constriction, as well as single ribs at the end of the last whorl.

Remarks. The specimens from the Los Catutos area are crushed; thus the better preserved material from Cerro Lotena and Cerro Caicayén has been used for the description. Paratype P 6351 MOZ is very close to the holotype, but is presumably a young specimen, not displaying single ribs at the end of the last whorl, as is the case with the giant adult macroconch and the microconch. The unnamed specimen P 3847 MOZ from a calcareous slab of level y (El Ministerio quarry) figured by Leanza & Zeiss (1990: pl. 36, fig. 2) may be ascribed to *M. garatei* sp. nov. *Catutosphinctes americanensis* (Leanza 1980: 41, pl. 7, fig. 1a-d), also from Cerro Lotena, differs from the new species by the presence of different ribbing stages with many bi- and trifurcate ribs, followed by a stage with bifurcate ribs and intercalatories, and then by single, distant, sharp collar ribs. The genus *Mapuchesphinctes* is fairly similar to the genus *Hegovisphinctes* Zeiss, Schweigert & Scherzinger, 1996 (130, pls. 19 figs. 1-2; pl. 20) from the Hangende Bankkalke Formation [Lower Tithonian Hybonotum Zone (eystettense horizon)] from the northern Hegau area, Baden-Württemberg, Germany (Schweigert 1996). It looks almost identical, except that the Andean genus exhibits in the body chamber a slightly greater number of bifurcate ribs and occasional trifurcation, which is not developed in the German species (cf. p.48, too).

Distribution. *Mapuchesphinctes garatei* sp. nov. is a characteristic species of the Tithonian Vaca Muerta Formation in the Neuquén Basin. In the Los Catutos region *M. garatei* sp. nov. was collected from level y (El Ministerio Quarry), and levels y and w (Pichi Moncol quarry). The better preserved specimens were collected in the Cerro Lotena and Cerro Caicayén areas.

Genus *Zapalia* Leanza & Zeiss, 1990

Type species. *Zapalia fascipartita* Leanza & Zeiss, 1990.

Diagnosis. Giant to medium sized, evolute shells. Inner whorls with dense or coarse, simple or bifurcate ribs; on the penultimate whorl ribs trifurcate or fascipartite. If they are fascipartite, the secondary ribs may be either very dense with equal interspaces between them, or the branching bundles are clearly separated and split up into a maximum of five branches. There are also some tendencies towards sigmoidal ribs. Ultimate whorl ornamented with coarse, distant, primary ribs, which may branch into bundles either bifurcate, trifurcate, polygyrate, or fascipartite. All species of the genus are macroconchs. Suture lines are not known.

Remarks. The genus *Virgatosphinctes* Uhlig, 1910, which is widely distributed in the Neuquén Basin at the base of the Vaca Muerta Formation, three ammonites zones below the beds with the genus *Zapalia*, differs in having a smaller size and virgatotome and polygyrate branched ribs, that are not present in *Zapalia*. The genus *Choicensisphinctes* Leanza, 1980 differs from *Zapalia* in having smaller and more involute shells. Although *Z. zapalensis* sp. nov. displays rib bundles as in *Choicensisphinctes*, the bundles in the latter genus consist of more and finer ribs, and the splitting point occurs in a higher position of the whorl height.

The Andean genus *Zapalia* includes five species: *Z. fascipartita* Leanza & Zeiss, *Z. zapalensis* sp. nov., *Z. triplex* sp. nov., *Z. poultoni* sp. nov., and *Z. thomsoni* sp. nov.

Distribution. Vaca Muerta Formation, Upper Tithonian. Zapala region, Neuquén Province.

Zapalia fascipartita Leanza & Zeiss, 1990
Pl. 10, Figs. 1-5

1990 *Zapalia fascipartita* sp. nov. – Leanza & Zeiss: 176, pl. 36, fig. 7.

Material. 12 specimens from the El Ministerio Quarry, level y (P 1763 MOZ, P 3793 MOZ (holotype), P 3799 = 3800 MOZ (imprint), P 3801 MOZ, P 3806 MOZ, P 3813 MOZ, P 3814 MOZ, P 3815 MOZ), level w (P 3833 MOZ), and the Pichi Moncol quarry, level w (P 5146 MOZ, P 5154 MOZ, P 5157 MOZ).

Specimen	D	WH	UW	IR	ER
P 3793 MOZ, holotype	290	80(0.27)	140(0.48)	17	33
P 5154 MOZ	325	100(0.30)	145(0.44)	15	-
P 3799 MOZ	~345	~90(0.26)	~200(0.57)	12	36

Measurements (in mm, better preserved specimens only; holotype revised).

Description. This is one of the largest species within the genus *Zapalia*. The giant forms reach nearly 350 mm in diameter. The cross-section is higher than wide, oval. The

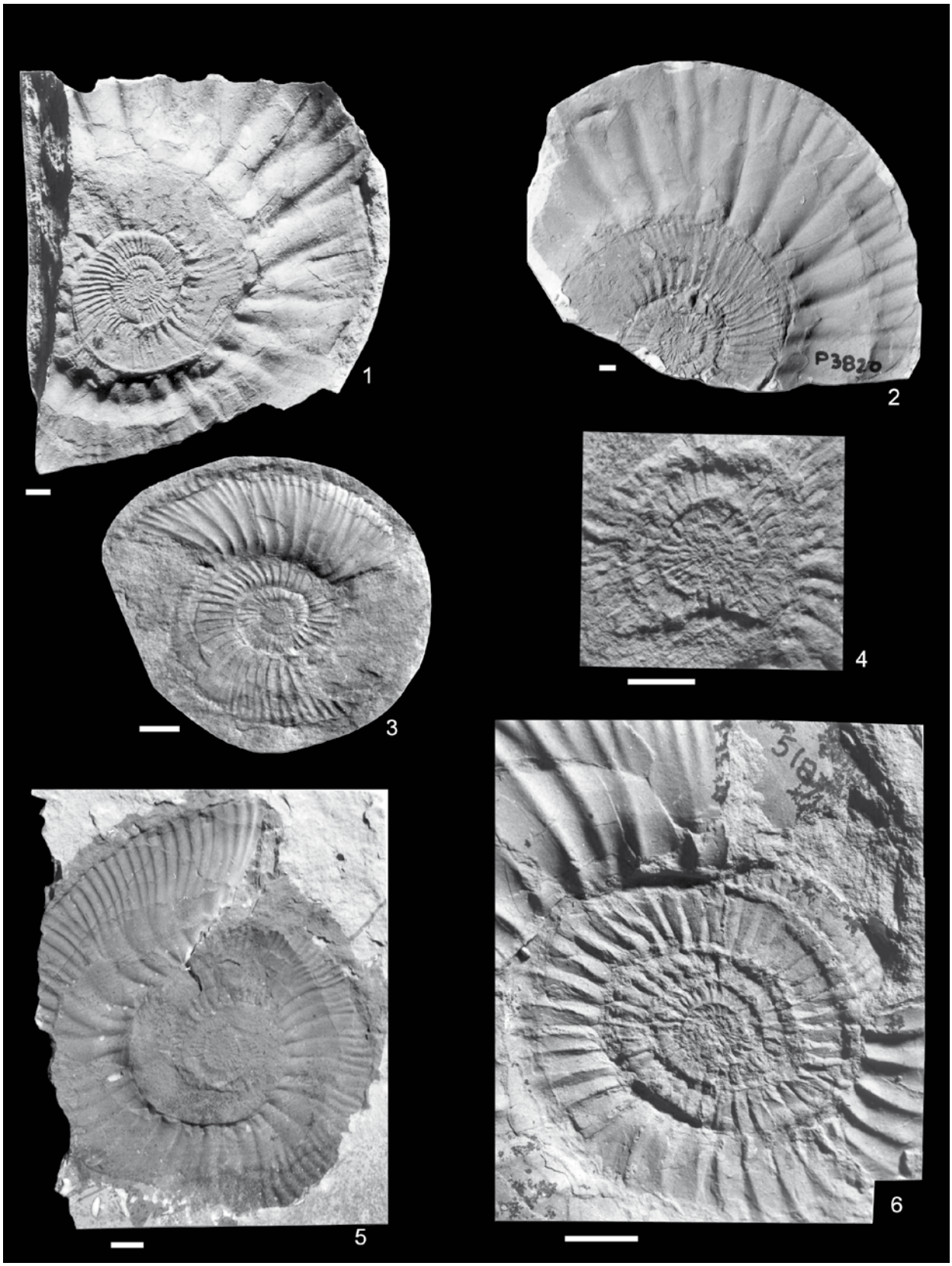


Plate 9. *Zapalia* and *Parazapalia* gen. nov.
Figs. 1-2. *Zapalia thomsoni* sp. nov. from the Los Catutos Member, Pichi Moncol quarry 1. Paratype P 5155 MOZ. Level w. 2. Holotype P 3820 MOZ. Level z.
Fig. 3. *Parazapalia perezi* sp. nov., holotype P 3803 MOZ. Level y, Los Catutos Member, El Ministerio quarry.
Figs. 4-6. *Zapalia poultoni* sp. nov. from the Los Catutos Member, El Ministerio quarry. 4. Holotype P 5143 MOZ, internal whorls. Level z. 5. Holotype P 5143 MOZ. Level z. 6. Paratype P 5187 MOZ, detail of the internal whorls. Level w. In all figures the bar corresponds to 10 mm.

flanks are somewhat convergent. The largest width is just above the umbilical margin. The umbilicus is wide, the umbilical wall inclined between 40º and 60º, and the umbilical border is rounded. The ventral region is rather narrow. The apertural margin is not preserved.

The inner whorls display prominent, mostly rectiradiate ribs with large interspaces. On the penultimate whorl bifurcate ribs can be recognized, which on the last whorl turn into slightly arched trifurcate and fascipartite bundles. On the outer part of the last whorl ribs are coarser; they are trifurcate, prominent, and rectradiate. They may also be thickened at the umbilicus. Bifurcate ribs with or without an intercalatory rib can also be seen (Pl. 10, Figs. 1, 4). At the end of the last whorl single ribs may occur. The specimen figured on Pl. 10, Fig. 5 differs from the other specimens in having denser ribbing on the inner whorls, which is interpreted as an intraspecific variation.

Remarks. *Zapalia fascipartita* Leanza & Zeiss differs from *Z. zapalensis* sp. nov. (see below) by its stronger ribs on the inner whorls, its greater evolution, different kind of rib branching, and the very prominent ribs on the outer whorl. A certain similarity exists with *Lithacoceras riedense* (Schneid, 1914: 160, pl. 5, fig. 3) from the southern Frankenalb, Germany, as the ribbing style of the inner whorls, especially of the penultimate whorl is nearly homoeomorph. At the beginning of the outer whorl the ribs are arched, and split up into five branches, passing later into three-branched ribs, and then, in the final part of the outer whorl, to strong, prominent, simple ribs. In contrast, bi- and trifurcate ribs in *Z. fascipartita* are always rectiradiate. Also *Euvirgalithacoceras supremum* (Schneid, 1914: 161, pl. 4, fig. 4) from the same region, which is not so evolute, shows arched, prominent, tri- to quinquefurcate ribs on the last whorl.

Distribution. *Zapalia fascipartita* was collected at levels y and w (El Ministerio quarry), and at level w (Pichi Moncol quarry), Los Catutos Member, Vaca Muerta Formation, Neuquén Province.

Zapalia zapalensis sp. nov.

Pl. 12, Figs. 2-4, 6; Pl. 13, Figs. 1-6

Holotype. P 3824 MOZ (level z, El Ministerio quarry), figured on Pl. 12, Fig. 2.

Further Material. 22 specimens from the El Ministerio quarry, level y (P 3761 MOZ, P 3798 MOZ, P 3811 MOZ), level z (P 3818 MOZ, P 3825 MOZ, P 5142 MOZ, P 5171 MOZ), level w (P 3809 MOZ, P 3829 MOZ, P 3835 MOZ, P 3838 MOZ, P 3839 MOZ, P 3840 MOZ, P 3842 MOZ, P 3844 MOZ, P 3845 MOZ) and the Pichi Moncol quarry, level w (P 5159 MOZ, P 5160 MOZ, P 5161 MOZ,P 5163 MOZ, P 5165 MOZ, P 5178 MOZ).

Locus typicus. El Ministerio quarry, Los Catutos region, Zapala Department, Neuquén Province.

Stratum typicum. Level z, Los Catutos Member, Vaca Muerta Formation, Mendoza Group.

Derivatio nominis. After the city of Zapala, where many houses and sidewalks ("veredas") are decorated with ammonite-bearing slabs from the Los Catutos region.

Specimen	D	WH	UW	IR	ER
P 3824 MOZ, holotype	210	68(0.32)	82(0.39)	15	~45
P 5142 MOZ	175	55(0.31)	70(0.40)	15	~50
P 5160 MOZ	175	65(0.37)	65(0.37)	18	75
P 5171 MOZ	135	40(0.29)	62(0.45)	-	-

Measurements (in mm, better preserved specimens only).

Diagnosis. Medium to large, evolute shells. Dense, fine, bifurcate ribs on inner whorls. Penultimate whorl with tri- and quadruplicate ribs. On outer whorl primary ribs form characteristic bundles with up to five secondary ribs, which are equally spaced.

Description. The material consists of mostly medium sized, evolute specimens, but many of them are not very well preserved, and incomplete. Moreover, the holotype is somewhat fragmentary on the outer whorl, but it is the only specimen which shows the adult distant rib bundles. Shells are of medium size (maximum D=210 mm), and not very evolute (UW=0.37-0.45). Cross-section probably high and oval; umbilical border rounded, and umbilical wall steep, but not vertical.

Internal ribs begin on the umbilical wall, they are somewhat sinuous at the umbilical border to continue from there in a prorsicostate fashion. On inner whorls ribs are dense and fine, presumably bifurcate. At the beginning of the outer whorl, ribs can split up into five, equally spaced secondary ribs. Primaries are pronounced; secondaries tend to become weaker; all are prorsicostate. On the outermost part of the last whorl (Pl. 13, Fig. 2) there are distant primaries, while the secondaries are not very well recognizable. It can be assumed that they are mainly trifurcate and projected; intercalatories may be present.

Remarks. *Zapalia zapalensis* sp. nov. can be separated clearly from *Z. fascipartita* Leanza & Zeiss, 1990 by the higher number of secondary ribs on the outer whorls and by the much more densely ribbed inner whorls. The interspaces of outer ribs on the ventral region are always equally spaced. *Z. poultoni* sp. nov. (described below) has fewer secondary ribs which are mostly bifurcate with intercalatories. On outer whorls this species displays trifurcate ribs, the anterior branch of which is deeply split (polygyrate) and strongly projected. Inner whorls are similar, but with some tendencies to develop swellings as in *Windhauseniceras*. *Z. zapalensis* can be distinguished from *Z. triplex* sp. nov. as the latter has a typical polygyrate ribbing style. *Z. thomsoni* sp. nov. (described below) has similar inner whorls, but the splitting up of the branches is more irregular. Ornamentation on the last half of the outer whorl displays more prominent primaries in relationship with weaker secondaries, which are always bifurcate, and rectiradiate.

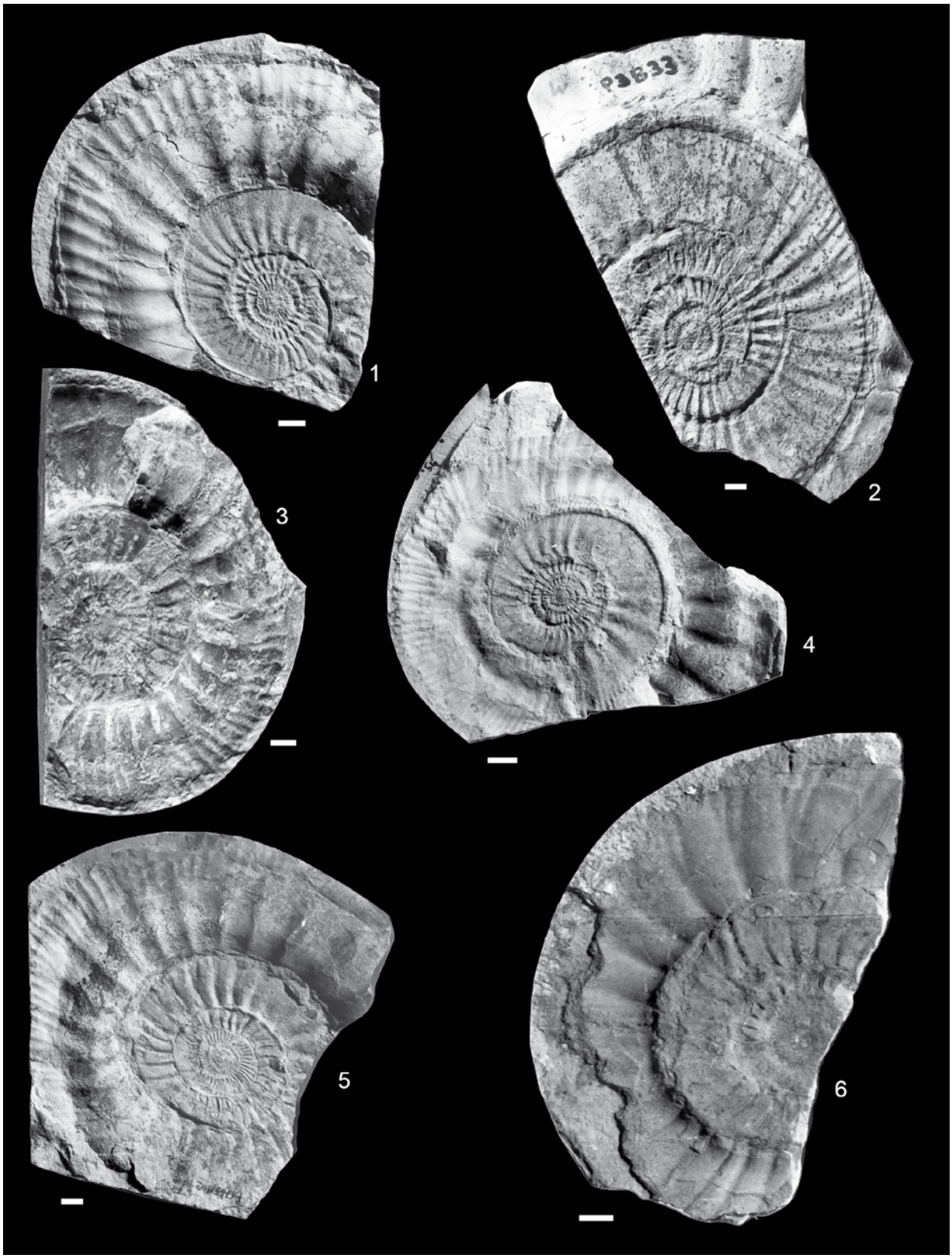


Plate 10. *Zapalia*

Figs. 1-5. *Zapalia fascipartita* Leanza & Zeiss from the Los Catutos Member. 1. Reproduction of the holotype (Leanza & Zeiss 1990: pl. 36, fig. 7) P 3793 MOZ. Level y, El Ministerio quarry. 2. Topotype P 3833 MOZ. Level w, El Ministerio quarry. 3. Topotype P 3799 MOZ. Level y, El Ministerio quarry. 4. Topotype P 5154 MOZ. Level w, Pichi Moncol quarry. 5. Topotype P 1763 MOZ. Level y, El Ministerio quarry.

Fig. 6. *Zapalia triplex* sp. nov., Paratype P 3802 MOZ. Level y, Los Catutos Member. El Ministerio quarry. In all figures the bar corresponds to 10 mm.

There is some superficial similarity with certain lithacoceratids of the Hybonotum Zone, such as *L. eystettense* (Schneid, 1914: 161, pl. 3, fig. 5, pl. 4, figs. 2-2a); but the latter species is more involute, and the fasciparite stage begins earlier. Primaries are more prominent. The branching of the ribs occurs lower on the flank, and the ribbing is denser on the last part of the outer whorl, where no reduction in the number of the external ribs is observed. *Danubisphinctes palatinus* Zeiss (1968: pl. 24, figs. 2-3) has somewhat similar rib bundles in the adult stage, but the branching style, especially on the inner half of the last whorl, is more virgatotome-like, and the point of branching is always in the middle of the flanks. *Lithacoceras ulmense* Oppel (1863: pl. 74, fig. 1) re-illustrated by Schweigert & Zeiss (1999: fig. 2) from the Zementmergel Formation (Upper Kimmeridgian Ulmense Subzone) of the Swabian Alb, closely resembles *Zapalia zapalensis*, and it might be considered as an heterochroneous homeomorph development within the Ataxioceratidae. The genus "*Phanerostephanus*" as illustrated by Howarth (1992: pl. 1, figs. 7-8), which occurs above the Pseudolissoceras beds in the Tithonian Chia Gara Formation of northern Iraq, is considered to belong to the genus *Zapalia* Leanza & Zeiss (Leanza 1996), and although being a fragment, closely resembles *Z. zapalensis* sp. nov.

Distribution. *Zapalia zapalensis* sp. nov. was collected from levels y, z, and w (El Ministerio quarry), and from level w (Pichi Moncol quarry), Los Catutos Member, Vaca Muerta Formation, Neuquén Province.

Zapalia triplex sp. nov.

Pl. 10, Fig. 6, Pl. 11, Figs. 1-6, Pl. 12, Figs. 1, 5

Holotype: P 5136 MOZ (Pl. 11, Fig. 1).

Further Material. 20 specimens from the El Ministerio quarry, level y (P 3794 MOZ, P 3797b MOZ, P 3802 MOZ, P 3805 M.O.Z, P 5134 MOZ, P 5139 MOZ, P 5141 MOZ, P 5186 MOZ, Level z: P 3822 MOZ, P 3823 MOZ, P 5177 MOZ), level w (P 3834 MOZ, P 3843 MOZ, P 5145 MOZ, P 5157/58 MOZ, P 5166 MOZ, P 5177 MOZ) and the Pichi Moncol quarry, level z (P 5263 MOZ) and level w (P 5262 MOZ, P 5164 MOZ).

Locus typicus. El Ministerio quarry, Los Catutos region, Zapala Department, Neuquén Province.

Stratum typicum. Level z, Los Catutos Member, Vaca Muerta Formation, Mendoza Group.

Derivatio nominis. After the latin word *triplex* = triple, referring to the dominating trifurcate rib branching of this species.

Specimen	D	WH	UW	IR	ER
P 5136 MOZ, holotype	~155	~55(0,35)	~75(0,48)	15	~37
P 5141 MOZ	145	50(0,34)	65(0,45)	~14	~40
P 5186 MOZ	390	95(0,24)	205(0,52)	15	~32

Measurements (in mm, better preserved specimens only).

Specimen	D	WH	UW	IR	ER
P 5139 MOZ	110	30(0,27)	58(0,52)	15	-
P 5145 MOZ	85	30(0,35)	40(0,47)	~15	--
P 3822 MOZ	215	56(0,26)	100(0,46)	11	~29
P 5164 MOZ	~150	~45(0,30	~75(0,50)	15	-
P 5177 MOZ	130	40(0,30)	70(0,53)	15	~40
P 3802 MOZ	175	55(0,31)	85(0,48)	16	-
P 3805 MOZ	110	45(0,40)	45(0,40)	16	35
P 3823 MOZ	~115	~40(0,34)	~50(0,43)	15	34

Measurements (in mm, better preserved specimens only).

Diagnosis. Inner whorls more or less coarsely ribbed, bifurcate. Penultimate whorl with triplicate bundles, developing on the last whorl into prominent polygyrate ribs, of which the anterior branch splits up very low. At the very end of the outer whorl again bifurcate ribbing sets in.

Description. Medium to giant shells (D=85-390 mm); evolute (UW=0.43-0.53). Cross-section presumably oval, as can be observed in fragmentary specimens P 5157/58 MOZ Umbilical border rounded. Umbilical wall slightly inclined. Inner whorls not densely ribbed, bifurcate, somewhat arched forward. On the last part of the penultimate whorl trifurcate branching ribs appear, which dominate on the last whorl (Pl. 11, Figs. 5-6). The first branch splits up at 1/3, the second and third ones at 2/3 of the whorl height (Pl. 11, Figs. 1, 4; Pl. 12, Fig. 1). At the very end of the last whorl, again bifurcate ribs may appear (Pl. 11, Figs. 1-2). On the penultimate and outer whorls the primaries may develop a conspicuous crest. The transition from tri- to bifurcate ribs may be marked by a constriction. The aperture is simple, slightly projected on the ventral side. Specimens P 3805 MOZ and P 3823 MOZ have a narrower umbilicus and appear to be young specimens. Specimen P 3805 MOZ displays a constriction at the end of the last whorl, accompanied by three collar ribs behind the apertural margin, which is slightly projected.

Remarks. *Zapalia triplex* sp. nov. is dominated by trifurcate and polygyrate ribs and, therefore, cannot be confounded with other species of *Zapalia*. The allied genus *Mapuchesphinctes* is characterized by a bifurcate-dominated ribbing pattern, with only very rare trifurcate ribs.

Distribution. *Z. triplex* sp. nov. was collected from levels y, z, and w (El Ministerio quarry), and from levels z and w (Pichi Moncol quarry); Los Catutos Member, Vaca Muerta Formation, Neuquén Province.

Zapalia poultoni sp. nov.

Pl. 8, Figs. 3-5, Pl. 9, Figs. 4-6

Holotype. P 5143 MOZ (level z, El Ministerio quarry), figured on Pl. 9, Fig. 5.

Further Material. Three specimens. El Ministerio quarry, level w (P 3830 MOZ, P 5162 MOZ, P 5187 MOZ).

Locus typicus. El Ministerio quarry, Los Catutos region, Zapala Department, Neuquén Province.

Plate 11. *Zapalia*

Figs. 1-6. *Zapalia triplex* sp. nov. from the Los Catutos Member. El Ministerio quarry. 1. Holotype P 5136 MOZ. Level z. 2. Paratype P 5141 MOZ. Level y. 3. Paratype P 5134 MOZ, internal whorls. Level y. Fig. 4. Paratype P 5166 MOZ, body chamber. Level w. Fig. 5. Paratype P 3822 MOZ. Level z. 6. Paratype P 5177 MOZ. Level z. In all figures the bar corresponds to 10 mm.

Stratum typicum. Level z, Los Catutos Member, Vaca Muerta Formation, Mendoza Group.

Derivatio nominis. In honour of Dr. Terry P. Poulton (Calgary, Canada).

Specimen	D	WH	UW	IR	ER
P 5143 MOZ, holotype	165	55(0.33)	~65(0.39)	19	~42
P 5187 MOZ	~165	~50(0.30)	~60(0.36)	14	~63
P 5162 MOZ	~180	~68(0.37)	-	-	-
P 3830 MOZ	145	~48(0.33)	55(0.37)	14	14

Measurements (in mm), better preserved specimens only.

Diagnosis. Shells of medium size, not very evolute. Internal ribs not densely arranged, with some swellings at the point of branching on the four innermost whorls. On the outer whorl ribs bifurcate or occasionally trifurcate. Very low splitting point on the flanks, and strongly projected ribs unlike in any other species of *Zapalia*.

Description. The holotype is, as are the other specimens, somewhat distorted. Shells are of medium size (D=145-~180 mm) and not very evolute (UW=~0.36-~0.39). Cross-section probably oval. Umbilical border rounded. On the inner whorls the ribs are rather distant, and rectiradiate. When favourably illuminated, they exhibit some thickening at the branching point. This feature disappears on the fourth whorl (Pl. 9, Fig. 6). From there onwards the ribs are in general more and more forward inclined, which is a diagnostic feature. At the end of the last whorl of very large specimens (Pl. 8, Fig. 3, and Pl. 9, Fig. 6), the ribs become rectiradiate again. Branching of the ribs on the inner whorls is presumable bifurcate; subsequently single external ribs intercalate. Occasionally trifurcate ribs are present, especially near the end of the last whorl. The point of branching is situated at 2/3 of whorl height on inner whorls, but descends to 1/3 on the last whorl, a characteristic feature that is not present in other species of *Zapalia*. On the last whorl the internal ribs thicken at the umbilical margin. Sinus-shaped constrictions may be responsible for some irregularities of the ribbing.

Remarks. *Zapalia poultoni* sp. nov. can be distinguished from the other species of the genus *Zapalia* Leanza & Zeiss,1990 by its inner whorls not being densely ribbed, and by the presence of strongly projected bifurcate ribs with very low points of splitting on the outer whorl. In fact, *Z. fascipartita* Leanza & Zeiss,1990 displays tri- and fascipartite ribs, whereas *Z. zapalensis* sp. nov. shows characteristic bundles with up to five ribs. *Z. triplex* sp. nov. has trifurcate to polygyrate branching ribs. *Z. thomsoni* sp. nov. displays tri- to quadrifurcate rib branching on the penultimate and first half of the outer whorl, and bifurcate branching on the outer half of the last whorl, but with higher splitting points, and mostly rectiradiate ribs. Finally, it should be noted that the thickenings on the ribs of the inner whorls resemble those of the genus *Windhauseniceras*.

Distribution. *Z. poultoni* sp. nov. was collected from levels z and w, El Ministerio quarry, Los Catutos Member, Vaca Muerta Formation; Upper Tithonian; Neuquén Province.

Zapalia thomsoni sp. nov.

Pl. 9, Figs. 1-2

Holotype. P 3820 MOZ (level z, El Ministerio quarry), figured on Pl. 9, Fig. 2.

Further Material. Three specimens from the El Ministerio quarry, level z (P 3797a MOZ) (fragment) and the Pichi Moncol quarry, level w (P 5155 MOZ). The specimen P 5133a/b MOZ (El Ministerio quarry, level y) is interpreted as *Z.* cf. *thomsoni* (see below).

Locus typicus. Pichi Moncol quarry, Los Catutos region, Zapala Department, Neuquén Province.

Stratum typicum. Level z, Los Catutos Member, Vaca Muerta Formation, Mendoza Group.

Derivatio nominis. In honour of Dr. Michael R. A. Thomson (Cambridge, England).

Specimen	D	WH	UW	IR	ER
P 3820 MOZ, holotype	~195	~55(0.28)	~90(0.46)	13	~28
P 5155 MOZ	~240	~80(0.33)	~95(0.39)	14	~30

Measurements (in mm), better preserved specimens only.

Diagnosis. Medium to large species. Inner whorls densely ribbed, somewhat irregular. Penultimate and first half of last whorl with tri- and quadrifurcate ribs. Outer half of last whorl with distant, bifurcate ribs.

Description. Shell of medium to large size (maximum D=~240 mm) and rather evolute (UW=~0.39-0.46). Inner whorls very densely ribbed, bifurcate; the penultimate whorl displays tri- and quadrifurcate ribs with some intercalatories. Adult sculpture on the outer half of last whorl consists of widely spaced, prominent, bifurcate ribs and intercalatories. A similar form is specimen P 5133 MOZ, but it exhibits already on inner whorls widely spaced ribs; for this reason we interpret this specimen as *Z.* cf. *thomsoni*. The specimen P 3797a MOZ is poorly preserved, but belongs to *Z. thomsoni* sp. nov. as can be recognized by the characteristic distant tri- and quadrifurcate bundles on the penultimate whorl.

Remarks. *Zapalia thomsoni* sp. nov. differs from *Z. zapalensis* sp. nov. and *Z. fascipartita* Leanza & Zeiss, 1990 by its bifurcate ribs on the last whorl. *Z. triplex* sp. nov. can be distinguished by its polygyrate and trifurcate ribbing style. *Z. poultoni* sp. nov. is different, as it has bifurcate and strongly projected ribs with a very low branching point on the outer whorl.

Distribution. *Z. thomsoni* sp. nov. has been collected from level z (El Ministerio quarry), and level w (Pichi Moncol quarry), Los Catutos Member, Vaca Muerta Formation; Upper Tithonian; Neuquén Province.

Plate 12. *Zapalia*

Figs. 1, 5. *Zapalia triplex* sp. nov. from Level y, Los Catutos Member, El Ministerio quarry. 1. Paratype P 5186 MOZ. 5. Paratype P 3794 MOZ.

Figs. 2-4. *Zapalia zapalensis* sp. nov. 2. Holotype P 3824 MOZ. Level z, Los Catutos Member. El Ministerio quarry. 3. Paratype P 5159 MOZ. Level w, Los Catutos Member. Pichi Moncol quarry. 4. Paratype P 5165 MOZ, internal whorls. Level w, Los Catutos Member, Pichi Moncol quarry.

Fig. 6. *Zapalia zapalensis* sp. nov., Paratype P 5160 MOZ. Level w, Los Catutos Member, Pichi Moncol quarry. In all figures the bar corresponds to 10 mm.

Genus *Parazapalia* gen. nov.

Type species. *Parazapalia hillebrandti* sp. nov.

Derivatio nominis. Refers to a genus, which co-occurs with *Zapalia*, and probably is related to it.

Diagnosis. A genus of medium size, with bi- or trifurcate ribbing. In general, accentuated single ribs are present before the apertural margin, which is decorated with large, lateral lappets.

Remarks. This genus consists of microconch forms. Their assignment to one of the macroconch genera *Catutosphinctes*, *Zapalia*, or *Djurjuriceras* is at present not possible; therefore we prefer to place the microconchs in the new morphogenus *Parazapalia*.

Similar prominent pairs of ribs at the end of the last whorl are displayed also by *Windhauseniceras internispinosum* (Krantz) as figured by Leanza (1980: pl. 9, fig. 1 a-b) and Zeiss & Leanza (2008), which indicate that the specimens are adult and represent the microconch of *Windhauseniceras internispinosum*. Until now, two species of the new genus *Parazapalia* are known: *P. hillebrandti* sp. nov. and *P. perezi* sp. nov.

Distribution. Vaca Muerta Formation (middle part); lowermost Upper Tithonian; Neuquén Basin.

Parazapalia hillebrandti sp. nov.

Pl. 14, Figs. 1-7

Holotype. P 3804 MOZ (level y, El Ministerio quarry) figuerd on Pl. 14, Figs. 2-3.

Further Material. 10 specimens from the El Ministerio quarry, level y (P 5137 MOZ), level w (P 3828 MOZ, P 3831 MOZ, P 3841 MOZ, P 5169 MOZ, P 5170 MOZ, P 5178 MOZ, P 5179 and P 5180 MOZ (imprint)), the Pichi Moncol quarry, level w (P 5259 MOZ), and the Los Catutos region, unknown level (P 3215 MOZ).

Locus typicus. El Ministerio quarry, Los Catutos region, Zapala Department, Neuquén Province.

Stratum typicum. Level z, Los Catutos Member, Vaca Muerta Formation, Mendoza Group.

Derivatio nominis. In honour of Prof. Dr. Axel von Hillebrandt (Berlin).

Specimen	D	WH	UW	IR	ER
P 3804 MOZ, holotype	~93	~28(0.30)	~38(0.40)	18	31
P 3828 MOZ	85	25(0.29)	38(0.44)	-	-
P 5137 MOZ	54	15(0.27)	24(0.44)	15	-
P 5169 MOZ	90	30(0.33)	38(0.42)	19	25
P 5170 MOZ	~80	~30(0.37)	~38(0.47)	14	-
P 5179 MOZ	68	22(0.32)	30(0.44)	18	31

Measurements (in mm), better preserved specimens only

Diagnosis. A species of medium size, evolute. Inner whorls with bifurcate ribs. Outer whorls with bifurcate and single ribs, terminating with two prominent single ribs. Aperture with large lappets.

Description. Medium sized (D=54-~93 mm), rather evolute (UW= 0.40-0.47) shells. Cross-section not recognizable because of lateral compression. Umbilical border rounded; umbilical wall steep, but not very deep. Ribs on inner whorls distinct, moderately spaced. On the penultimate whorl bifurcate, and very occasionally trifurcate ribs are observable; the latter ones occur at constrictions; single ribs may also be present. On the ultimate whorl some irregularities are present, and intercalation of external ribs may occur. On the last quarter of the last whorl mostly bifurcate ribs are developed, but single ribs may also appear (Pl. 14, Fig. 1). Before the aperture, there are two prominent single ribs, rather broad on the external part of the shell; the outer rib is sigmoidal in shape. Between these two ribs, a furrow can be developed. The apertural margin is double-arched, developing a large, lateral, spoon-like lappet in the middle of its length (Pl. 14, Fig. 2). On the external side the margin is somewhat projected forming a small rostrum.

Remarks. The single ribs at the end of the last whorl of *Parazapalia hillebrandti* sp. nov. resemble somewhat those of *Simplisphinctes rivasi* and *S. sandovali* (Tavera, 1985: pl. 29, fig. 7, pl. 30, fig. 3) from the Betic Ranges of southern Spain. The inner whorls of the new species are similar to those of *Zapalia fascipartita* Leanza & Zeiss, 1990 and *Z. triplex* sp. nov. during the bifurcate stage. The occurrence of prominent single ribs before the aperture can be considered as a characteristic of an adult microconch specimen and can also indicate a possible relationship with *Djurjuriceras catutosense*.

Distribution. *Parazapalia hillebrandti* sp. nov. has been collected from levels y and w (El Ministerio quarry) and level w (Pichi Moncol quarry) of Los Catutos Member, Vaca Muerta Formation; Neuquén Province.

Parazapalia perezi sp. nov.

Pl. 9, fig. 3

Holotype. P 3803 MOZ (level y, El Ministerio quarry) figured on Pl. 9, Fig. 3.

Locus typicus. El Ministerio quarry, Los Catutos region, Zapala Department, Neuquén Province.

Stratum typicum. Level y, Los Catutos Member, Vaca Muerta Formation, Mendoza Group.

Derivatio nominis. In honour of Dr. Ernesto Pérez-Angelo (Santiago, Chile).

Specimen	D	WH	UW	IR	ER
P 3803 MOZ, holotype	~80	~26(0.33)	~18(0.44)	?	?

Measurements (in mm).

Diagnosis. Of medium size. Ribs on the inner whorls bifurcate as in *P. hillebrandti*, but those on the outer whorl bi- and trifurcate.

Description. Shell of medium size (D=~80 mm), rather evolute (UW=~0.44). Innermost whorls displaying widely spaced ribs with small external nodes, resembling *Windhauseniceras*. Constrictions are also present.

Plate 13. *Zapalia*

Figs. 1-6. *Zapalia zapalensis* sp. nov. from the Los Catutos Member. 1. Paratype P 5171 MOZ. Level z, El Ministerio quarry. 2. Paratype P 5161 MOZ. Level w, Pichi Moncol quarry. 3. Paratype P 3761 MOZ, last whorl fragment. Level y, El Ministerio quarry. 4. Paratype P 3844 MOZ. Level w, El Ministerio quarry. 5. Paratype P 3809 MOZ. Level w, El Ministerio quarry. 6. Paratype P 5142 MOZ. Level z, El Ministerio quarry. In all figures the bar corresponds to 10 mm.

Only on the last half of the penultimate whorl bifurcate branching-points can be recognized. On the ultimate whorl they are situated on the middle of the flanks. The trifurcate ribs are slightly prorsicostate, more projected forward at the end of the last whorl. The aperture is not preserved.

Remarks. Although the outermost part of the last whorl in *Parazapalia perezi* sp. nov. is missing, we assume that this specimen represents a microconch. The small nodes on the innermost whorls are reminiscent of those of *Windhauseniceras*; but further material is necessary to clear up the problem whether there exists a true relationship between these forms. *P. perezi* sp. nov. can be distinguished from *P. hillebrandti* sp. nov. by the presence of trifurcate ribs on the outer whorl, which are also much more projected.

Distribution. *Parazapalia perezi* sp. nov. was collected from level y (El Ministerio quarry) of Los Catutos Member, Vaca Muerta Formation; Neuquén Province.

Family Aspidoceratidae Zittel, 1895
Subfamily Aspidoceratinae Zittel, 1895
Genus *Aspidoceras* Zittel, 1868

Type species. *Ammonites rogocznicensis* Zeuschner, 1846.

Diagnosis. Whorls rounded, sub-quadrate or depressed, with two rows of lateral tubercles. Peri-umbilical row always present, usually more widely spaced in direction of the aperture; outer row placed nearly at the middle of the whorl flank, and soon fading in many species. Some species also ribbed (Arkell et al. 1957; Checa 1985).

Distribution. Upper Oxfordian to Lower Berriasian. Cosmopolitan, except for Boreal regions.

Aspidoceras quinchaoi sp. nov., with Laevaptychus
Pl. 15, Figs. 1-5, Pl. 16, Figs. 2-3, 6

1987 *Aspidoceras* aff. *altum* Biró-Bagoczky – Cione et al.: fig. 5.
1990 *Aspidoceras* aff. *altum* Biró-Bagoczky – Leanza & Zeiss: 176, pl. 36, fig. 3.
2007 *Aspidoceras* cf. *euomphalum* Steuer – Parent et al.: 14, figs. 2-7.

Holotype. P 1910 MOZ [Ma], a very well preserved phragmocone from Cerro Lotena, figured on Pl. 15, Figs. l, 4.

Further Material. 16 specimens from the El Ministerio quarry, level y (P 3783 MOZ, P 3784 MOZ, P 3785 MOZ (figured by Leanza & Zeiss 1990: pl. 36, fig. 3), P 3787 MOZ, P 3788 MOZ, P 3789 MOZ, P 5174 MOZ, P 5182 MOZ (with attached Laevaptychus), P 5185 MOZ), level z (P 3817 MOZ), level w (P 5173 MOZ, P 5174 MOZ), the Pichi Moncol quarry, level w (P 5135 MOZ, P 5172 MOZ), Cerro Lotena, unknown level L P 1678 MOZ [mi], P 4050 MOZ [mi]), and the Los Catutos area, unknown level (P 0547 MOZ, a giant Laevaptychus, figured on Pl. 16, Figs. 2-3).

Locus typicus. Cerro Lotena, Zapala Department, Neuquén Province.

Stratum typicum. Vaca Muerta Formation, Mendoza Group.

Derivatio nominis. Dedicated to the memory of Manuel Quinchao, the late Mapuchean 'Great Chief' of Los Catutos village. In the area of this village most of the studied ammonites have been found.

Specimen	D	WH	WW	UW	IT	ET
P 1910 MOZ[Ma] holotype	370	166(0.44)	200(0.54)	110(0.29)	6	8
P 5182 MOZ[Ma]	310	125(0.40)	-	90(0.29)	8	11
P 1678 MOZ[mi]	180	65(0.36)	100(0.55)	65(0.36)	8	8
P 4050 MOZ[mi]	100	40(0.40)	60(0.60)	35(0.35)	-	-

Measurements (in mm, better preserved specimens only).

Diagnosis. Dimorphic species. Macroconchs large to giant in size, rather involute. Whorl-section rounded, somewhat depressed, wider than high. With peri-umbilical and lateral rows of spiniferous tubercles, the latter ones being usually fewer in number. Coarse, external, rectiradiate ribs originating at the external tubercles and intercalatories, fading at the middle of the whorl height. Microconchs smaller in size with the same ornamental pattern, but with stronger tubercles and ribs. Aptychi very large, of Laevaptychus type.

Description. Shell globular, large to giant in size (maximum D=370 mm), but in the outcrops we could observe several fragments which were considerably larger. Rather involute (UW=0.29-0.36). Whorl-section rounded, somewhat depressed in shape, always wider than high (WW=0.54-0.60). Flanks gently convex, converging slightly towards the rounded ventral region. Ornamentation characterized by strong, spiny peri-umbilical and lateral tubercles. The lateral row is situated nearly at the middle of the whorl height. These tubercles do not correspond exactly to the tubercles of the peri-umbilical row, which are more numerous. The outer row of tubercles, which tends to be more widely spaced in direction to the aperture, fades in some specimens. Another important characteristic of this new species are the coarse, rectiradiate ribs, which cross the venter without interruption. The ribbing begins mostly at the height of the outer row of tubercles with two or three coarse ribs. Intercalatories of the same thickness, fading also at the middle or inner part of the flank, are also present (Pl. 15, Fig. 3). Microconchs are characterized by a smaller size and by the same ornamental pattern, but by stronger tubercles and ribs (Pl. 15, Fig. 5).

The specimen of *A. quinchaoi* sp. nov. figured on Pl. 16, Fig. 6 (D=310 mm) shows an attached Laevaptychus, which possesses the following dimensions: L=155 mm, B=140 mm, B/L=~0.90. The surface, which is gently convex, shows numerous small pores and is ornamented with faint radial and concentric striae.

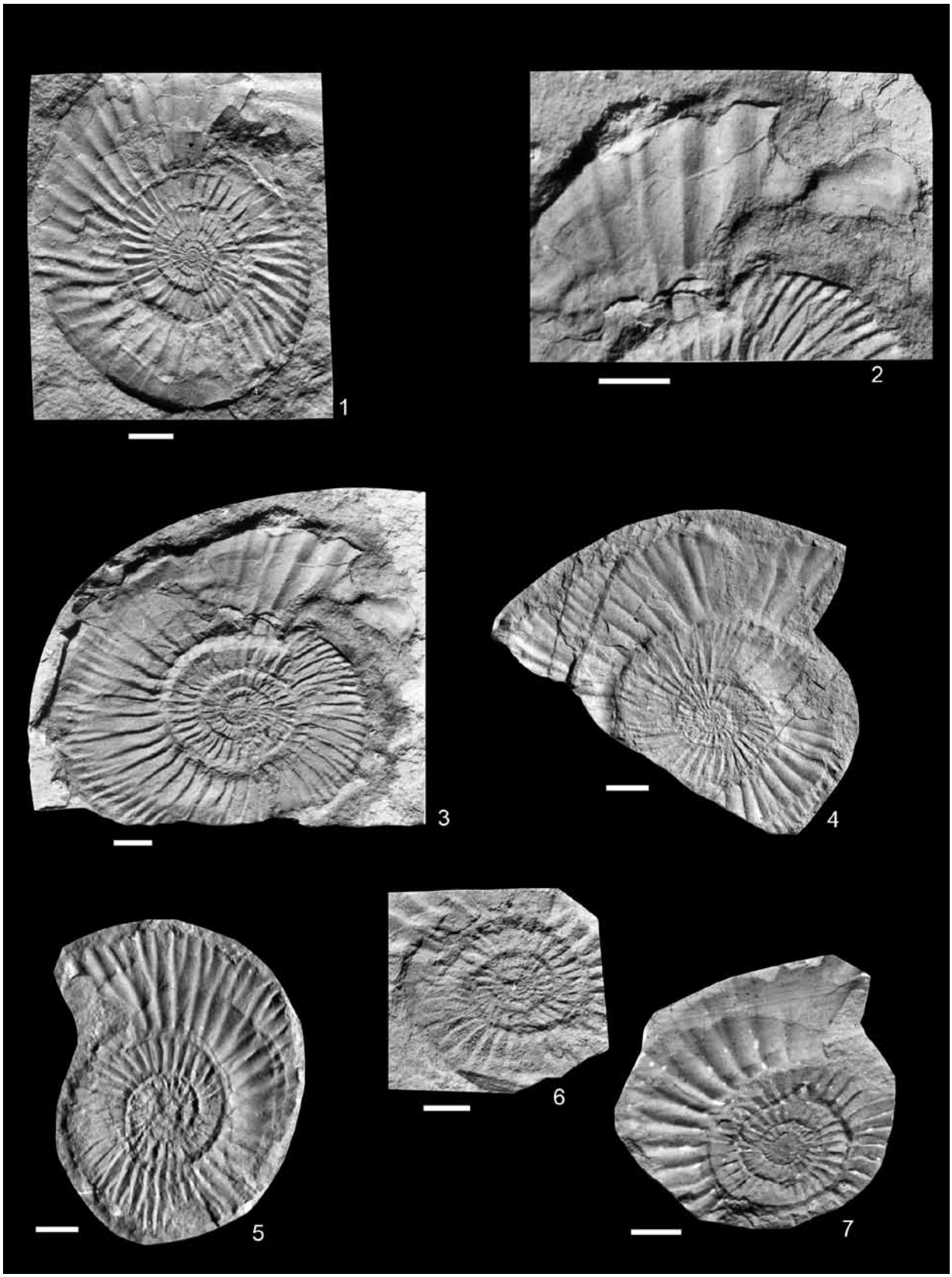


Plate 14. *Parazapalia*
Figs. 1-7. *Parazapalia hillebrandti* sp. nov.from the Los Catutos Member. El Ministerio quarry. 1. Paratype P 5169 MOZ. Level w. 2. Holotype P 3804 MOZ, detail of the aperture. Level y. 3. Holotype P 3804 MOZ. Level y. 4. Paratype P 3828 MOZ. Level w. 5. Paratype P 5180 MOZ. Level w. 6. Paratype P 3841 MOZ, detail of the internal whorls. Level w. 7. Paratype P 5170 MOZ. Level w. In all figures the bar corresponds to 10 mm.

A giant Laevaptychus (P 0547 MOZ) (L=350 mm, B=270 mm, B/L=~0,80) from an unknown level of the Los Catutos area, is figured on Pl. 16, Figs. 2-3. This Laevaptychus strongly resembles in shape and ornamentation the Laevaptychus attached to a shell of *Aspidoceras quinchaoi* sp. nov. figured on Pl. 16, Fig. 6. The shell is gently curved and very thick, reaching 65 mm at the highest point, approximately at the middle of the valve. In sectors, in which the original shell surface is preserved, numerous very small pores can be observed. Under suitable light conditions, it is possible to observe weak concentric striae, which are crossed by radial ones. Considering the 350 mm length of this giant Laevaptychus, it can be assumed that the shell of *A. quinchaoi* sp. nov. originally associated with it had a diameter of more than 500 mm (= 0.50 m). On some parts of the shell surface, small cemented oysters are preserved, probably implying that this specimen, which also is not flattened, does not come from Los Catutos Member proper, but from some marginal region or a higher level.

Remarks. *Aspidoceras quinchaoi* sp. nov. resembles somewhat *Aspidoceras rafaeli* (Oppel, 1863) from the Tithonian of the Mediterranean region, which has been extensively illustrated by Checa (1985: pl. 16, fig. 5; pl. 17, figs. 1-2; pl. 18, fig. 1). However, this species clearly differs from the Andean species in having (1) a more evolute shell, (2) a much rougher ornament, (3) inner and mid-lateral tubercles united by a prominent crest, and (4) far fewer secondary ribs. It has been attributed to *Pseudhimalayites* by Schweigert (1997).

Aspidoceras altum Biró-Bagoczky (1978: 227, pl. 2, fig. 1a-d) [D=210, WH=99(0.47), WW=58(0.27), UW=60(0.28)] from the Tithonian of Central Chile appears, if observed laterally, to be a very closely related species; but the whorl section considerably differs from that of *A. quinchaoi* sp. nov. by being much higher than wide, with a somewhat fastigate venter (Biró-Bagoczky 1978: pl. 2, fig. 1b). In addition, the arrangement of the two rows of tubercles of *A. quinchaoi* sp. nov. is somewhat more irregular: they do not occupy corresponding positions as in *A. altum*, but often alternate. Other well known Andean species of *Aspidoceras*, such as *A. euomphalum* Steuer, 1897 or *A. andinum* Steuer, 1897 show still bigger differences with regard to *A. quinchaoi* sp. nov. in size, shape, and ornamentation. Parent et al. (2007) already noticed the main differences between *A. euomphalum* and his *A.* cf. *euomphalum* i.e., the different stratigraphic levels and the complete lack of ribs on the holotype. The ribbing is still more prominent in our specimens, which demonstrate a strong ribbing until the inner whorl (cf. Pl. 15, Figs. 2 and 5). We think that this character is sufficiently distinct and therefore established a new species for these forms.

As some of the aptychi are preserved together with shells of *Aspidoceras quinchaoi* sp. nov. (Pl. 16, Fig. 6) we consider it appropriate to describe them together with the new species, also in order to avoid unnecessary disturbance in ammonite nomenclature (cf. Arkell 1957). Cloos (1961) had made a very complete revision of the aptychi from Argentina. The described forms clearly belong to the parataxon *Laevaptychus* Trauth (1927), and more precisely to *Laevaptychus latus* (Parkinson) originally described from Solnhofen, Germany (cf. Trauth:1931, pl. 1, fig. 3; Moore & Sylvester-Bradley 1957: fig. 558/12; Kennedy & Cobban 1976: pl. 3, fig. 2a-b; Cloos 1961: pl. 2, figs. 1-6; pl. 3, figs.1-3, 7; and Zakharov & Lominadze 1983: fig. 7c).

Distribution. *Aspidoceras quinchaoi* sp. nov., partly with Laevaptychus, was collected from levels y, z, and w (El Ministerio quarry) and level w (Pichi Moncol quarry). Los Catutos Member, Vaca Muerta Formation (in the same formation also at Cerro Lotena), Neuquén Province.

Aspidoceras aff. *euomphalum* Steuer, 1897, with Laevaptychus

Pl. 16, Figs. 1, 4-5, 7

aff. 1897 *Aspidoceras euomphalum* sp. nov. – Steuer: 69: pl. 5 figs. 1-4.

Material. Three specimens, two of them with Laevaptychus, and two single, complete Laevaptychi from the El Ministerio quarry, level y (P 5175 MOZ (*A.* with Laevaptychus), P 3719 MOZ (complete, single Laevaptychus), P 5183 MOZ (complete, single Laevaptychus) and the Los Alazanes quarry, level unknown (P 2612 MOZ (*A.* with Laevaptychus), P 5233 MOZ (*A.* without Laevaptychus)).

Description. Imprints of small specimens of *Aspidoceras* (maximum D=150 mm). Ornamentation consists of two rows of small spines, one peri-umbilical and one mid-lateral; the latter being more strongly developed. From the upper row of spines faint prorsiradiate striae cross over the shell surface. The aptychi are very well preserved; they belong to the Laevaptychus type. The specimens figured on Pl. 16, Figs. 5 and 7 both show an attached Laevaptychus. In addition, two complete Laevaptychus are figured on Pl. 16, Figs. 1 and 4. The valves are of relatively small size, semi-circular in shape, somewhat larger than wide (P 3719 MOZ: L=142 mm, B=97 mm, B/L=0.68; P 5183 MOZ: L=130 mm, B=92, B/L=0.70). The valves are not very thick; the external convex surface displays characteristic small pores, whereas the internal concave surface is ornamented with conspicuous concentric striae.

Remarks. Although the preservation of the ammonites precludes measurements, the ornamentation consisting of two rows of small spines, the upper one being more strongly developed, and the presence of prorsiradiate striae on the flanks suggest affinities with *A. euomphalum* Steuer (1897: 69, pl. 5, figs. 1-4). It should be noted, however, that *A. euomphalum* Steuer as figured by Leanza (1980: 41, pl. 8, fig. 1a-b) from Cerro Lotena was considered by Checa (1985) to be synonymous with *A. rogoznicense* Zeuschner, 1846 from the Hybonotum Zone of Europe. This view is not accepted since the Andean species can be easily distinguished from *A. rogoznicense* (cf. Checa 1985: pl. 16, figs. 1-4) by (1) a more delicate ornamentation, (2) more numerous peri-umbilical and mid-lateral tubercles, (3) a higher position

Plate 15. *Aspidoceras*

Figs. 1-5. *Aspidoceras quinchaoi* sp. nov. 1. Paratype P 5174 MOZ [Ma],whorl fragment. Level w, Los Catutos Member, El Ministerio quarry. 2. Holotype P 1910 MOZ [Ma], lateral view. Vaca Muerta Formation, Cerro Lotena. 3. Paratype P 3785 MOZ [Ma]. Level y, Los Catutos Member, El Ministerio quarry (same specimen as figured by LEANZA & ZEISS 1990: pl. 36, fig. 3). 4. Holotype P 1910 MOZ, anterior view. Vaca Muerta Formation, Cerro Lotena. 5. Paratype P 1678 MOZ [mi], lateral view. Vaca Muerta Formation, Cerro Lotena. In all figures the bar corresponds to 10 mm.

on the flank of the upper row of tubercles, which are larger in size, and (4) faint prorsiradiate striae crossing the shell surface.

The aptychi attached to the shells of *A.* aff. *euomphalum* Steuer (1897: pl. 16, figs. 5, 7) belong to the parataxon Laevaptychus Trauth, 1927. They differ from the Laevaptychus of *A. quinchaoi* by (1) a smaller size, (2) sub-circular shape, just a little larger than wide, and (3) valves which are not very thick. The Laevaptychus-pairs figured herein on Pl. 16, Figs.1 and 4, agree with those illustrated by Cione et al. (1987: fig.7) and Leanza & Zeiss (1990, pl. 3, fig.7), which had been provisionally placed in L. brevis (Dollfuss).

Distribution. *Aspidoceras* aff. *euomphalum* Steuer (with Laevaptychus) was collected from level y (El Ministerio quarry) and level y and an unknown level (Los Alazanes quarry); Los Catutos Member, Vaca Muerta Formation; Neuquén Province.

Family Simoceratidae Spath 1924

Simoceratidae indet.
Pl. 5, Fig. 5

Material. Two specimens (3832 MOZ, P 3836 MOZ).

Specimen	D	WH	UW	IR	ER
P 3832 MOZ	~120	~25(0.20)	~70(0.58)	14	-

Measurements (in mm, better preserved specimen only).

Description. The poorly preserved fragments consist of very evolute shells (UW=0.58). Some constrictions may be present. The ribs are faint on the inner whorls, rectiradiate and always simple. On the penultimante whorl an umbilical thickening can be observed. At constrictions the ribs may be somewhat arched and projected. On the preserved fragment of the outer whorl only thickening of the ribs at the umbilical margin can be observed.

Remarks. The interpretation of the specimens is rather doubtful, but the simple ribs and the constrictions with combined arched ribs point probably to a simoceratid, most likely allied with *Volanoceras* Geyssant, 1985. The same conclusion can be reached from the arrangement of the whorls. A problem remains because no marginal tubercles are observable. Therefore the specimens are named only as Simoceratidae indet.

Distribution. The Simoceratidae indet. were collected from level w (El Ministerio quarry), Los Catutos Member, Vaca Muerta Formation; Neuquén Province.

Superfamily Haploceratacea Zittel, 1884
Family Oppeliidae Douvillé, 1890

Oppeliidae indet.
Pl. 1, Fig. 10

Material. One specimen (P 3782 MOZ).

Description. Poorly preserved and flattened specimen with rather evolute shell. Some sculptural elements can be observed on the internal whorl; the outer whorl becomes gradually smooth. The whorl height does not seem to be very large.

Remarks. The impression of this specimen is very poorly preserved. The coiling resembles somewhat the genus *Glochiceras* s.l. and especially the subgenus *Neoglochiceras*, but this interpretation is very doubtful, and therefore the specimen is named only Oppeliidae indet.

Distribution. Oppeliidae indet. was collected from level y (El Ministerio quarry), Los Catutos Member, Vaca Muerta Formation; Neuquén Province.

Qualitative and quantitative analysis of the Zapala ammonite fauna

The material described in this paper represents five families, three subfamilies, nine genera, and 19 species. Of these, one subfamily (divided into two tribes), two genera, and eleven species are new. Taxa directly related to this study have been previously described by the authors, including *Zapalia fascipartita*, *Djurjuriceras catutosense*, and *Catutosphinctes rafaeli* (cf. Leanza & Zeiss 1990, 1992). Due to their poor preservation, representatives of the families Simoceratidae and Oppelidae remained indeterminate at the generic level.

The whole material collected and studied by us from the Los Catutos Member of the Vaca Muerta Formation consisted of 194 specimens. Some specimens housed in the Zapala Museum and collected from the Vaca Muerta Formation at the localities of Cerro Lotena and Cerro Caycayén were also included in our studies, as they are mostly better preserved and this offered valuable supplementary information.

The fossil localities and stratigraphic units of the described species and their distribution in the different horizons are given in the following list:

1. Cerro Caicayén (37°25‘ S - 70°26‘ W; Fig. 1)
   Mapuchesphinctes garatei sp. nov.
2. Cerro Lotena (39°10‘ S - 69°38‘ W; Fig. 1)
   Mapuchesphinctes garatei sp. nov.
   Catutosphinctes callomoni sp. nov.
   Windhauseniceras stipanicici sp. nov.
   Aspidoceras quinchaoi sp. nov.
3. Los Catutos region (38°71‘ S - 70°12‘ W) with the El Ministerio, Pichi Moncol, Loma Negra, El Pozo, and Los Alazanes quarries (Fig. 5).

a. El Ministerio quarry

Within the Los Catutos Member of this quarry Leanza & Zeiss (1990) had recognized, from base to top, five ammonite-bearing levels: x+a, x, y, z, and w (Fig. 6).

Level x + a
Aulacosphinctes proximus (Steuer) [M] and [m]
A. aff. *proximus* (Steuer)
Corongoceras cf. *praecursor* Zeiss

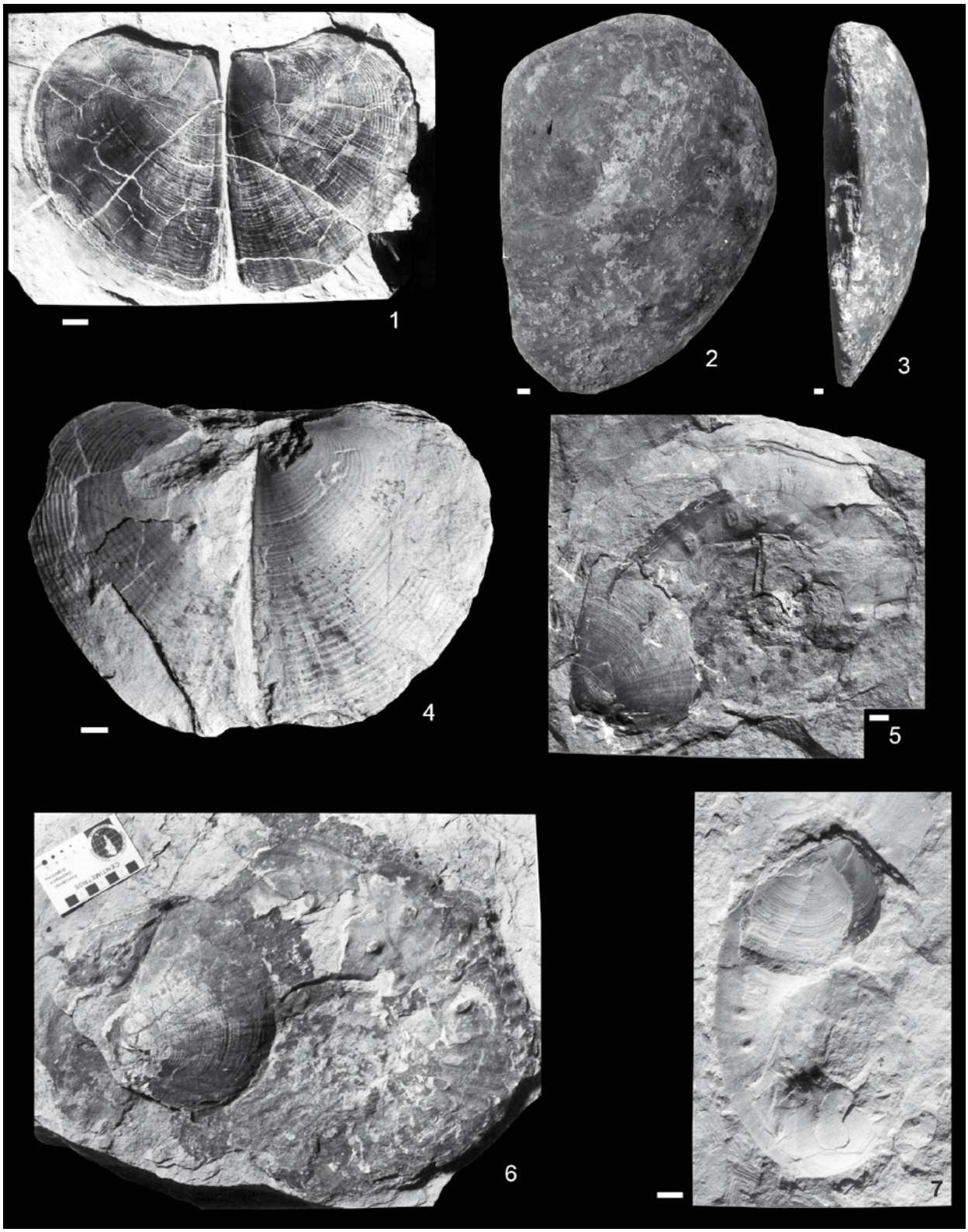


Plate 16. *Aspidoceras* and Laevaptychus

Figs. 1, 4. Complete Laevaptychus of *A.* aff. *euomphalum* Steuer from Level y, Los Catutos Member. 1. Hypotype P 3719 MOZ. Already figured by Leanza & Zeiss (1990: pl. 37, fig. 7) as Laevaptychus brevis (Dollfus). Los Alazanes quarry (orientation according to Trauth). 4. Hypotype P 5183 MOZ. El Ministerio quarry (orientation according to Trauth).

Figs. 2-3. Laevaptychus of *A. quinchaoi* sp. nov. Paratype P 0547 MOZ. 2. Left side (note its giant size). 3. Anterior view. Unknown level (Los Catutos Member?) Los Catutos.

Figs. 5, 7. *Aspidoceras* aff. *euomphalum* Steuer with *Laevaptychus* from the Los Catutos Member. 5. Hypotype P 2612 MOZ. Level unknown. Los Alazanes quarry. 7. Hypotype P 5175 MOZ. Level y, El Ministerio quarry.

Fig. 6. *Aspidoceras quinchaoi* sp. nov. with *Laevaptychus*. Paratype P 5182 MOZ. Level y, Los Catutos Member, El Ministerio quarry.

In all figures the bar corresponds to 10 mm.

Level x

Catutosphinctes rafaeli Leanza & Zeiss [M] and [m]

Level y

Mapuchesphinctes garatei sp. nov.
Parazapalia perezi sp. nov.
Zapalia fascipartita Leanza & Zeiss
Zapalia triplex sp. nov.
Zapalia zapalensis sp. nov.
Zapalia cf. *thomsoni* sp. nov.
Parazapalia hillebrandti sp. nov.
Aspidoceras quinchaoi sp. nov. [M] and [m]
Aspidoceras aff. *euomphalum* Steuer with Laevaptychus
Aspidoceras quinchaoi sp. nov. with Laevaptychus
Laevaptychus of *A. quinchaoi* sp. nov.
Oppeliidae indet.

Level z

Zapalia thomsoni sp. nov.
Zapalia poultoni sp. nov.
Zapalia triplex sp. nov.
Zapalia zapalensis sp. nov.
Windhauseniceras internispinosum (Krantz)

Level w

Simoceratidae indet.
Djurjuriceras catutosense Leanza & Zeiss
Zapalia poultoni sp. nov.
Zapalia fascipartita Leanza & Zeiss
Zapalia triplex sp. nov.
Zapalia zapalensis sp. nov.
Parazapalia hillebrandti sp. nov.
Windhauseniceras internispinosum (Krantz)

Unknown level

Giant Laevaptychus of *A. quinchaoi* sp. nov.

b. Pichi Moncol quarry

Level y

Catutosphinctes westermanni sp. nov.
Mapuchesphinctes garatei sp. nov.

Level z

Zapalia triplex sp. nov.

Level w

Catutosphinctes westermanni sp. nov.
Djurjuriceras catutosense Leanza & Zeiss
Mapuchesphinctes garatei sp. nov.
Zapalia thomsoni sp. nov.
Zapalia fascipartita Leanza & Zeiss
Windhauseniceras internispinosum (Krantz)

c. Loma Negra quarry

Level y

Zapalia zapalensis sp. nov.

d. El Pozo quarry

Level y

Windhauseniceras internispinosum (Krantz)

Level w

Windhauseniceras internispinosum (Krantz)
Windhauseniceras stipanicici sp. nov.

e. Los Alazanes quarry

Level y

Laevaptychus of *Aspidoceras* aff. *euomphalum* Steuer

Unknown level

4. *Aspidoceras* aff. *euomphalum* Steuer with Laevaptychus.

The ammonite succession of Los Catutos Member as described in this monograph is summarized in Fig. 7. The numbers of specimens studied from the individual levels are as follows: 20 (x+a), 57 (x), 49 (y), 11 (z), and 57 (w).

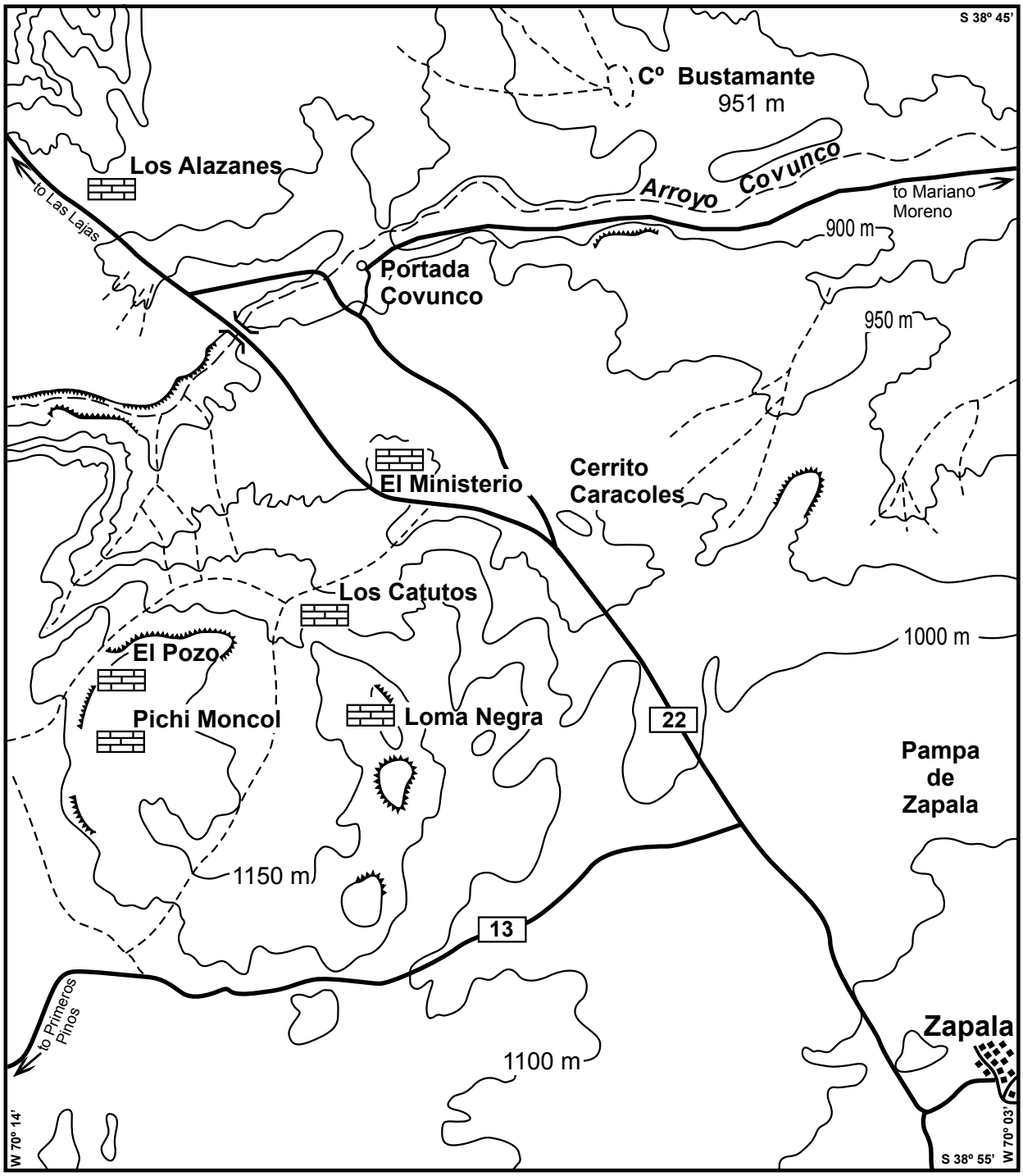
A taxonomic overview of the taxa collected from the different horizons provides the following results (first position: number of genera; second position: number of species): 2/3 (x+a x), 1/1 (x), 8/12 (y), 2/5 (z), and 7/13 (w).

Comparison with other ammonites from time-equivalent strata of the Neuquén Basin

The ammonites studied in this paper can be most reliably compared with those described from the Vaca Muerta Formation in the surroundings of the Cerro Lotena. In contrast to our material they are three-dimensionally preserved (Haupt 1907; Douvillé 1910; Weaver 1931; Leanza 1980), occurring mostly in the Proximus and Internispinosum zones.

Haupt (1907) was the first to introduce, in the geological literature, the name of Cerro Lotena, while describing and illustrating ammonites and bivalves from that area. Regarding ammonites, he reported '*Perisphinctes*' *proximus* (Steuer), first transferred together with *Hoplites koellickeri* Haupt non Oppel to *Aulacosphinctes* by Krantz (1926) L; *H. koellickeri* had been already, designated as the type species of the genus *Corongoceras* by Spath (1925), *Aspidoceras steinmanni* Haupt ascribed to *Pseudhimalayites* by Spath (1925), and *Neumayria pseudooolithica* Haupt, later placed in the genus *Pseudolissoceras* by Krantz (1926).

Krantz (1926, 1928) studied a great number of Middle and Upper Tithonian ammonites collected by Gerth (1925) from Tithonian strata considered to belong to the Vaca Muerta Formation, not only from the classical localities between the Atuel and Rio Grande rivers in the southern Mendoza province, but also from the Cerro Lotena area. Of particular interest for our study are those ammonites illustrated and classified by Krantz (1926, 1928) from the Cerro Lotena area, such us *Aspidoceras euomphalum* Steuer, *Aspidoceras haupti* Krantz, *Aspidoceras* (*Pseudhimalayites*) *steinmanni* (Haupt), *Corongoceras lotenoense* Spath, *Aulacosphinctes proximus* (Steuer), and especially '*Perisphinctes*' *internispinosus* Krantz, the type species of *Windhauseniceras* Leanza 1945.

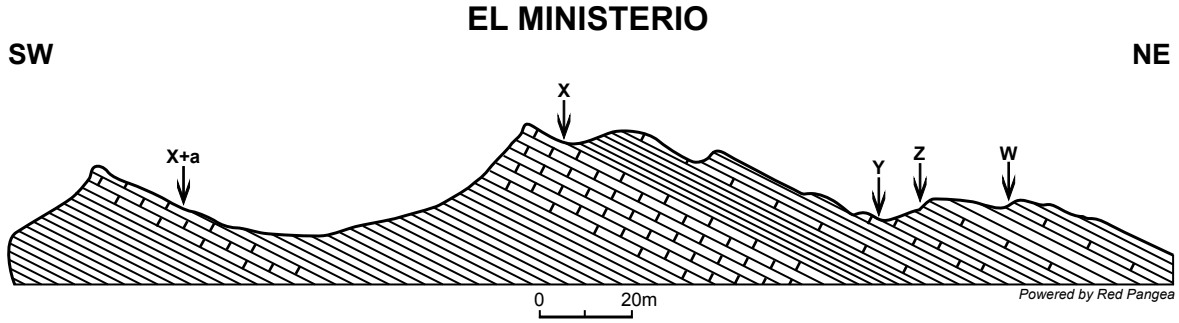


Text-Fig.5. Location map of Los Catutos quarries cited in the text.

Weaver (1931) mentioned from time-equivalent strata at Cerro Lotena *Aulacosphinctes windhauseni* Weaver, considered by Leanza (1980) as a representative of *Subdichotomoceras* Spath (1925), and *Aspidoceras euomphalum* Steuer. Other ammonites described by Weaver are from the Late Lower Tithonian Virgatosphinctinae Beds (Leanza 1980).

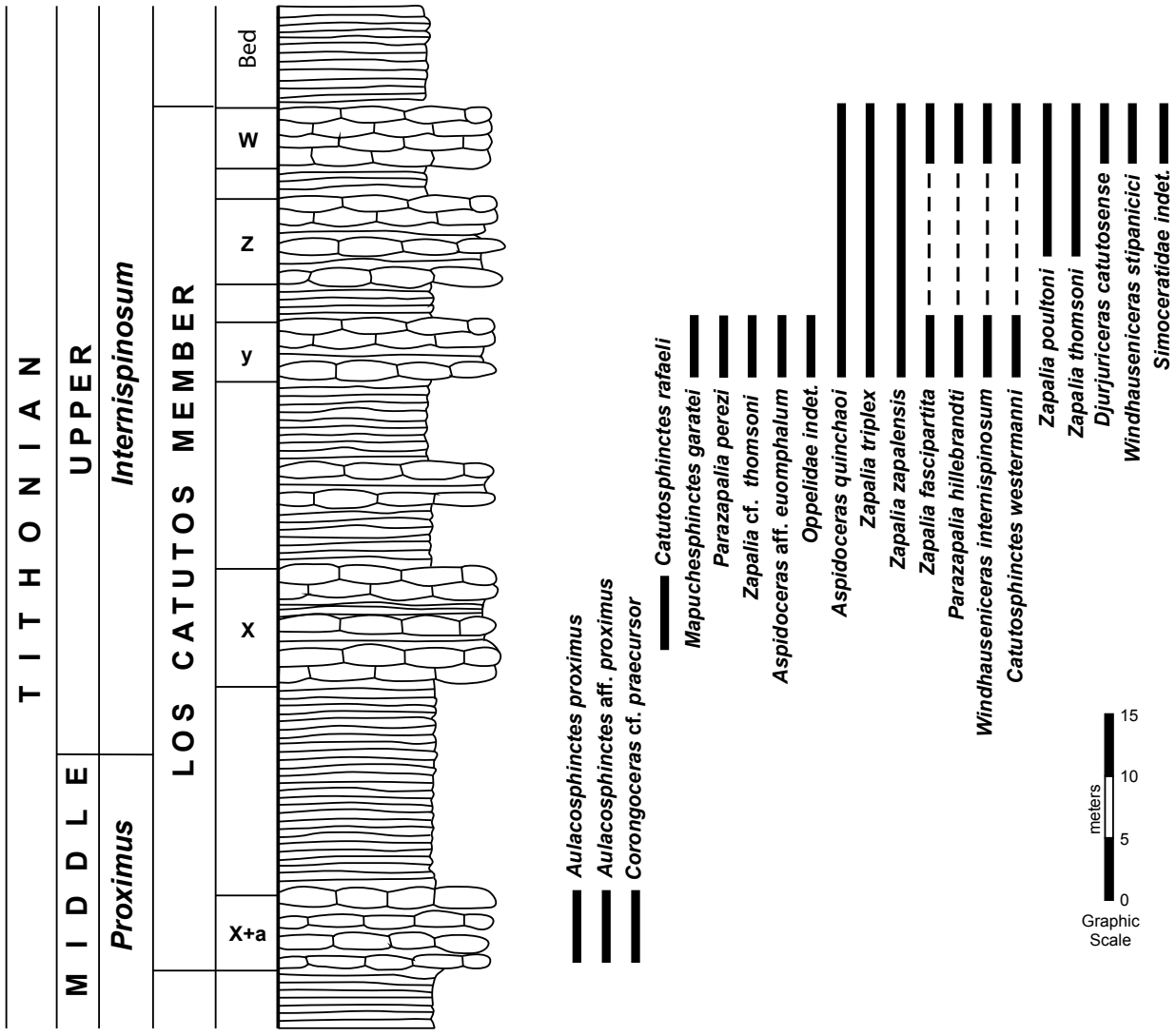
Leanza (1980) also illustrated ammonites from the Cerro Lotena area. As a result of the present study, some of his interpretations have been partly modified. In the case of *Subdichotomoceras*, its type species *S. lamplughi* comes from the Upper Kimmeridgian (Autissiodorensis Zone) of southern England. In this paper it is thought to be a possible microconch of *Windhauseniceras*. Also, as the genus *Pachysphinctes* is a truly Kimmeridgian genus, '*P.*' *americanensis* Leanza (1980) has been also reconsidered and ascribed some time ago to *Catutosphinctes* by Leanza & Zeiss (1992).

Parent (2003) presented a taxonomic and biostratigraphic re-evaluation of '*Perisphinctes*' *internispinosus* Krantz from the Cerro Lotena, placing *Aulacosphinctes proximus* (Steuer) in *Torquatisphinctes* but, as discussed in the systematic section, this assignation is discarded as the latter genus is considered to be Kimmeridgian in age.



Text-Fig.6. Section through the Los Catutos Member at El Ministerio quarry, showing the stratigraphic position of the horizons x+a, x, y, z, and w.

Other Tithonian time-equivalent ammonite-bearing strata in regions not far from the Los Catutos area were studied at Cañadón de los Alazanes (PARENT 2001) and Portada Covunco (PARENT & COCCA 2007). Of particular interest for our study is the study by PARENT et al. (2007), in which the spatio-temporal distribution of morphospecies related to *Aspidoceras euomphalum* STEUER in the Barda Negra area within the Internispinosum Zone is shown (PARENT et al. 2007: fig. 11). Based on the excellent preservation of aptychi attached to shells and on morphological differences, our new results indicate that in Los Catutos the aspidoceratid formerly described as *Aspidoceras* aff. *altum* BIRÓ-BAGOCZKY by CIONE et al. (1987: fig. 5) and LEANZA & ZEISS (1990: pl. 36, fig. 3) differs not only from *A. euomphalum* but also from *A. al-*



Text-Fig.7. The ammonite succession in the Los Catutos Member as described in this monograph.

tum. As a result the new species *Aspidoceras quinchaoi* has been established herein including '*A.* cf. *euomphalum*' of Parent et al. (2007).

Zeiss & Leanza (2008) recently described the new species *Simplisphinctes* (*Lotenia*) *neuquenensis* at Cerro Lotena from the Internispinosum Zone, shifting it to the lowermost Upper Tithonian and providing arguments for its correlation with the Simplisphinctes [abnormis] Zone of the Mediterranean Province.

In the southern Mendoza province, Leanza (1945) described ammonites of comparable Tithonian strata from the southern end of the Sierra Azul (e.g., *Windhauseniceras* cf. *internispinosum* Krantz in Leanza 1945: 23, pl. 21, fig. 6) leaving no doubt that the Internispinosum Zone is also present there.

Other Tithonian ammonites of not exactly time-equivalent strata from the Vaca Muerta Formation of the Neuquén Basin have been illustrated in papers by Steuer (1897), Burckhardt (1900a, b, 1903), Douvillé (1910), Indans (1954), Leanza (1949), and Leanza & Olóriz (1987). Their relationships with the fauna described herein are discussed in the systematic descriptions.

Time-equivalent strata with specimens probably belonging to the Internispinosum Zone have also been recorded from the Río Leñas section in central Chile (Corvalán: 1959: 16, pl. 4, figs. 16-17) and from Paso Los Bayos (Aguirre Urreta & Charrier 1990: 265, pl. 1, fig. 9). The northernmost occurrence of this species in Chile has been recorded at Quebrada de los Asientos, Atacama (Pérez d'Ángelo in García 1967).

In northern South America, Bürgl (1960: pl. 1, fig. 5) figured a specimen from Boyacá (Colombia) resembling *W. internispinosum*, although its stratigraphic position is uncertain.

Biochronological correlations of the Zapala ammonite fauna around the Middle/Upper Tithonian boundary

The ammonite assemblages described in this paper belong to the Andean Province of the Jurassic. They have been found in the Neuquen Basin, and mostly in the surroundings of the city of Zapala. By lying between the Zitteli and Alternans assemblage zones (Text-Fig. 4), they allow a refinement of ammonite biostratigraphy around the Middle/Upper Tithonian boundary. Zeiss & Leanza (1999, 2008) discussed this boundary at a global scale based on ammonites, calpionellids (chitinoidelids), radiolarians, calcareous nannofossils and dinoflagellates and concluded that these fossil groups can be used to arrive at a good global correlation of the base of the Upper Tithonian.

Global correlations of the above mentioned boundary by ammonites were rather limited until the second half of the last century. Only through the thorough description of a stratigraphically well-collected ammonite fauna from the lowermost Upper Tithonian of southern Spain by Olóriz & Tavera (1981) and especially by Tavera (1985), it was possible to propose more precise correlations between different parts of Mediterranean Europe and elsewhere (Olóriz & Tavera 1981: 229; Zeiss 1983: 431; Tavera 1985: 344, fig. 27). Tavera (1985) proposed a correlation of three regional zones for the lowermost Upper Tithonian, namely the Simplisphinctes Zone of 'S España', the Scruposus Zone of the 'Submediterranean' and the Internispinosum Zone of 'C. and S. America', apparently assuming for them the same time range (Zeiss & Leanza 2008). The recent find in Argentina of *Simplisphinctes* (*Lotenia*) *neuquenensis* Zeiss & Leanza in an association with *Windhauseniceras internispinosum* within the Vaca Muerta Formation at the southern slope of the Cerro Lotena (cf. Zeiss & Leanza 2008) provides further arguments for the correlation between the Internispinosum Zone of the Andean Province of the Jurassic and the Simplisphinctes [abnormis] Zone of the Mediterranean Province. Concerning the Scruposus Zone, Zeiss (2001) demonstrated that only the lower part can be considered as equivalent of the Simplisphinctes Zone.

The possible correlation between the Simplisphinctes/Oloriziceras magnum Zone of southern Spain and the Internispinosum Zone is based on early species of the genus *Corongoceras* (e.g., *C. lotenoense*, *C. mendozanum*) which occur in the Simplisphinctes/O. magnum Zone of Europe and Northern Africa as well as in the Internispinosum Zone of southern South America (Tavera 1985). Similar forms have also been found in Antarctica (Ross Island, det. A. Zeiss 1985, unpublished; Whitham & Doyle 1989), Madagascar (Collignon 1960), the Himalayas (Krishna et al. 1982) and Japan (Sato 1962). A related, but apparently somewhat older species, *Corongoceras praecursor* Zeiss, has been described from Austria (Zeiss 2001) and, in accordance with the results of this paper, it is apparently also present in Argentina.

The great similarity between the related species *Simplisphinctes* (*S.*) *rivasi* Tavera from southern Spain and the Argentinian species *Simplisphinctes* (*Lotenia*) *neuquenensis* Zeiss & Leanza and their associated fauna suggest that the time intervals in which these two species existed are more or less equivalent. Additionally, another related species, *Simplisphinctes* (*Paralytohoplites*) *caribbeanus* (Imlay 1942) from the Tithonian Stage of Cuba, is similar to *Simplisphinctes* (*S.*) *abnormis* from southern Spain and North Africa and is apparently of the same age. Therefore, the genus *Simplisphinctes* and in particular these four species are very useful correlation tools between southern Europe and North Africa and Central and South America (Table 3).

The himalayitid genus *Simplisphinctes* is rather widespread at the base of the Upper Tithonian stage of Europe and North Africa, where it is known from southern Spain (Tavera 1985), northern Italy (Sarti 1988; Zeiss 2001), Morocco (Benzaggagh & Atrops 1995, 1997), and Algeria (Roman 1936). Tavera (1985) introduced for this genus the "Zona de Simplisphinctes" as "taxon-range zone". This is the lowermost zone of the Upper Tithonian Stage in southern Europe (Table 3). A time-equivalent in Central Europe is the Oloriziceras magnum Zone (Zeiss

		Southern Europe, Northern Africa	Cuba	Mexico		Argentina, Chile	Antarctic Peninsula		Pakistan	Himalaya
Upper Tithonian		*Durangites vulgaris*	*Durangites, Micranthoceras, Hildoglochiceras, Salinites, Corongoceras*	*Substeueroceras, Durangites, Salinites*		*Substeueroceras koeneni*	*Blanfordiceras*	*Substeueroceras*	*Protacanthodiscus, Himalayites*	*Blanfordiceras, Spiticeras*
	Micracanthum	*Paraulacosphinctes transitorius*		*Corongoceras, Micranthoceras, Acevedites, Suarites*		*Corongoceras alternans, Lytohoplites*	*Lytohoplites weaveri*		*Blanfordiceras, Uhligites*	*Himalayites, Corongoceras*
		Simplisphinctes, Co. lotenoense	*Simplisphinctes caribbeanus*	*Proniceras neohispanicum*		*Simplisphinctes neuquenensis, Windhauseniceras internispinosum, Co. lotenoense*	*Corongoceras involutum*		*Micracanthoceras, Aulacosphinctes, Haploceras*	
Middle Tithonian		*Ponti/Peroni*	*Pseudolissoceras*	*Volanoceras, Mazatepites, Kossmatia victoris, Pseudolissoceras*		*Aulacosphinctes proximus*	*Aulacosphinctes*		*Aulacosphinctes aff. lauri, Aspidoceras aff. haupti*	*Aulacosphinctes, Uhligites*
		Admirandum / Biruncinatum				*Pseudolissoceras zitteli*	*Kossmatia tenuistriata, Virgatosphinctes denseplicatus*	*Hildoglochiceras*	*Virgatosphinctes denseplicatus*	*Hildoglochiceras, Virgatosphintes denseplicatus*
		Richteri							*Indodichotomoceras sparsicostatum*	*Virgatosphinctes broilii - raja, Aulacosphinctoides*
		Semiforme / Verruciferum								
Lower Tithonian		*Darwini / Alberti-num*	*Parakeratinites*	*M. zitteli*	*V. mendozanus*	*Choicensisphinctes choicensis*	*V. mendozanus*			
				M. symonensis						
		Hybonotum	*Hybonoticeras, Mazapilites*	*Mazapilites*		*„L.“ malarguense*	*Neochetoceras, Katroliceras, Pachysphinctes*		*Aulasimoceras, Katroliceras, Metagravesia*	*Kossmatia, Katroliceras, Hybonoticeras*

Tab.3. Correlation chart of the Tithonian stage embracing southern Europe (Alps) - Northern Africa, Cuba, Mexico, Argentina - Chile, Antarctic Peninsula, Pakistan and Himalaya (after Zeiss & Leanza (2008), modified and supplemented.

& Bachmayer 1989; Zeiss 2001), and in Central América the Simplisphinctes (Paralytohoplites) caribbeanus Zone of Cuba (Myczyński 1989, 1999; Myczyński & Pszczółkowski 1994), which actually is considered as being Upper Tithonian in age (Zeiss & Leanza 2008). As already documented by Tavera (1985: 344), *Corongoceras lotenoense* and other early micracanthoceratids appear in the Simplisphinctes Zone of lowermost Upper Tithonian age in Spain, allowing the age calibration of the Internispinosum Zone in Argentina (see also above).

Based on this evidence, Zeiss & Leanza (2008) stated the reintegration of the Internispinosum Zone (with *Wichmanniceras*) in the lowermost Upper Tithonian, as had been correctly proposed by A.F. Leanza (1945) more than 60 years ago. Therefore, the late Middle Tithonian age for the Internispinosum Zone, first proposed by Arkell (1956) followed by Leanza (1980) and later by Parent (2003b) and Parent et al. (2007), cannot be maintained.

Phylogenetic considerations

The subfamily Windhauseniceratinae, with its tribes Windhauseniceratini and Catutosphinctini, is considered to be a descendant of the subfamiliy Virgatosphinctinae and is included in the family Ataxioceratidae Buckman (Callomon in Donovan et al. 1981: 150). Together with the Paraulacosphinctinae and Pseudosubplanitinae, they represent the last ataxioceratid offspring in the geological record of the Tethyan and Indopacific regions. In the case of the Andean ammonite fauna, it stratigraphically overlies the haploceratid *Pseudolissoceras zitteli* and the himalayitids *Aulacosphinctes proximus* (Steuer) and *Corongoceras* cf. *praecursor* Zeiss, faunal assemblages considered to be Middle Tithonian in age (Barthel 1962; Zeiss 1968, 2001; Leanza 1980, among others)

Most striking is a certain resemblance of some genera of ataxioceratids of the Tethyan Late Kimmeridgian Beckeri Zone and Early Tithonian Hybonotum Zone of southern Germany (Dimke & Zeiss 1997; Zeiss et al. 1996; Schweigert & Zeiss 1999) to those of the fauna here described. This can be observed especially between the genera *Lithacoceras*/*Euvirgalithacoceras* and *Zapalia* and between *Hegovisphinctes* and *Mapuchesphinctes*, as has been already mentioned in the taxonomic part. But again, the Andean ammonite assemblages described here overlie the Pseudolissoceras horizons and are late Middle Tithonian to early Upper Tithonian in age; therefore we consider them as heterochroneous homeomorph developments within the Ataxioceratidae.

As already noticed by Leanza (1996), strong similarities exist also between the Iraqui Kurdistán Chia Gara Formation and the Vaca Muerta Formation both in lithology and ammonite succession. According to Howarth (1992), *Phanerostephanus* Spath 1950 and its close allies *Nothostephanus* Spath, 1950 and *Nannostephanus* Spath, 1950 occur at the base of the Tithonian Stage. Leanza (1996) pointed out the affinities existing between the group of *Phanerostephanus* and its allies with the Early Tithonian genus *Choicensisphinctes* Leanza, 1980. Also Zeiss & Schweigert (1999) made interesting comments on *Notostephanus* while describing *Lithacoceras nothostephanoides* Zeiss & Schweigert from the youngest Kimmeridgian (Ulmense Subzone) of the southwestern Swabian Alb (Germany). Most relevant to this study is the presense of the genus "*Phanerostephanus*" (cf. Howarth 1992: pl. 1, figs. 7-8) above the *Pseudolissoceras* beds, which is considered as a coeval equivalent of the genus *Zapalia* Leanza & Zeiss (cf. Leanza 1996).

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