Upper Bathonian ammonites from Chacay Melehué (Neuquén Basin, Argentina) and the chronostratigraphy of the Steinmanni Zone

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Abstract. It is here presented the study of a collection of Upper Bathonian ammonites sampled bed-by-bed from a new section of Chacay Melehué (Neuquén Basin, Argentina). Most of the specimens are macroconch females moderately well preserved, belonging to the following genera: *Oxycerites*, *Alcidellus*, *Choffatia*, *Neuqueniceras*, *Iniskinites*, *Stehnocephalites*, *Lilloettia*, and *Eurycephalites*. The new species *Choffatia irregularis* and *Eurycephalites belgranoi* are described. The microconch of *Iniskinites crassus* is described for first time. From the occurrence of ammonites very close to *Eurycephalites gottschei* the stratigraphic range of the genus is extended downwards into the upper part of the Steinmanni Subzone. The Steinmanni Zone is subdivided in two new standard subzones: Steinmanni Subzone and Gerthi Subzone. The base of this latter is the *crassus* Hz. (emended).
Key words: Upper Bathonian ▪ Steinmanni Zone ▪ Ammonoidea ▪ Neuquén Basin ▪ Chacay Melehué.

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Resumen. **Amonites del Bathoniano Superior de Chacay Melehué (Cuenca Neuquina, Argentina) y la cronoestratigrafía de la Zona Steinmanni**. Se presenta el estudio de una colección de amonites del Bathoniano Superior obtenida mediante un muestreo capa por capa de una nueva sección de Chacay Melehué (Cuenca Neuquina). La mayoría de los amonites son hembras macroconchas bien preservadas asignables a especies de los géneros: *Oxycerites, Alcidellus, Choffatia, Neuqueniceras, Iniskinites, Stehnocephalites, Lilloettia,* y *Eurycephalites*. Se describen dos nuevas especies: *Choffatia irregularis* y *Eurycephalites belgranoi*. El macho microconcha de *Iniskinites crassus* es descripto por primera vez. A partir de la ocurrencia de amonites muy cercanos a *Eurycephalites gottschei* en la parte alta de la Zona Steinmanni, el rango estratigráfico del género se extiende notablemente. La Zona Steinmanni es subdividida en dos subzonas estándar: Subzona Steinmanni y Subzona Gerthi. La base de esta última es el Horizonte *crassus* (enmendado).
Palabras clave: Bathoniano Superior ▪ Zona Steinmanni ▪ Ammonoidea ▪ Cuenca Neuquina ▪ Chacay Melehué.

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INTRODUCTION

The Neuquén Basin (Fig. 1) has a vast record of Jurassic ammonitiferous rocks. The well known locality Chacay Melehué comprises a relatively large area showing extensive Middle to Upper Jurassic outcrops (Fig. 2). The stratigraphy and the ammonite fauna of the Toarcian-Callovian Los Molles Formation in Chacay Melehué have been studied by many authors (e.g., Keidel 1910, Stehn 1923, Groeber 1953, Stipanicic 1965, Westermann 1967, Zöllner & Amos 1973, Riccardi et al. 1989, Riccardi & Westermann 1991a-b, Parent 1997, 1998). The Andean chronostratigraphy of the Upper Bathonian-Upper Callovian interval (Fig. 3) is rather well established in its essential terms (see Hillebrandt 1970, Gröschke & Hillebrandt 1985, 1994, Riccardi et al. 1989, Hillebrandt & Gröschke 1995, Parent 1998, Hillebrandt et al. 2000, Parent & Garrido 2015 and references therein), providing a convenient framework for improving and expanding the knowledge of the fauna along with the refinement by identifying ammonite biohorizons. However, the Upper Bathonian-Lower Callovian deposits of the Chacay Melehué area are exposed in an extensive area and are locally very fossiliferous, so that it will take much time until a comprehensive, detailed knowledge of the whole ammonite fauna is attained. Indeed, almost every new collection (sample), no matter the size, provides new significant information with new morphotypes of known species or new forms attributable to new species. Additional collections sometimes indicate the latter forms to be variants or transients of known species from previously not sampled horizons. This situation is well known in many other time intervals and regions of the world (e.g., Callomon 1985a, Westermann & Callomon 1988, Jakobs et al. 1994, Scherzinger et al. 2015, 2018).

In this paper we present the results of the study of a recent bed-by-bed collection of ammonites from a new Upper Bathonian (upper Steinmanni Zone) section of the Los Molles Fm at Chacay Melehué. The stratigraphy is based on a recent geological survey of the study area (Fig. 2). The ammonite collection has produced much new information, including first descriptions of new species as well as records of others which had remained poorly known. Furthermore, the study improves knowledge on the classification and evolution of already known taxa. In addition to the dominant East Pacific Eurycephalitinae, the fauna includes perisphinctids and oppeliids which are concentrated in few scattered levels. The taxonomic composition of the assemblages and their modes of preservation are analyzed in the framework of the lithology and palaeogeography of the study area.

The following stratigraphic units are distinguished throughout the text: (a) biozone, a body of rock characterized by its fossil content; (b) chronostratigraphic zone, a sheet of rock (one or more strata) bounded by two time-planes and recognized by its fossil content; (c) standard chronostratigraphic zone, a chronostratigraphic zone defined only by an ammonite biohorizon at its base, thus forming a succession of standard zones without gaps or overlaps; and (d) ammonite horizon or biohorizon (Hz.), a bed or series of beds characterized by a fossil assemblage within which no further stratigraphical differentiation of fauna can be distinguished. Thus, biohorizons as the shortest distinguishable biostratigraphic subdivision, must be considered time-planes, and in this sense they are the base for the elaboration of a chronostratigraphic classification from the biostratigraphy of the fossil successions.

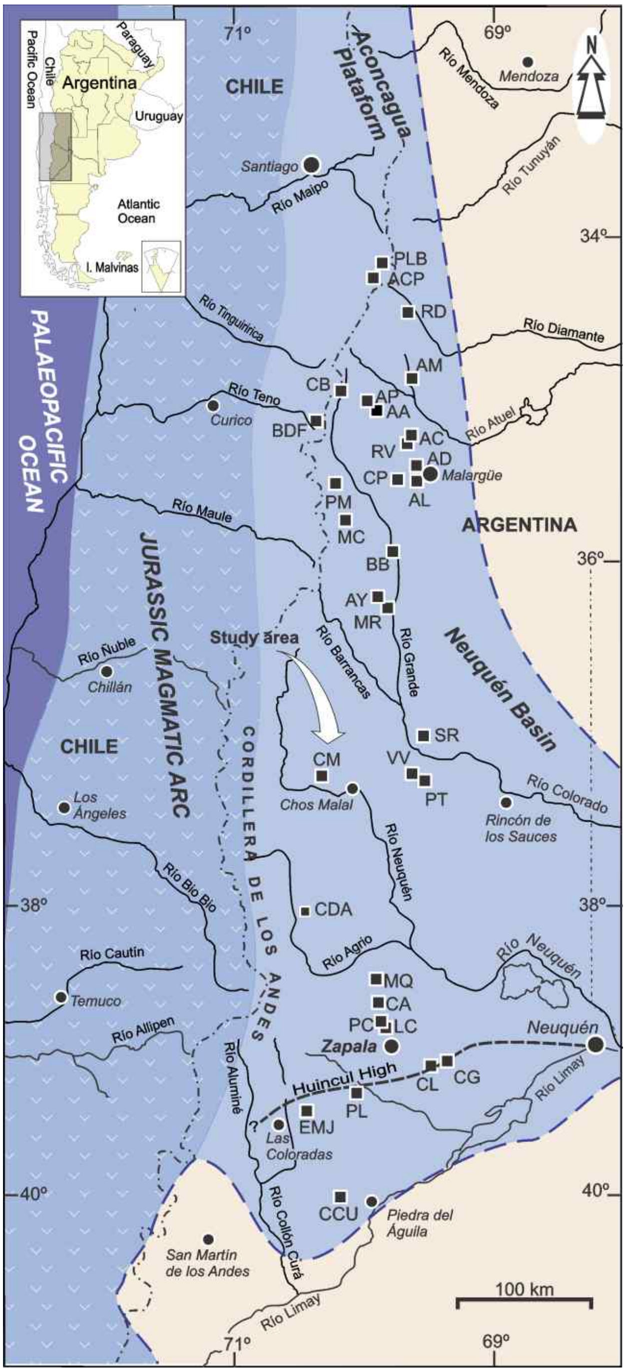
Biohorizons are the empirical, observable links between chrono- and biostratigraphy. Further discussion about the meaning and nomenclature of these units can be found in, e.g., Gabilly (1971), Mouterde et al. (1971), Callomon (1985a-b, 1995), Cariou & Hantzpergue (1997), Garrido & Parent (2013), Parent et al. (2015), Schweigert (2015).

STRATIGRAPHY

The studied section. The studied section (Fig. 4) consists of a succession of black shales and marls belonging to the Los Molles Fm., exposed in the cliffs at the right side of the Chacay Melehué stream, about 2 km north of the hill Loma Baya (Fig. 2A). It is a monotonous succession of black shales with calcareous concretions, becoming more calcareous through the upper part, close to the base of the Gottschei Zone. The total observed thickness is 64.6 m, which includes from below: (1) the upper part of the Steinmanni Subzone (new), 7.7 m; (2) the Gerthi Subzone (new), 43.7 m; and (3) a basal part of the Gottschei Zone, 13.2 m.

There are several concretionary levels with many of the calcareous concretions containing ammonites, usually very well preserved and complete. All throughout the succession more or less thin beds of fine, whitish tuffaceous sandstones are intercalated (Fig. 5). This volcanic material undoubtely originated in the western volcanic arc as indicated by the facies distribution and basin geometry (Fig. 6): a steep western slope (close to the volcanic arc) towards the depocentre, slowly shallowing eastwards through the slope towards the distal platform (see details in Digregorio & Uliana 1980, Digregorio et al. 1984, Gulisano & Gutierrez 1995, Legarreta & Uliana 1996, Franzese et al. 2003, Howell et al. 2005).

The sequence gives the impression of being very "continuous" up to the level of the bedding plane. Nevertheless, detailed observations show the existence of many discontinuity surfaces indicating non-sequences, mainly in shale beds. In these beds the upper sides of the ammonites are eroded, the bodychamber is well preserved and the phragmocone poorly preserved or replaced by calcite and shale (Fig. 5). This setting with erosive



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

Figure 1. **A**: Map of the Neuquén Basin superimposed on the Recent geogragphy with indication of the study area, the Chacay Melehué (CM) locality, and other important localities with Middle and Upper Jurassic outcrops.

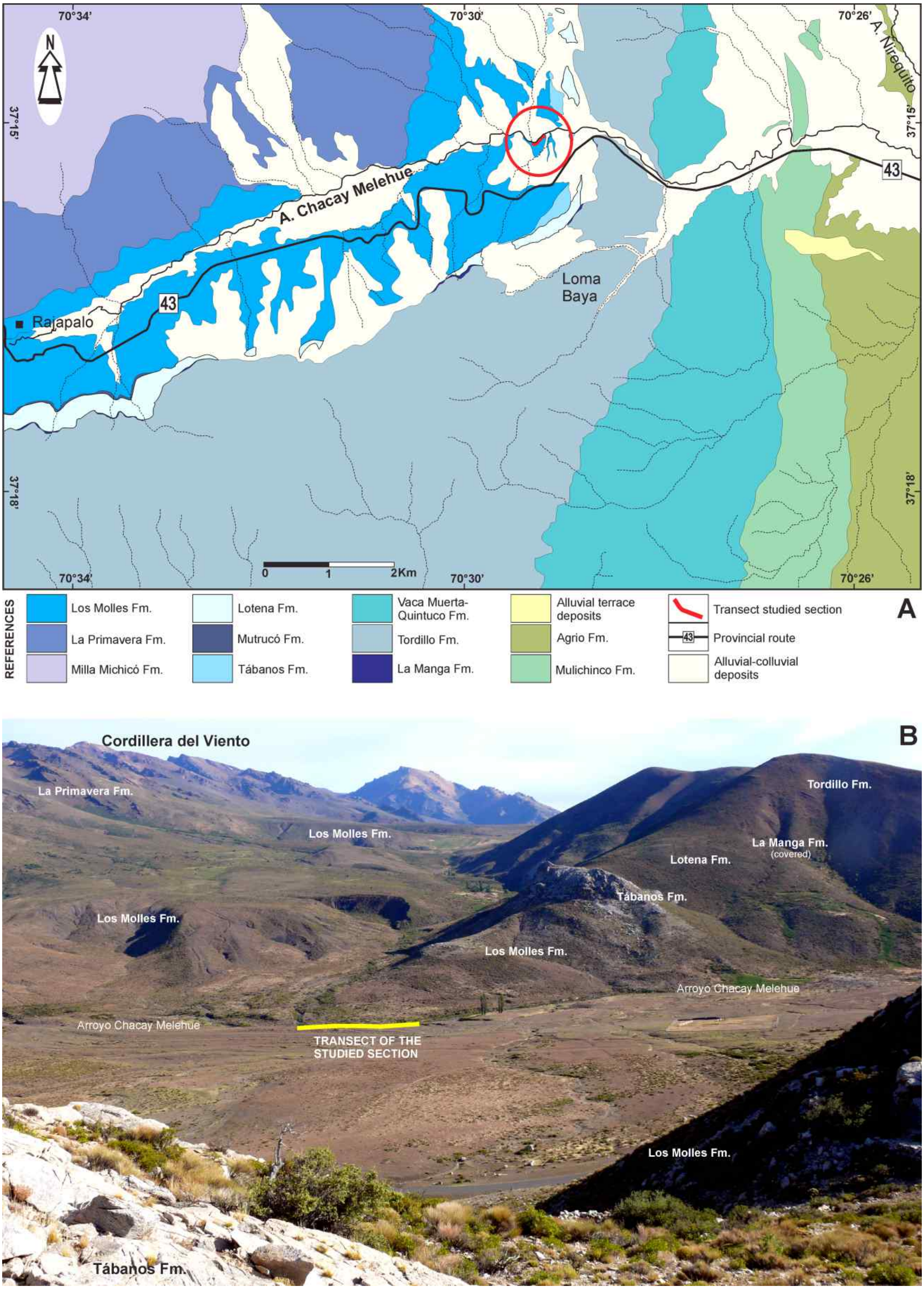


Figure 2. A: Geological map of the study area with location of the studied section (into the red circle). Lithostratigraphy according to Dellapé et al. (1979), Garrido & Parent (2013), Parent et al. (2019b), and our new observations made for a more general survey of the region. The Mutrucó Fm (Garrido & Parent 2013) occurs as conglomerates eroding partially or totally the gypsiferous Tábanos Fm in some areas, especially towards the western border of the basin. These conglomerates have been mapped as part of the base of the Lotena Fm by Leanza & Hugo (2004). **B**: Panoramic (northern) view of the study area.

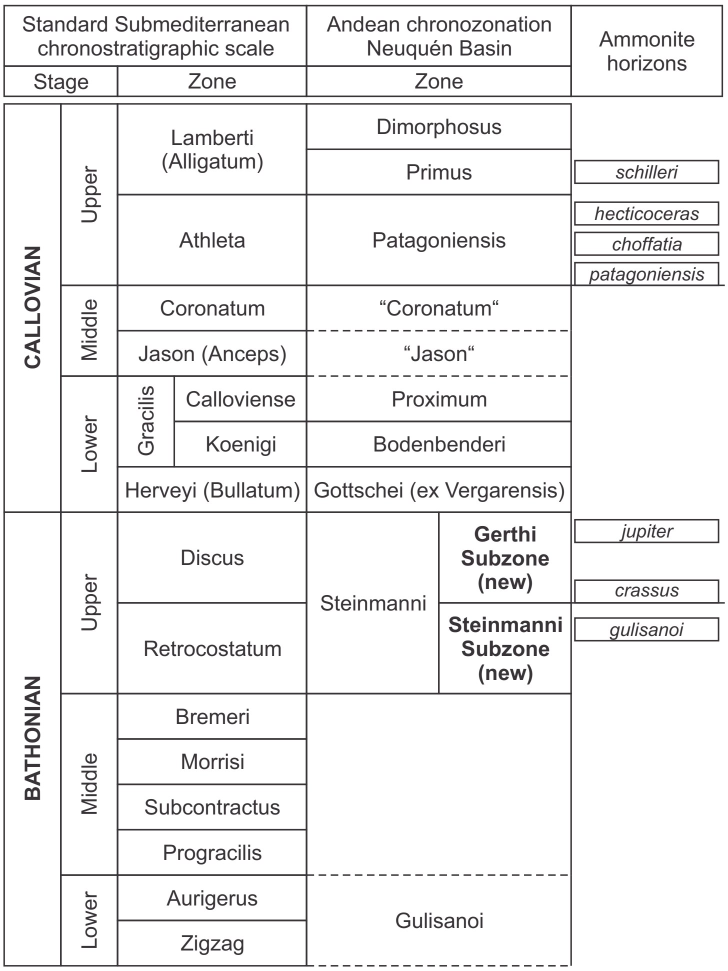


Figure 3. Andean chronostratigraphic zonation of the Bathonian-Callovian interval in the Neuquén Basin, time-correlated approximately with the Submediterranean zonation; updated from Parent & Garrido (2015) with the new Steinmanni and Gerthi subzones, and the *gulisanoi* and *crassus* emended biohorizons. Solid lines indicate the base of standard zones and subzones. The *schilleri*, *hecticoceras*, *choffatia*, and *patagoniensis* horizons (Upper Callovian) have been recognized in southern (Picún Leufú, Manzano Escondido) and northern (Vega de la Veranada, Chacay Melehué) localities of the Neuquén Basin (see Parent 2006, Garrido & Parent 2013, Parent & Garrido 2015). The *crassus* Hz. and the *gulisanoi* Hz. (Upper Bathonian) have not been recognized yet outside their type locality Chacay Melehué. The *jupiter* Hz., whose type locality is Caracoles (northern Chile-southern Bolivia) has been recognized in Cordillera Domeyko, northern Chile (Hillebrandt 1970, Gröschke & Hillebrandt 1985) and in the study area at Chacay Melehué (Riccardi et al. 1989). See text for further explanation.

discontinuities, pointing to gaps in the record, indicates erosional to non-depositional episodes. However, such a situation seems to be normal and expected in shale successions where the preserved rocks represent only a small part of the time actually elapsed during the accumulation of the sediments. A state frequently quoted as "more gap than record" (e.g., Ager 1973, Trabucho-Alexandre 2014, Bailey 2017).

Faunal succession. The studied section was divided into 47 levels of which 20 yielded ammonites. These ammonite-bearing levels occur scattered throughout the succession, separated by rather long, unfossiliferous intervals (Fig. 4: fossiliferous spectrum). Interestingly, the only macrofossils recorded from the succession are ammonites. In general, the fossiliferous levels are not very rich in individuals and poor in species, with the notable exception of the richest level CM-35 (Fig. 4: number of species per level). The recorded associations of species are depicted in Table 1. The chronostratigraphic meaning of the associations is discussed in the last chapter.

In the Gerthi Subzone (new, levels CM-6b to CM-37) 11 species have been recorded (Fig. 4), which is a moderately high number. However, the distribution of these occurrences is uneven. The diversity is low in most levels (one or two species), slightly higher in level CM-6b (3 species, *crassus* Hz.), and highest in level CM-35 (7 species, *jupiter* Hz.?). A very similar number of species for the part or the succession equivalent to the Gerthi Subzone (see discussion below) was (nominally) listed by Riccardi & Westermann (1991a: 11) but with no details.

The succession is dominated by eurycephalitines, which occur in every fossiliferous level with the exception of levels CM-3 and CM-8 where only oppeliids and/or perisphinctids have been found. In level CM-35 perisphinctids and oppeliids occur associated with abundant *Stehnocephalites gerthi*. These isolated occurrences of perisphinctids and/or oppeliids concentrated in few specific levels are an

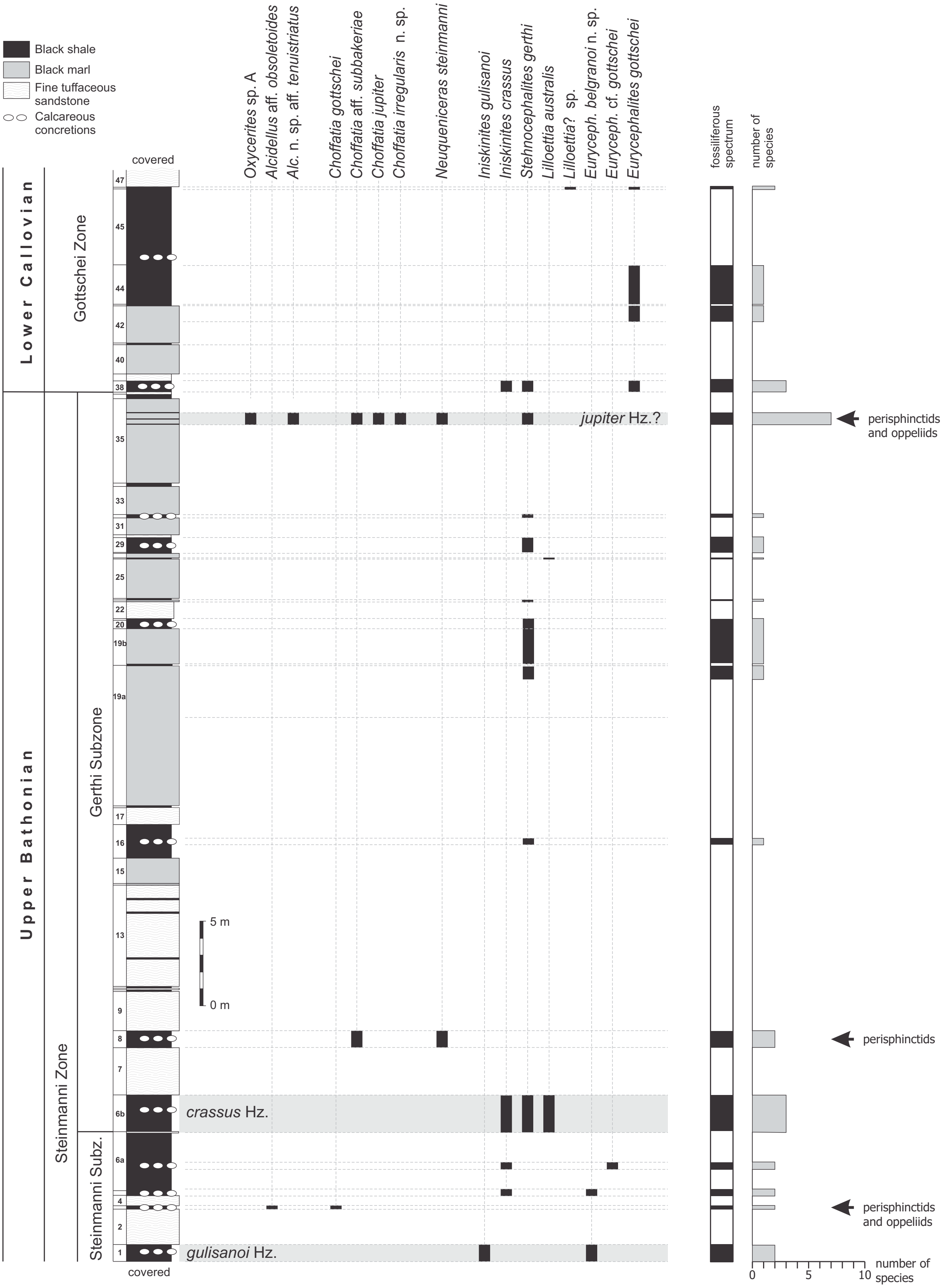
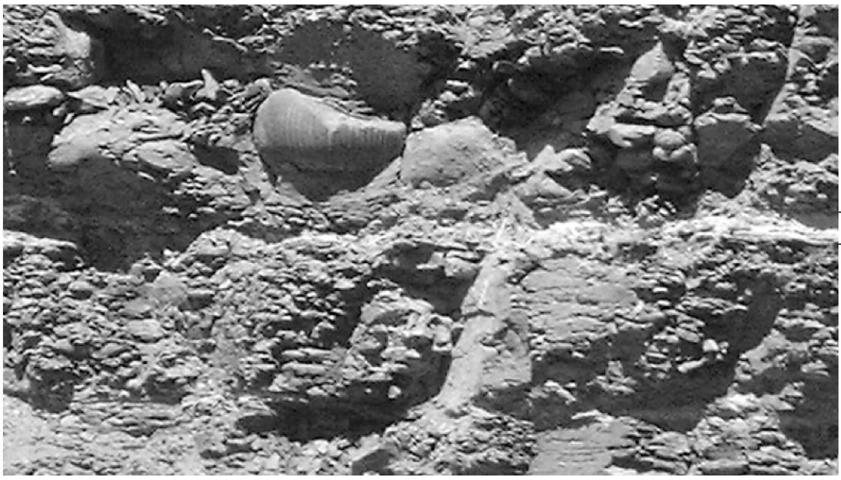


Figure 4. Studied section of the Los Molles Fm (pars) at Chacay Melehué showing the ammonite occurrences (solid bars), local zonation and ammonite horizons based on Fig. 3. At the right side the features of the ammonite record discussed in the text: the fossiliferous spectrum (white: non-fossiliferous levels; black: levels with ammonites), species diversity as number of species per level. See Table 1 for ammonite associations. The only three levels where oppeliids and/or periphinctids occur are marked.

Table 1. Stratigraphic distribution of the ammonites with the distribution of the occurrences per subfamily summarized at right columns. Levels indicated as NF are non-fossiliferous. In the last right column are indicated the occurrences of oppeliids (O) and/or perisphinctids (P).

Zone / Subzone	Level	Species	Oppeliinae	Grossouvrinae	Neuqueniceratinae	Eurycephalitinae	Events
Gottschei Zone	CM - 47	NF					
	CM - 46	*Eurycephalites gottschei* [M&m], *Lilloettia*? sp.				■	
	CM - 45	NF					
	CM - 44	*Eurycephalites gottschei* [M&m]				■	
	CM - 43	NF					
	CM - 42	*Eurycephalites gottschei* [M&m]				■	
	CM - 41	NF					
	CM - 40	NF					
	CM - 39	NF					
	CM - 38	*Stehnocephalites gerthi* [M], *Iniskinites crassus* [M], *Eurycephalites gottschei* [M]				■	
Steinmanni Zone, Gerthi Subzone	CM - 37	NF					
	CM - 36	NF					
	CM - 35	*S. gerthi* [M], *Oxycerites* sp. A [M], *Alcidellus* n. sp. aff. *tenuistriatus* [M], *Choffatia* aff. *subbakeriae* [M], *C. jupiter* [M], *C. irregularis* n. sp. [M], *Neuquen. steinmanni* [M&m]	■	■	■	■	PO-II
	CM - 34	NF					
	CM - 33	NF					
	CM - 32	*Stehnocephalites gerthi* [M&m]				■	
	CM - 31	NF					
	CM - 30	NF					
	CM - 29	*Stehnocephalites gerthi* [M]				■	
	CM - 28	NF					
	CM - 27	NF					
	CM - 26	*Lilloettia australis* [M]				■	
	CM - 25	NF					
	CM - 24	NF					
	CM - 23	*Stehnocephalites gerthi* [M]				■	
	CM - 22	NF					
	CM - 21	NF					
	CM - 20	*Stehnocephalites gerthi* [M]				■	
	CM - 19b	*Stehnocephalites gerthi* [M]				■	
	CM - 19a	*Stehnocephalites gerthi* [M]				■	
	CM - 18	NF					
	CM - 17	NF					
	CM - 16	*Stehnocephalites gerthi* [M]				■	
	CM - 15	NF					
	CM - 14	NF					
	CM - 13	NF					
	CM - 12	NF					
	CM - 11	NF					
	CM - 10	NF					
	CM - 9	NF					
	CM - 8	*Choffatia* aff. *subbakeriae* [M], *Neuqueniceras steinmanni* [M]		■	■		P
	CM - 7	NF					
	CM - 6b	*Iniskinites crassus* [M], *Lilloettia australis* [M], *Stehnocephalites gerthi* [M]				■	
Steinmanni Zone, Steinmanni Subz.	CM - 6a	*Iniskinites crassus* [M], *Eurycephalites* cf. *gottschei* [M]				■	
	CM - 5	*Iniskinites crassus* [M], *Eurycephalites belgranoi* n. sp. [M]				■	
	CM - 4	NF					
	CM - 3	*Alcidellus* aff. *obsoletoides* [M], *Choffatia* aff. *subbakeriae* [m?]	■	■			PO-I
	CM - 2	NF					
	CM - 1	*Iniskinites gulisanoi* [M], *Eurycephalites belgranoi* n. sp. [M]				■	



level CM-38 Black shales with calcareous concretions showing a macroconch specimen of *Stehnocephalites gerthi* [M] eroded equatorially

level CM-37 Fine, tuffaceous sandstone

level CM-36 Black shales with no fossils

Figure 5. Close-up view of level CM-38 showing an adult macroconch of *Stehnocephalites gerthi* eroded equatorially, above the thin level CM-37 of very tuffaceous, fine sandstone.

interesting phenomenon which can be discriminated only by sampling under high stratigraphic control, otherwise these occurrences are hidden in collections from thicker, undivided intervals consisting of several levels. However, this kind of sampling has produced for the present study few specimens in most levels, whereas a fine study of the diversity dynamics would need larger samples. Under these circumstances we can only assume that the occurrence of only oppeliids and/or perisphinctids in some few levels is significant with respect to the absence of spherocones there, considering the greater abundance of spherocones through most of the section. On the other hand, the sample from level CM-35, collected with the same effort of sampling, contains plenty of specimens of the three morphotypes together (see Table 1 and Fig. 4).

Mode of occurrence and preservation. The fossiliferous levels are relatively thin, intercalated between thicker levels without fossils, representing barren intervals. Almost all the ammonites are adult macroconchs, especially in the Gerthi Subzone (new; levels CM-6b to CM-37), where only two specimens are microconchs (complete adults of *S. gerthi* and *N. steinmanni*). The preservation and mode of occurrence are not the same throughout the succession. There are several concretionary levels from which many concretions contain ammonites, usually complete and well preserved. All throughout the succession the ammonites lay in horizontal position. In the more calcareous, marly beds the ammonites are nearly complete, mostly with the phragmocone moderately to well preserved. From levels CM-6b and CM-19b specimens of *I. crassus* and *S. gerthi* with the last whorl of the phragmocone collapsed were collected, whereas their bodychambers are intact. In level CM-35 many ammonites, mostly the perisphinctids, are preserved as bodychambers with the phragmocones collapsed or missing. These features characterize the fossil record of the levels CM-1 to CM-35 (upper Steinmanni and Gerthi subzones) with ammonite assemblages dominated by adult macroconchs occurring in thin levels separated by long barren intervals. In the shale levels CM-38 to CM-46 in the uppermost part of the section (base of the Gottschei Zone), the preservation is quite different with most of the ammonites being crushed.

There is a number of possible explanations given by Westermann (1996: 659; see also Callomon 1981, 1985a) for similar settings. The present observations suggest synchronized spawning events with dead animals and empty shells drifting for several kilometers from (eastern) shallower areas (platform) to the slope and depocentre (west) where they became embedded.

Taphonomy. As indicated above, the succession is dominated by eurycephalitines with sporadic occurrences of oppeliids and/or perisphinctids (Table 1, Fig. 4). The location of the biotopes can be inferred from the postulated habitats for the different ammonite morphotypes as they were highly dependent of their shell-shape (e.g., Ziegler 1967, 1980, Cecca 1992; recent reviews by Westermann 1996, Hoffmann et al. 2015, Naglik et al. 2015, Lukeneder 2015). The principal habitats according to shell-shape were discussed in detail by Westermann (1996). According to his models (Westermann 1996: figs 1, 14) the three main morphotypes –serpenticone, spherocone, oxycone– should have had rather well delimited biotopes in epeiric seas like the Neuquén Basin. The more or less inflated serpenticonic ammonites belonging to *Choffatia* and *Neuqueniceras* and the oxyconic *Oxycerites* and *Alcidellus* would have been mostly demersal (nekto-benthonic) in shallow areas, the oxycones would have lived somewhat deeper. The spheroconic ammonites (*Lilloettia*, *Eurycephalites*, *Iniskinites*, and *Stehnocephalites*) would have been vertical-migrants (partially planktonic and nekto-benthic) in deeper waters and/or open areas. This correlation of the habitat with the shell-shape is strongly supported by the distribution of the morphotypes of a single highly variable species along depth gradients demonstrated from reliable data by Wilmsen & Mosavina (2011).

According to the palaeogeography of the Neuquén Basin (see above), Figure 6 shows a model for the distribution of the presently studied ammonoids in their respective assumed habitats, that is the location of the main biotopes. The drifting and sinking of dead cephalopods and their shells are represented by the gray arrows which are derived from the model of Maeda & Seilacher (1996). Drifting and sinking of dead animals and shells are mainly determined by the depth at which the animal died with respect to the "depth

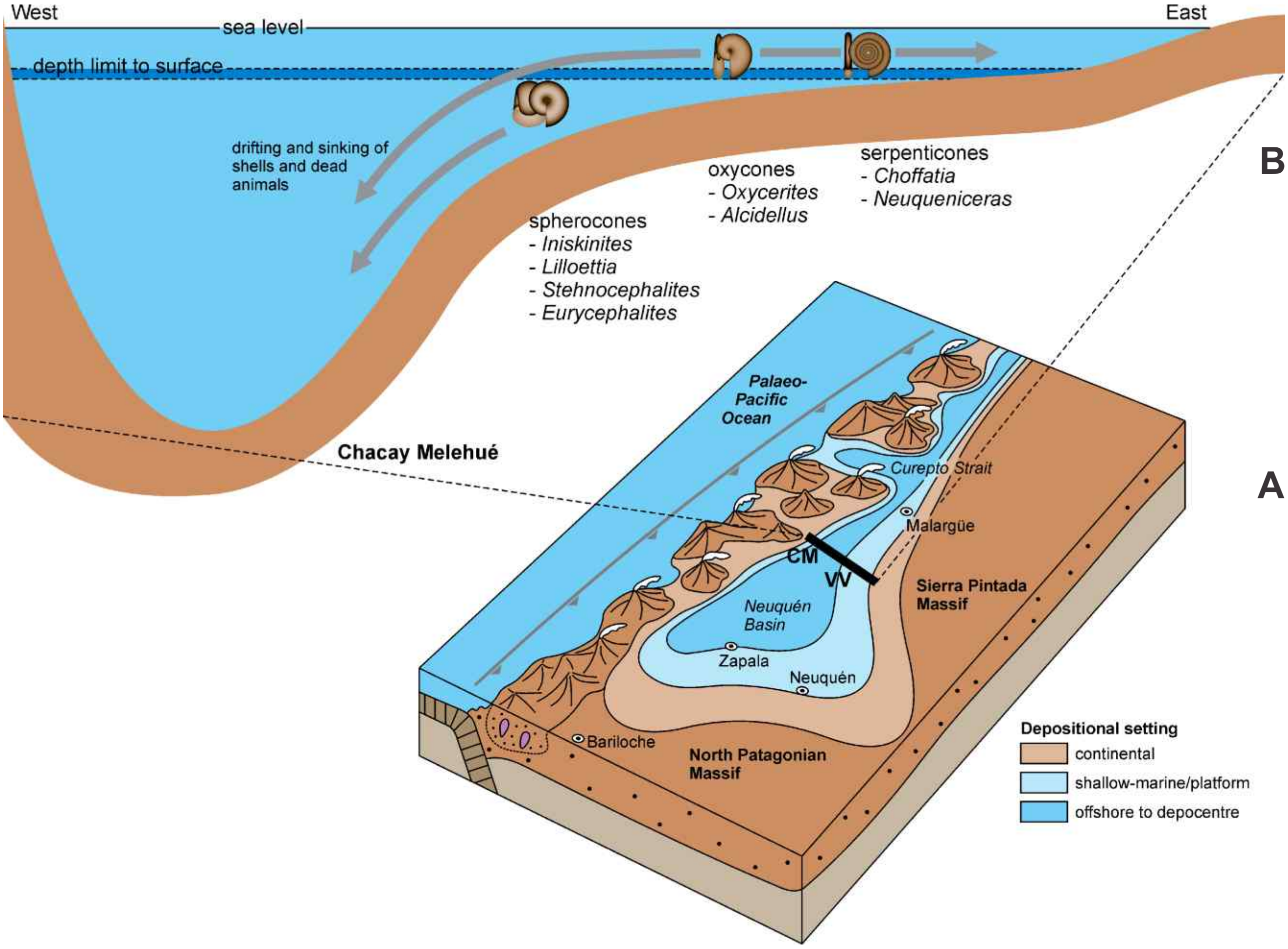


Figure 6. A: Palaeogeographic reconstruction for the Neuquén Basin during the Middle Jurassic (modified after Howell et al. 2005, Vicente 2005, Parent 2006). **B**: Biocoenoses model for the Late Bathonian in the Chacay Melehué (depocentre)-Vega de la Veranada (platform) transect indicated CM-VV in A. Schematic representation of the distribution of the inferred biocoenoses during the times of accumulation of the deposits of the Gerthi Subzone (new), upper Steinmanni Zone, Los Molles Fm at Chacay Melehué (studied section). The depth limit to surface depends mainly of the hydrostatic pressure in the point at which the animal died. Not in scale.

limit to surface" (DLS, determined mainly by hydrostatic pressure). Since oxycones (*Oxycerites* and *Alcidellus*) and serpenticones (*Choffatia* and *Neuqueniceras*) would have inhabited relatively shallow waters, thus rather far from the studied area, they would have died normally above the DLS, thus reaching longer distances (as empty shells) than spherocones (as dead animals) which would have died mostly below the DLS drowning much sooner.

Nevertheless, this drifting should have been a regular process - transporting dead shells into the deeper parts of the basin constantly, but the occurrence of oppeliids and perishinctids in the sampled taphocoenoses does not show this regularity (Fig. 4). If marine currents and other processes transported the dead shells into the study area, then this should have happened more constantly - leading to a more regular distribution of shallow-water ammonites in the section. At least three possible and non-exclusive factors could have been determinant to the configuration of the actual fossil record: (1) it is possible that oppeliids and perisphinctids did not live permanently in the area, (2) storm events, and (3) size of the populations, the abundance of collected specimens of spherocone species suggest the populations of eurycephalitines should have been the larger. The composition of the sample of level CM-35 (Table 1) including abundant representatives of the three morphotypes, suggest that it is possible that in fact exceptional storm events led to the transport of shallow-water ammonite shells into deeper water where they formed beds concentrated with these allochthonous forms. The absence of bivalve shells or other shallow-water organisms might indicate that the storm waves transported drifting shells and not transported hardparts/shells, which were already deposited on the sea floor. However, none of these situations explain the absence of spherocones in the levels where only oppeliids and/or perisphinctids occur. In order to reach a more consistent and complete explanation for the formation of the actual fossil record it seems necessary that more studies of high stratigraphic resolution in other sections of the transect Chacay Melehué-Vega de la Veranada are conducted (Fig. 6).

These inferences are based on the presented, detailed observations with the highest possible stratigraphical resolution. However, they are in agreement with observations of Riccardi et al. (1989: 569) who noted the abundance of forms of *Choffatia* in the Gerthi Subzone (new, formerly "*Stehnocephalites gerthi*" Hz.), naming it as the

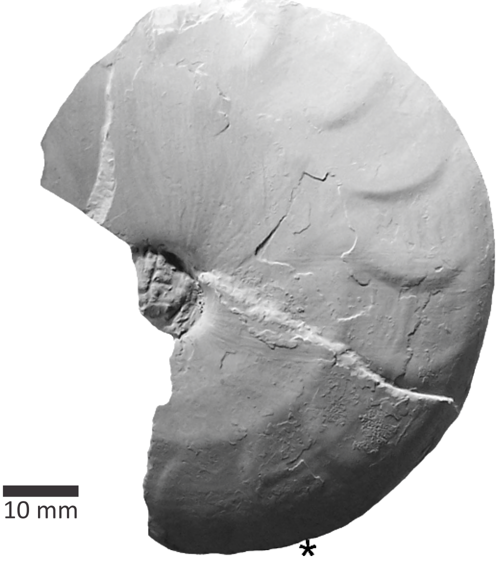


Figure 7. *Oxycerites* sp. A. Adult macroconch bodychamber (MOZ-PI-7430/3), level CM-35, *jupiter* Hz.?, upper Gerthi Subzone, Steinmanni Zone. – Natural size (x1). Asterisk at last septum.

Choffatia-acme, further noting that it could likely be facies-controlled and so of poor value for biostratigraphic time-correlation. The levels CM-8 and CM-35, which include all perisphinctids of the Gerthi Subzone (new) in the present section, strongly suggest that the *Choffatia*-acme actually corresponds to two (or more) events well separated in time and possibly facies-controlled. However, modelling the formation of the local taphocoenoses on the basis of our biocoenoses model (Fig. 6) needs more studies, mainly from sections located west and east of that herein studied. Outcrops of the Los Molles Fm between Chacay Melehué and Vega de la Veranada (Lajas Fm, see below) have not been reported, since it is mainly covered in this transect. Some kilometers east of the present section, yet far west from Vega de la Veranada, there are only few small outcrops of the Los Molles Fm, consisting of black shales apparently without fossils, except for scarce small bivalves. On the other hand, cursory observations made in sections west of the study area show that the predominant ammonites in levels equivalent to those studied herein belong to the Eurycephalitinae.

SYSTEMATIC PALAEONTOLOGY

The material described is housed at the Museo Provincial de Ciencias Naturales “Prof. Dr. Juan A. Olsacher”, Zapala (MOZ-PI). Bodychamber is abbreviated with Bc and phragmocone with Ph; macroconch (female shell): [M], microconch (male shell): [m]. Measurements: diameter (*D*), diameter at the last adult septum (D_{ls}) and diameter at adult peristome (D_p), all given in millimeters [mm]; umbilical width (*U*), whorl width (*W*), whorl height (H_1), and whorl ventral (or apertural) height (H_2), all given as dimensionless proportions of *D*; length of bodychamber (L_{BC}) in degrees [°]. Number of primary (*P*) and ventral (*V*) ribs per half whorl. These measurements per half whorl are more sensitive to changes in density, and less exigent with quality of material. The biometric features of the shell-shape are given in the form of dimensionless numbers or "indexes", mainly relative to the diameter (*D*) which allow comparisons in a range of sizes. Abbreviations are used in synonymy lists for holotype or lectotype (*), neotype (+), do-not-belong to the species (*n*), and doubtful attribution (*?*). Levels of occurrence of the specimens denoted by the level number in Fig. 4 and the prefix CM (Chacay Melehué). Zones, Subzones, and biohorizons refer to Figs. 3-4 (discussed in the next chapter).

Lists of synonymy are given at length only in the cases where new information and/or changes in attributions with respect to those published are proposed. In the remaining cases we refer to papers where the lists are already published.

Order Ammonitida Fischer, 1882
Suborder Ammonitina Fischer, 1882
Superfamily Haploceratoidea Zittel, 1884
Family Oppeliidae Douvillé, 1890
Subfamily Oppeliinae Douvillé, 1890

Genus *Oxycerites* Rollier, 1909

Type species. *Ammonites aspisoides* Oppel, 1857; by original designation.

Oxycerites sp. A
Fig. 7

Material. One adult macroconch bodychamber (MOZ-PI-7430/3) from level CM-35 (upper part).

Description and remarks. The specimen consists of the final part of the phragmocone and a half-whorl of bodychamber. Oxyconic, compressed lanceolate with high flanks passing indistinctly, with no shoulders into a sharp single keeled venter from the last whorl of adult phragmocone. Strong, well spaced lunuloid ribs originate above a mid-ventral ridge and fade away a little below the keel. The septal suture line, poorly preserved, is finely frilled and complex.

The combination of a sharp, single keeled venter with concave lunuloid ribs, and the complex suture line lead to the assignation to *Oxycerites* rather than to *Alcidellus*. The specimens from the Bodenbenderi Zone of Caracoles, Chile described as *Oxycerites* cf. *oppeli* Elmi, 1967 by Riccardi et al. (1989: 562, pl. 7: 5-7) are more narrowly umbilicate and weakly ornamented. This latter species was reported as *Oxycerites* aff. *oppeli* Elmi, 1967 from younger levels of the studied secion, in the lowermost Middle Callovian "Jason" Zone (Parent et al. 2019b: 40).

The adult macroconch figured by Hahn (1968: pl. 1: 2) as *Oxycerites aspidoides* (Oppel) from the *Aspidoides*-Oolith of Balingen, Germany matches our specimen in size, ornamentation and whorl section. However our incomplete specimen can not be compared more closely for a definite determination.

Occurrence and distribution. The specimen comes from the upper part of level CM-35, Gerthi Subzone (new), Steinmanni Zone (Upper Bathonian); probably *jupiter* Hz.

Genus *Alcidellus* Westermann, 1958

Type species. *Ammonites tenuistriatus* Grossouvre, 1888; by original designation. Krystin (1972: 237) cited the

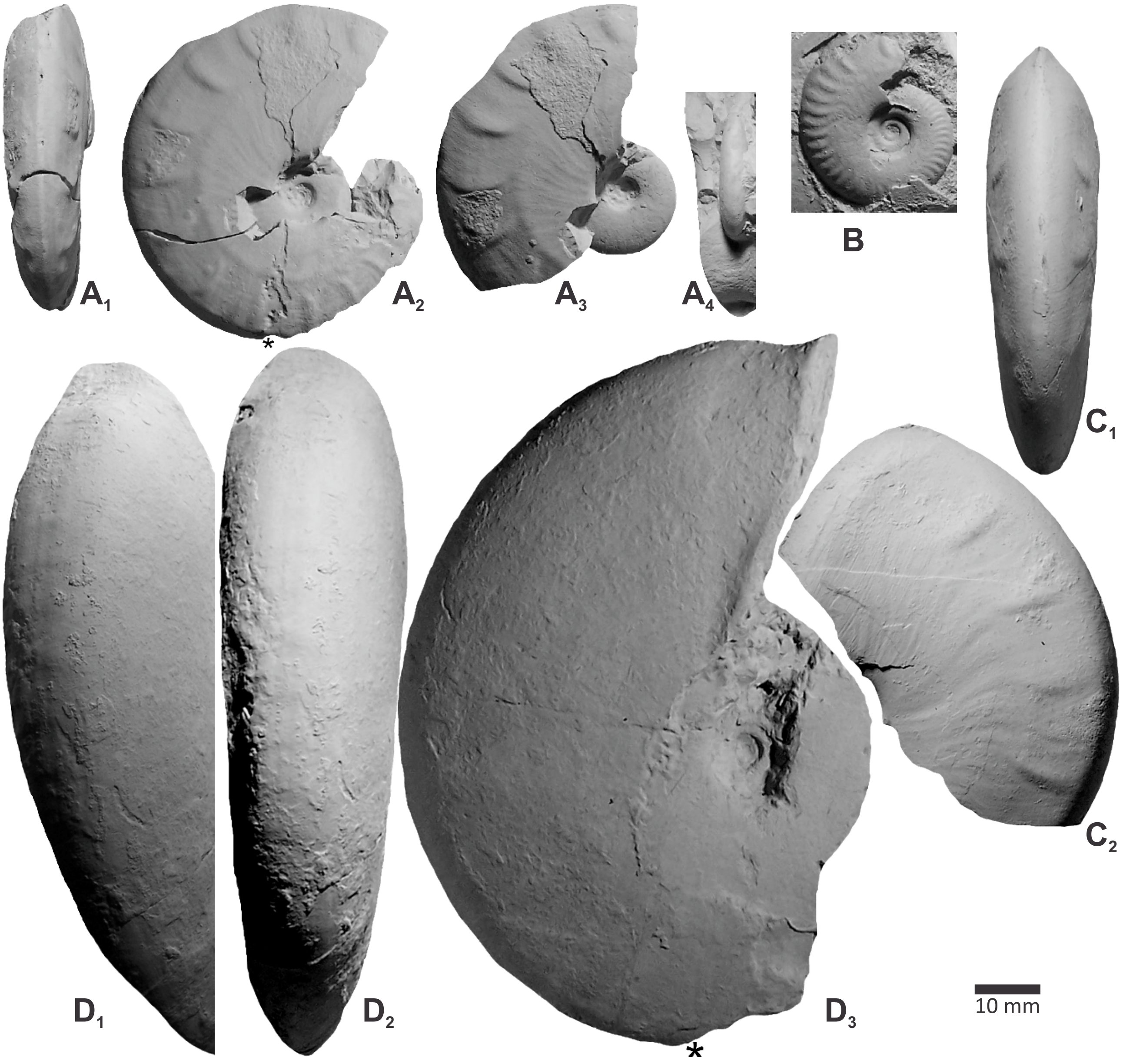


Figure 8. **A**-**B**: *Alcidellus* aff. *obsoletoides* Riccardi, Westermann & Elmi, 1989, level CM-3, Steinmanni Subzone, Steinmanni Zone. **A**: complete adult macroconch (MOZ-PI-7412/1); ventral (A_1) and lateral (A_2) views, A_3: lateral view with last part of the phragmocone removed showing the inner whorls, A_4: ventral view of the inner whorls. **B**: adult macroconch phragmocone (MOZ-PI-7412/3). **C**-**D**: *Alcidellus* n. sp. aff. *tenuistriatus* (Grossouvre, 1888), level CM-35, Gerthi Subzone, Steinmanni Zone. **C**: adult macroconch beginning of bodychamber (MOZ-PI-7430/4), C_1: ventral view showing a weak tricarination, C_2: lateral view showing distant lunuloid ribs on the upper flank. **D**: adult macroconch with peristome (MOZ-PI-7430/7); D_1-D_2: ventro-lateral and ventral views of the bodychamber showing ventral tabulation; D_3: lateral view, note the wide and shallow constriction preceding the flared peristome. – All natural size (x1). Asterisk at last septum.

specimen figured by Grossouvre (1888: pl. 4: 7) as holotype, but Grossouvre did not designate a holotype from the two specimens he considered belonging to the species. Thus, it should be considered as a lectotype what seems to have not been done yet. In this case we designate as lectotype of *Ammonites tenuistriatus* the specimen figured by Grossouvre (1888: pl. 4: 7).

Remarks. *Alcidellus* includes macroconchs which are distinguished from those of *Oxycerites* by the simpler septal suture and the tricarinate (or sub-tricarinate) venter becoming more or less broadly rounded in the bodychamber. Most of the many specimens of the genus in literature are preserved without or with only parts of the bodychamber, and the tricarination may be very blunt or even inconspicuous in many cases (e.g., Krystin 1972: pl. 4: 3; Westermann & Callomon 1988: pl. 2: 2-3). *Alcidellus* is frequently considered a subgenus of *Oxycerites*. However, these taxa have been discussed at length by Westermann & Callomon (1988), who have concluded that *Oxycerites* and *Alcidellus* are two parallel but independent lineages. This latter interpretation is followed by the present authors and

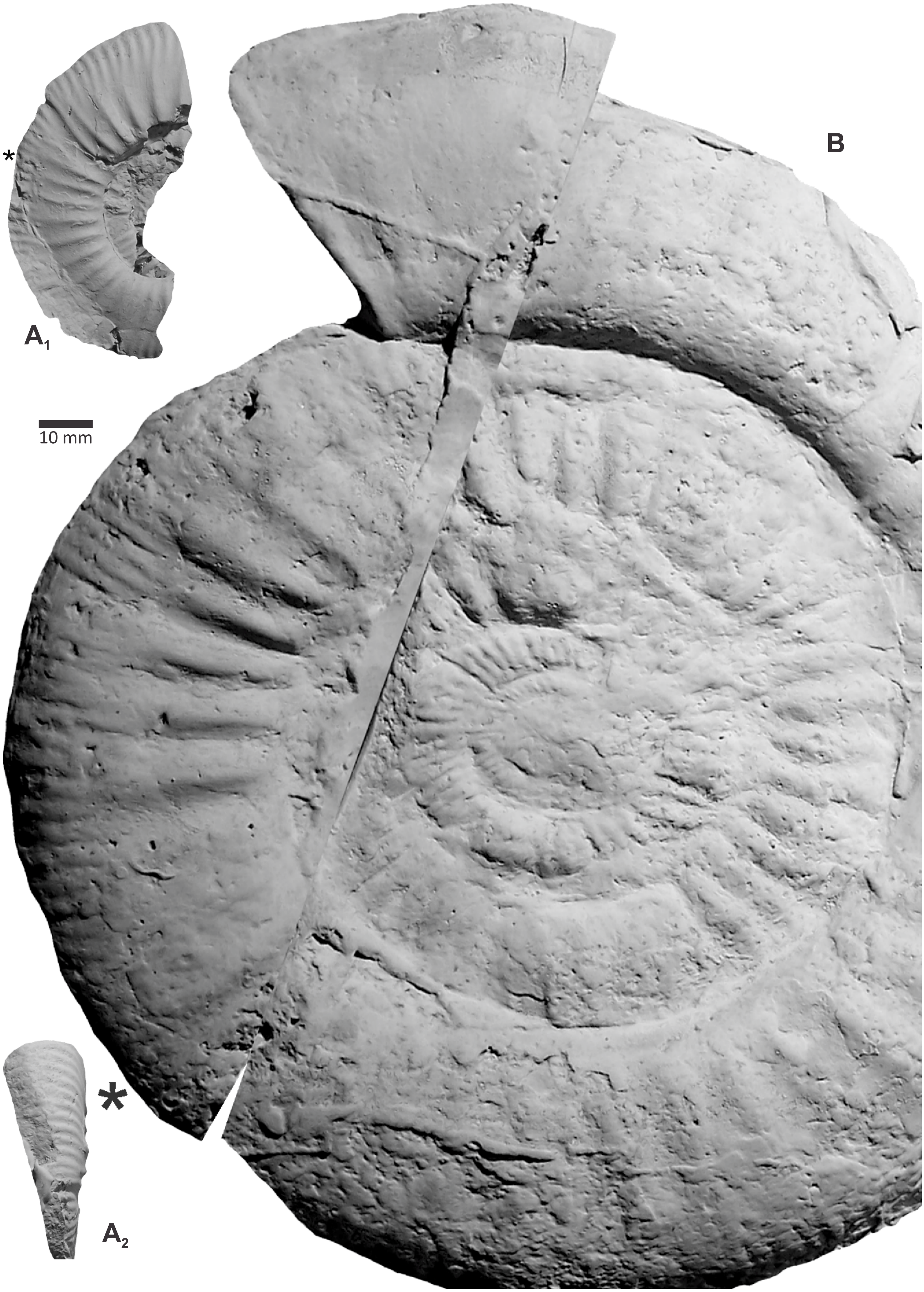


Figure 9. *Choffatia* aff. *subbakeriae* (d'Orbigny, 1850), Steinmanni Zone. **A**: possible adult microconch (MOZ-PI-7412/2), level CM-3, Steinmanni Subzone. **B**: complete adult macroconch with peristome (gypsum cast), level CM-8, Gerthi Subzone. – All natural size (x1). Asterisk at last septum.

Figure 10. *Choffatia* aff. *subbakeriae* (d'Orbigny, 1850), level CM-8, Gerthi Subzone, Steinmanni Zone. **A**: juvenile macroconch (MOZ-PI-7417/1). **B**: adult macroconch (MOZ-PI-7417/2), last whorl of phragmocone lost; **B$_1$**: bodychamber, **B$_2$**-**B$_3$**: phragmocone. – All natural size (x1). Asterisk at last septum.

we classify both groups as separate genera since we consider that independent lineages must be classified as different genera.

Paroxycerites Breistroffer, 1947 (type species: *Ammonites subdiscus* d'Orbigny, 1846) seems to have originated from *Alcidellus* (see discussion in Westermann & Callomon 1988). Macroconchs of *Paroxycerites* show the adult phragmocone and beginning of bodychamber sculpture and shell shape similar to *Oxycerites*, and differ from those of *Alcidellus* by having wider relative umbilicus and tertiary ribblets.

Sexual dimorphism and ontogeny, crucial features in

Figure 11. *Choffatia* aff. *subbakeriae* (d'Orbigny, 1850), level CM-35, Gerthi Subzone, Steinmanni Zone. **A**: adult macroconch with almost complete bodychamber (MOZ-PI-7430/9). **B**: incomplete phragmocone (MOZ-PI-7430/8). – All natural size (x1). Asterisk at last septum.

ammonite systematics, are poorly known for the species of these genera. In purely morphotypic grounds the microconchs of *Alcidellus* are commonly included in *Paroecotraustes* Spath, 1928 (type species: *Oecotraustes serrigerus* Waagen, 1869), a morphogenus which ranges from at least the Middle Bathonian up to the Upper Callovian.

Alcidellus aff. *obsoletoides*
(Riccardi, Westermann & Elmi, 1989)
Fig. 8A-B

Material. Two almost complete adult macroconchs (MOZ-PI-7412/1, 3) from level CM-3.

Description. Macroconch. Inner whorls, at least from *D* = 5-10 mm, platyconic, compressed, widely umbilicated, smooth; whorl section subrectangular with an incipient keel as a blunt ventral angularity. From *D* = 12-15 up to *D* = 25 mm, depending on the specimens, the shell is platyconic with a small keel and *Paroecotraustes*-like sculpture, i.e., dense, short rounded ribs in the uppermost flank. From *D* = 25 mm the sculpture changes into widely spaced lunuloid ribs covering the upper half of the flank, originating at a mid-flank ridge, and fading-off in the weak ventro-lateral keels of the tricarinate venter of the bodychamber (Fig. 8A_2). The adult bodychamber begins at D_{ls} = 35 mm with weak uncoiling. Septal suture line little frilled, with the typical structure of the subfamily.

Remarks and comparison. The present macroconchs can be assigned to *Alcidellus* by the ontogeny of their sculpture (Fig. 8B →8A_3-A_4 →8A_1-A_2) with tricarinate venter and the little frilled suture line. The outer whorls are almost indistinguishable from those of *A. obsoletoides*, only being more widely umbilicated. The holotype of *A. obsoletoides*, an adult? macroconch of which the inner whorls are not known, comes from the Bodenbenderi Zone of northern Chile. Riccardi & Westermann (1991a: 11) cited the species from the base of the Steinmanni Zone. It is very likely that these latter specimens together with the present ones represent a transient older than the holotype, but the inner whorls must be compared before the identity of these lower records can be established.

The adult macroconch of *A. tenuistriatus* differs from *A. obsoletoides* by its wider and more rounded bodychamber with very blunt to no ribs at the beginning, or vanishing towards the peristome. *Alcidellus cualacensis* (Sandoval & Westermann in Sandoval et al. 1990), from the Lower Callovian (Steinmanni and Bodenbenderi zones) of Mexico, is larger and the bodychamber more inflated with the tricarinate stage well marked through the phragmocone and almost all of the bodychamber. However, there are no significant differences between *A. obsoletoides* and *A. cualacensis* which could likely be a junior synonym, but the inner whorls of the type specimens of both nominal species need to be examined for a meaningful comparison.

The *Paroecotraustes*-like inner whorls of our macroconchs (Fig. 8B) are a clear indication of the sexual dimorphic correspondence with microconch ammonites usually assigned to that morphogenus, which is considered to include the microconchs of *Alcidellus* (see Westermann & Callomon 1988).

Occurrence and distribution. Level CM-3, Steinmanni Subzone, Steinmanni Zone, Upper Bathonian.

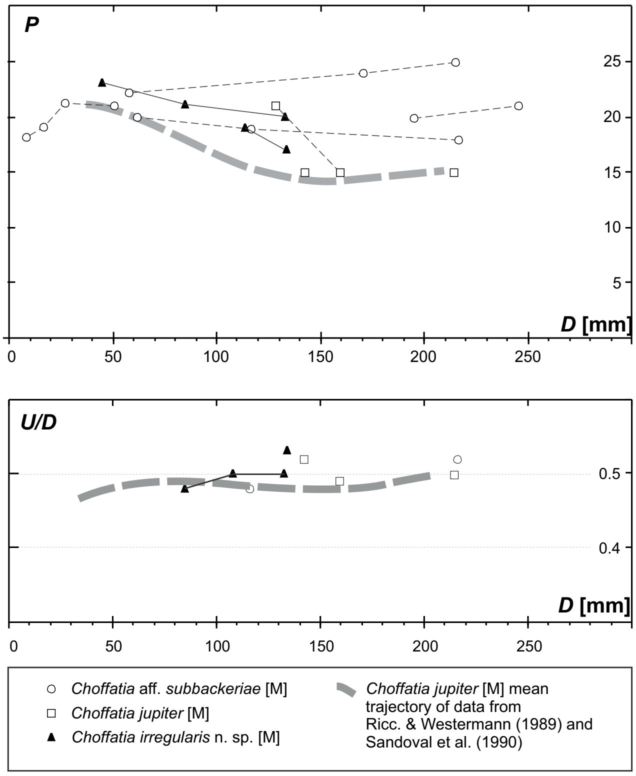


Figure 12. Ontogeny of the rib density (*P-D*) and relative umbilical width (*U/D*) of *Choffatia* aff. *subbakeriae*, *Choffatia jupiter*, and *Choffatia irregularis* n. sp.

Alcidellus n. sp. aff. *tenuistriatus* (Grossouvre, 1888)
Fig. 8C-D

Material. One adult macroconch and several fragmentary specimens (MOZ-PI-7430/4-7) from level CM-35 (upper part).

Description. Only macroconchs are available. Phragmocone, from *D* = 20 mm, suboxyconic, involute and compressed. Whorl section compressed suboval to subtriangular; the slightly convex flanks pass through blunt ventro-lateral shoulders into a rather narrow venter with a rounded angularity or blunt keel. The ribbing consists of feeble primary ribs which are slightly prosocline in the lower flank, becoming prominent and well spaced from the middle of the flank.

The adult bodychamber begins at D_{ls} = 60-80 mm, depending on the specimens. It is inflated, higher than wide suboval in whorl section; the flanks pass through rounded ventro-lateral shoulders into a wide subtabulate venter. Primary ribs very weak in the lower half of flank and more or less prominent on the upper flank, fading away towards the peristome. The peristome is flared, preceded by a wide shallow constriction. The length is one half-whorl.

Remarks and comparison. The uniqueness of this species is that the fine falcate primaries with upper lunuloid ribs are the only, simple ornamentation from the inner whorls. The secondary ribs by furcation of the lower primary after falcation and the early stage of *Paroecotraustes*-like ornamentation in the upper flank, typical for the phragmocones of species of *Oxycerites* or *Alcidellus*, are absent in the present specimens.

Occurrence and distribution. The species was recorded from the upper part of level CM-35, probably *jupiter* Hz., upper Gerthi Subzone (new), Upper Bathonian.

Superfamily Perisphinctoidea Steinmann, 1890
Family Perisphinctidae Steinmann, 1890
Subfamily Grossouvrinae Spath, 1930
Genus *Choffatia* Siemiradzki, 1898

Type species. *Perisphinctes cobra* Waagen, 1875; by subsequent designation of Buckman (1920).

Remarks. The classification of the Grossouvrinae (formerly Pseudoperisphinctinae Schindewolf, 1925, see Enay & Howarth 2019) remains problematic as can be seen in the most recent revision by Énay & Howarth (2019). Their classification is based on differences between genera that in many cases could be attributed to intraspecific variation. For example, the differences between *Choffatia* and *Subgrossouvria*, which have almost identical stratigraphic range and geographic distribution, are said to be that the representatives of the latter are more depressed and more coarsely ribbed. On the other hand, some features of the Andean Upper Bathonian-Lower Callovian perisphinctids are somewhat different from those of the Tethyan *Choffatia*, suggesting they could belong to an undescribed Andean genus (lineage). Among these features are the fine and dense, radial primaries dividing into three to four secondaries from the juvenile phragmocone, crossing the venter bundled, combined with strong phragmocone constrictions preceded by a prorsiradiate polyschizotomic rib (descriptions below). However, there is not yet enough well preserved material to disentangle the patterns and systematic meaning. A possible differentiation of the Andean forms would be not surprising since perisphinctids show marked provincialism (Énay & Howarth 2019), and have developed, during the Middle and Late Jurassic, local lineages in almost every marine basin (e.g., Donovan et al. 1981, Meléndez & Myczynsky 1987, Parent 2006, Parent et al. 2017). Under these circumstances, following Sandoval et al. (1990), Parent (1998), and Zatoń (2010), we provisionally adopt a wide concept, including *Subgrossouvria* Spath, 1924, *Grossouvria* Siemiradzki, 1898 (pars), *Homoeoplanulites* Buckman, 1922, and *Parachoffatia* Mangold, 1970, into the undivided genus *Choffatia*, since the differences are unclear or not sufficient for generic distinction. The genus *Grossouvria* should be restricted to the Upper Callovian forms close to its type species (*Ammonites sulciferus* Oppel, 1857, Late Callovian), as an independent lineage with macro- and microconchs (see, e.g. Dietl 1993) well differentiated from those of *Choffatia*.

The bulk of the Upper Bathonian perisphinctids studied herein form three well differentiated groups with coherent aspect and insignificant morpho-ornamental overlaping. These three groups are described as separate species.

Choffatia aff. *subbakeriae* (d'Orbigny, 1850)
Figs. 9-12

Material. One fragmentary microconch? (MOZ-PI-7412/2) from level CM-3; three fragmentary macroconchs (MOZ-PI-7417/1-3) and one complete adult macroconch (gypsum cast) from level CM-8; one adult macroconch and one phragmocone (MOZ-PI-7430/8-9) from level CM-35.

Description. Macroconch (Figs. 9B, 10-11). Large and compressed serpenticones, regularly and densely ribbed throughout the ontogeny.

Inner and middle whorls, about D = 10-80 mm, evolute (U/D = 0.50) with compressed suboval section (W/H_1 = 0.60-0.70); adult phragmocone (about D = 80 to 200 mm) little changed, passing into a rounded subrectangular whorl section. Primary ribs (P = 18-21) originate in the uppermost portion of the umbilical wall, running across the flank strong and straight, radially oriented, trifurcating from about the mid-height of the flank; secondaries and rare intercalatories cross the venter unchanged and evenly spaced.

The adult bodychamber begins at D_{ls} = 170-220 mm in the different specimens, showing more compressed whorl section (W/H_1 = 0.50-0.60) and moderate uncoiling in the last half (U/D_p = 0.55). The ribbing remains almost unchanged; the flanks and venter tend to become smooth near the peristome. The peristome is flared in one specimen, at D_p = 245 mm with L_{BC} = 250°.

Microconch? (Fig. 9A). One fragmentary specimen of about 65 mm in diameter, including the beginning of the bodychamber estimated at D_{ls} = 58 mm. The whorl section and ribbing as in the macroconch, only differing in that the primary ribs in the portion of bodychamber are somewhat curved and projected forward in the mid-flank. The lack of peristome prevents reliable sexing.

Remarks and comparison. The small fragmentary specimen in Fig. 9A could likely be a microconch as indicated by the flexuous ribs in the bodychamber, resembling the pattern seen in microconch perisphinctids.

The phragmocone of the present species is similar to the lectotype of *C. subbakeriae* (designated and refigurated by Fischer et al. 1994: 136-137, pl. 55: 1, Upper Callovian of Niort, France) at comparable size, but more evolute and coarsely ribbed and the whorl section is more rounded (suboval). The adult macroconchs are similar to analogous specimens from the Upper Bathonian of Europe (e.g. Hahn 1969: pls. 3: 2, 8: 8), but these latter are more inflated and involute, with the ribbing of the bodychamber vanishing in the venter and reinforced or swollen primaries. The overall similarity of our specimens with only small differences at different stages of the ontogeny in comparison with those of the Upper Bathonian of Europe suggest some degree of direct genetic relationships but not conspecificity (see Parent 1998).

Occurrence and distribution. The species ranges through the levels CM-3 to CM-35, that is from the upper Steinmanni Subzone (new) up to the upper Gerthi Subzone (new) in the Upper Bathonian. For the time being no similar or comparable specimens are known from other localities. The Lower? Callovian specimens of *Choffatia* sp. A from Vega de la Veranada (see below) are compressed and more finely ribbed macroconch phragmocones, but, although closer to the lectotype of *C. subbakeriae* they are too poorly preserved for advancing meaningful comparisons.

Choffatia jupiter (Steinmann, 1881)
Figs. 12-15

* 1881 *Perisphinctes jupiter* n.f. – Steinmann: 277, pl. 9: 6, 6a (holotype by monotypy).

Figure 13. *Choffatia jupiter* (Steinmann, 1881), level CM-35, *jupiter* Hz.?, Gerthi Subzone, Steinmanni Zone. Adult macroconch (MOZ-PI-7430/20). – Natural size (x1). Asterisk at last septum.

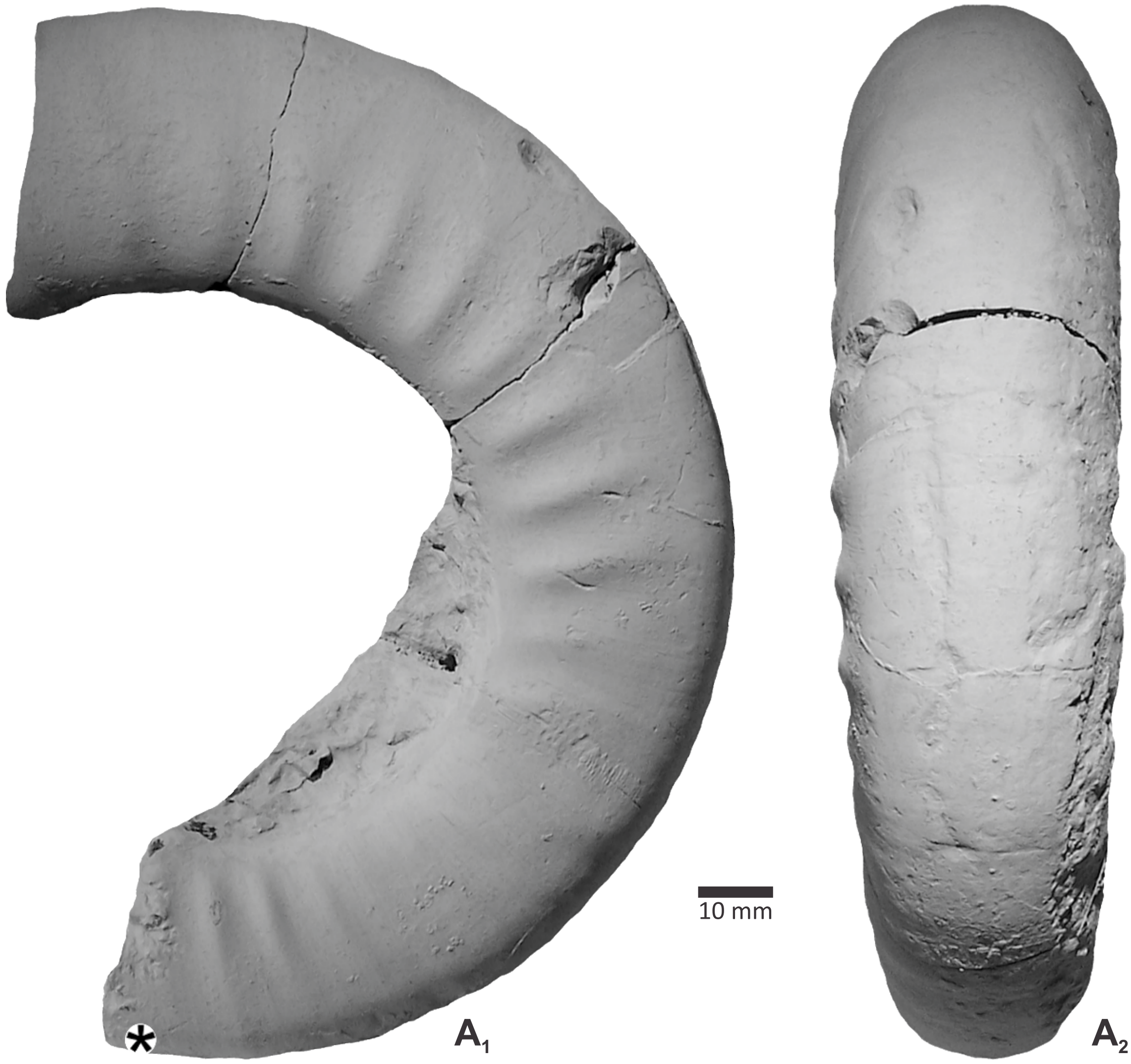


Figure 14. *Choffatia jupiter* (Steinmann, 1881), level CM-35, *jupiter* Hz.?, Gerthi Subzone, Steinmanni Zone. Adult macroconch (MOZ-PI-7430/21). – Natural size (x1). Asterisk at last septum.

n 1915 *Perisphinctes jupiter* Steinmann – Lóczy: 404, pl. 24(12): 4.
n 1960 *Subgrossouvria* cf. *jupiter* Lóczy – Raileanu & Nastaseanu: 7, pl. 6: 19.
+ 1989 *Choffatia jupiter* (Steinmann) [M] – Riccardi et al.: 568, pls. 5: 1 (neotype), 6: 3.
? 1989 *Choffatia jupiter* (Steinmann) [m] – Riccardi et al.: 568, pl. 4: 14-15.
1990 *Choffatia* cf. *jupiter* (Steinmann) – Sandoval et al.: 131, pls. 10: 1, 15: 3.
1992 *Choffatia jupiter* (Steinmann) [M] – Westermann: pl. 60: 6.
1998 *Choffatia jupiter* (Steinmann) [M] – Parent: 83, fig. 9.
? 2010 *Choffatia jupiter* (Steinmann) – Ramos et al.: 46, pl. 1: D-E.

Material. Four adult macroconch bodychambers (MOZ-PI-7430/20-23) from level CM-35 (upper part).

Description. Macroconchs. Adult phragmocone (D = 60-140 mm) evolute with rounded subrectangular whorl section. Primary ribs swollen, trifurcating, sometimes quadrifurcating, from about the middle of the flank; ventral ribs fine, evenly spaced, weakened in the siphonal line. The adult bodychamber begins at variable diameter, D_{ls} = 115-160 mm.

Adult bodychamber evolute (U/D = 0.50), gradually uncoiling towards the peristome, whorl section subtrapezoidal (W/H_1 = 0.90-1.00). From about the last adult septum secondary ribbing fades away completely leaving the venter smooth, whereas the primary ribs (P = 15) remain swollen and prominent in the flanks; in some small adults (D_{ls} = 114-130 mm) the primaries vanish from the middle of the flank. The peristome, preserved in one specimen at D_p = 214 mm, is flared.

Remarks and comparison. The present macroconchs match those described by Riccardi et al. (1989: pls. 5: 1 and 6: 3) in the subrectangular whorl section, swollen primaries and smooth venter in the bodychamber.

The macroconch figured by Steinmann (1881: pl. 9: 6)

Figure 15. *Choffatia jupiter* (Steinmann, 1881), level CM-35, *jupiter* Hz.?, Gerthi Subzone, Steinmanni Zone. Adult macroconch (MOZ-PI-7430/22). – Natural size (x1). Asterisk at last septum.

was the only originally included in *Perisphinctes jupiter* Steinmann, thus the holotype by monotypy. However, it seems to be lost, and Riccardi et al. (1989: pl. 5: 1) figured a large macroconch as a "neotype" but without the provisions of the Article 75.3 of the ICZN, neither providing an explicit proposal of designation in the text. This neotype was later accepted by Parent (1998), as well as here, after failing in finding the specimen, assuming the holotype is lost.

Thus, *C. jupiter* is based on a neotype which is an evolute ammonite with subrectangular whorl section, swollen primaries, and smooth venter from the end of the phragmocone. The lost holotype is significantly different, with rounded whorl section and well marked secondary ribbing crossing the venter unchanged in its last whorl (bodychamber?). The lost holotype of *C. jupiter* is indistinguishable from the lectotype of *Choffatia suborion* (Burckhardt 1927: pl. 31: 2-4; designated by Westermann et al. 1984: 107). The supposed microconch *C. jupiter* figured by Riccardi et al. (1989: pl. 4: 14-15) has conspicuous bundles of secondary ribs crossing the venter which does not seem characteristic of the species, but suggests comparison with the macroconchs of *Choffatia irregularis* n. sp. (described below) which do bear this sculpture.

Choffatia aff. *subbakeriae* (macroconchs) differs from *C. jupiter* (macroconchs) by its compressed suboval whorl section with marked constrictions and ventral ribbing well marked and persistent through the adult bodychamber.

The two specimens from the Nieves Negras Fm at the locality Las Minas (Mendoza Province) figured by Ramos et al. (2010: pl. 1: D-E) are in general similar to *C. jupiter* but

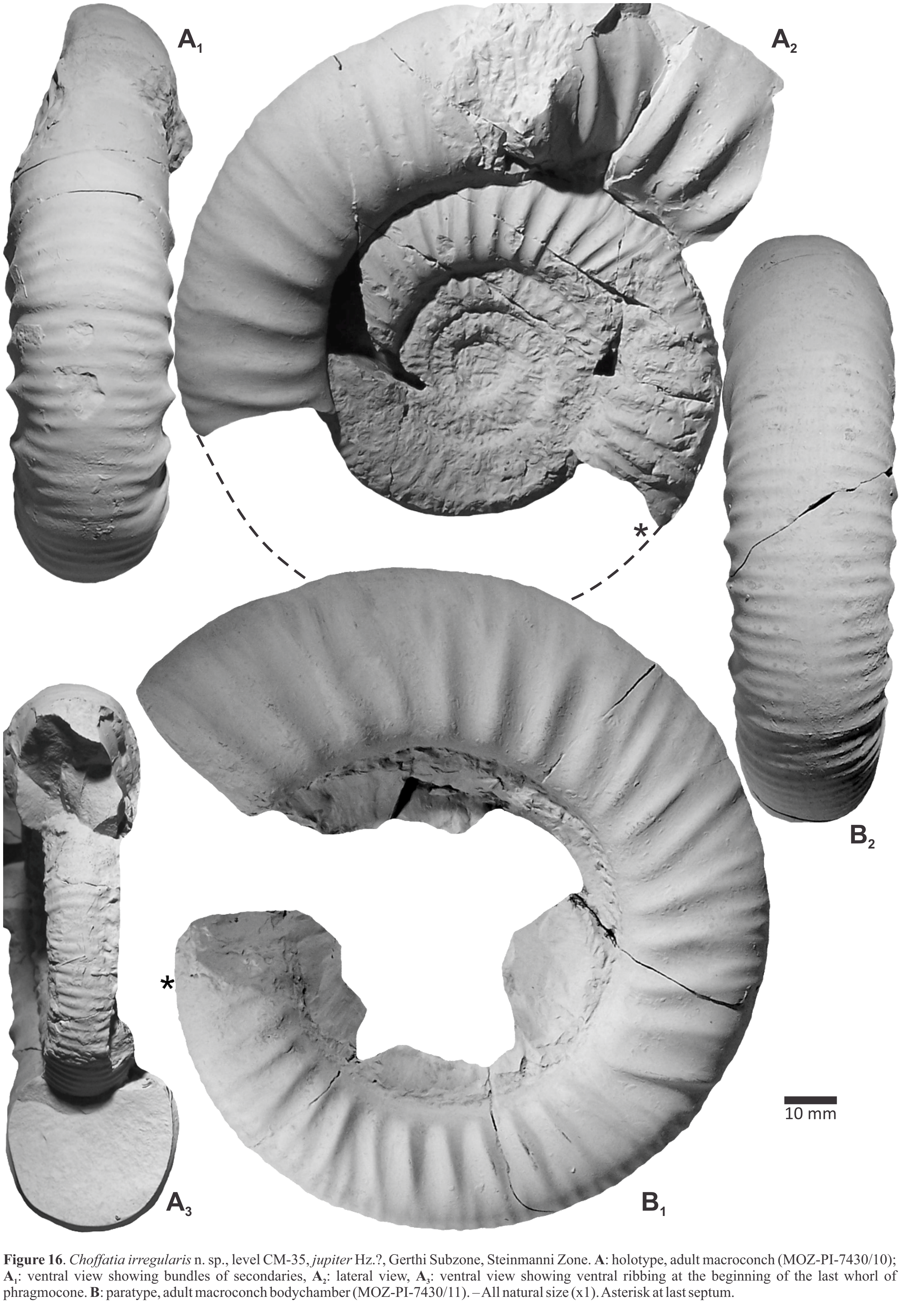


Figure 16. *Choffatia irregularis* n. sp., level CM-35, *jupiter* Hz.?, Gerthi Subzone, Steinmanni Zone. **A**: holotype, adult macroconch (MOZ-PI-7430/10); **A**$_1$: ventral view showing bundles of secondaries, **A**$_2$: lateral view, **A**$_3$: ventral view showing ventral ribbing at the beginning of the last whorl of phragmocone. **B**: paratype, adult macroconch bodychamber (MOZ-PI-7430/11). –All natural size (x1). Asterisk at last septum.

however exhibit some differences which cannot be understood clearly from the known material. These ammonites seem to be adult macroconchs as indicated by the slightly uncoiled bodychamber with an incipient variocostation. They are similar to *C. jupiter* in shell shape but the ribbing is finer and more prosocline from the innermost whorls up to the bodychamber. These ammonites could be local small adult variants of the species or belong to an undescribed species.

The misindentifications by Lóczy (1915) and Raileanu & Nastaseanu (1960) for Tethyan ammonites were already discussed in Parent (1998). This leaves the species confined to the Neuqúen Basin and probably by local variants in Mexico.

Occurrence and distribution. In the present section level CM-35 (*jupiter* Hz.?), Steinmanni Zone, Upper Bathonian.

***Choffatia irregularis* n. sp.**

Figs. 12, 16

Etymology. After the irregular ribbing which characterizes the species.

Type locality. Chacay Melehué, northern Neuquén Province, Argentina (Figs. 1-2).

Type horizon. Bed and level CM-35 (Fig. 4), Gerthi Subzone (new), Steinmanni Zone, Upper Bathonian; Los Molles Formation.

Material. Holotype (Fig. 16A), an adult macroconch with bodychamber (MOZ-PI-7430/10) from level CM-35. Paratype (Fig. 16B), an adult macroconch bodychamber (MOZ-PI-7430/11) from level CM-35.

Diagnosis. Macroconch evolute, with suboval whorl section throughout the ontogeny. Primary ribs of outer whorls sharp and prorsiradiate, irregular, tri- or bifurcating in strong secondaries which cross the venter in bundles.

Description. Macroconchs only. Phragmocone (D = 20-95 mm) evolute (U/D = 0.46) with suboval whorl section; primary ribs (P = 21-23) strong and wiry, subradial. Beginning of the bodychamber at D_{ls} = 95 mm. The adult bodychamber is slightly more evolute (U/D = 0.50-0.53) and uncoiled in the last part; suboval in whorl section (W/D = 0.23-0.27), slightly higher than wide (W/H_1 = 0.88-0.90). The primary ribs (P = 17-20) are strong, prorsiradiate, somewhat more prominent in the lower half, tri- or more rarely bifurcating from the upper half of the flank. The secondaries cross the venter forming bundles of three ribs. Some primaries are polyschizotomic, dividing near the umbilical shoulder and again in the upper flank. The maximum diameter preserved, probably at peristome in the paratype, is D = 133 and 134 mm.

Remarks and comparison. *C. jupiter* is larger in adult size with swollen primaries and smooth venter. *C.* aff. *subbakeriae* is larger in adult size, much more compressed, with the venter densely ribbed. Given the wide variety of morphotypes allocated within the genus, the diagnosis allows to distinguish the present species mainly from the known Andean forms. However, the strong secondaries crossing the venter in bundles are very distinctive from any other morphospecies. This latter feature is present in the coeval (*jupiter* Hz. of the Gerthi Subzone, new) ammonite described by Riccardi et al. (1989: pl. 4: 14-15) as a microconch of *C. jupiter*; nevertheless, this ammonite is very compressed and the secondaries are not as strong as in *C. irregularis* n. sp.

The ontogeny of primary rib density P and relative umbilical width U/D of the described species are compared in Fig. 12. The phragmocone rib density is very similar in the three species, but diverges in the bodychamber of *C.* aff. *subbakeriae*, becoming higher than in *C. jupiter* and *C. irregularis* n. sp. from about D = 120 mm. The relative umbilical width is very regular through the ontogeny of the three species, very narrowly around U/D = 0.50.

Among Tethyan forms, "*Orionoides*" [*Choffatia*] *samatrensis* Spath (1931: pl. 65: 6) has a similar whorl section and ribbing and could be related, but it comes from the Upper Callovian Athleta beds of Fakirwari, India. The Upper Bathonian-Lower Callovian *Choffatia recuperoi* (Gemmellaro, 1873), see e.g. Mangold (1970: pl. 10: 2-3) and Gálacz (2002: fig. 181), is also similar to *C. irregularis* n. sp., but more depressed and involute from middle whorls and variocostate in the adult whorls, with regular ribbing of stronger primaries and finer secondaries crossing the venter evenly spaced.

The macroconch figured as *Choffatia suborion* (Burckhardt, 1927) by Parent (1998: fig. 7) undoubtedly belongs to *C. irregularis* n. sp. This specimen comes from the same stratigraphic position of the holotype and paratype, and is indistinguishable from them.

Occurrence and distribution. The holotype and paratype come from level CM-35, upper Gerthi Subzone (new), Steinmanni Zone (Upper Bathonian), probably *jupiter* Hz. The specimen in Parent (1998: fig. 7) was collected from the same stratigraphic position as the type horizon in a nearby section. For the time being *C. irregularis* n. sp. is only known from the type locality.

Family Reinceckeiidae Hyatt, 1900

Subfamily Neuqueniceratinae Cariou, 1984

Genus *Neuqueniceras* Stehn, 1923

Type species. *Neuqueniceras steinmanni* Stehn, 1923; by original designation.

***Neuqueniceras steinmanni* Stehn, 1923**

Fig. 17

Synonymy. See Riccardi & Westermann (1991b).

Material. One fragmentary macroconch bodychamber (MOZ-PI-7417/3), three almost complete, well preserved macroconchs (MOZ-PI-7430/12-14) and four fragments, and one complete adult microconch (MOZ-PI-7430/15) from the upper part of level CM-35.

Description. Macroconch (Fig. 17A-B). Innermost whorls, D = 3 to 12 mm, widely umbilicate, depressed with the flanks covered by fine and dense, prosocline primary ribs. From D = 15-20 mm, all through the phragmocone the whorls remain evolute, with wider than high, suboval to subrectangular section. The primary ribs become stronger and more widely spaced, beginning in the umbilical wall and crossing the shoulder with no twist, projected straight forward; in the upper third or middle of the flanks, depending on the

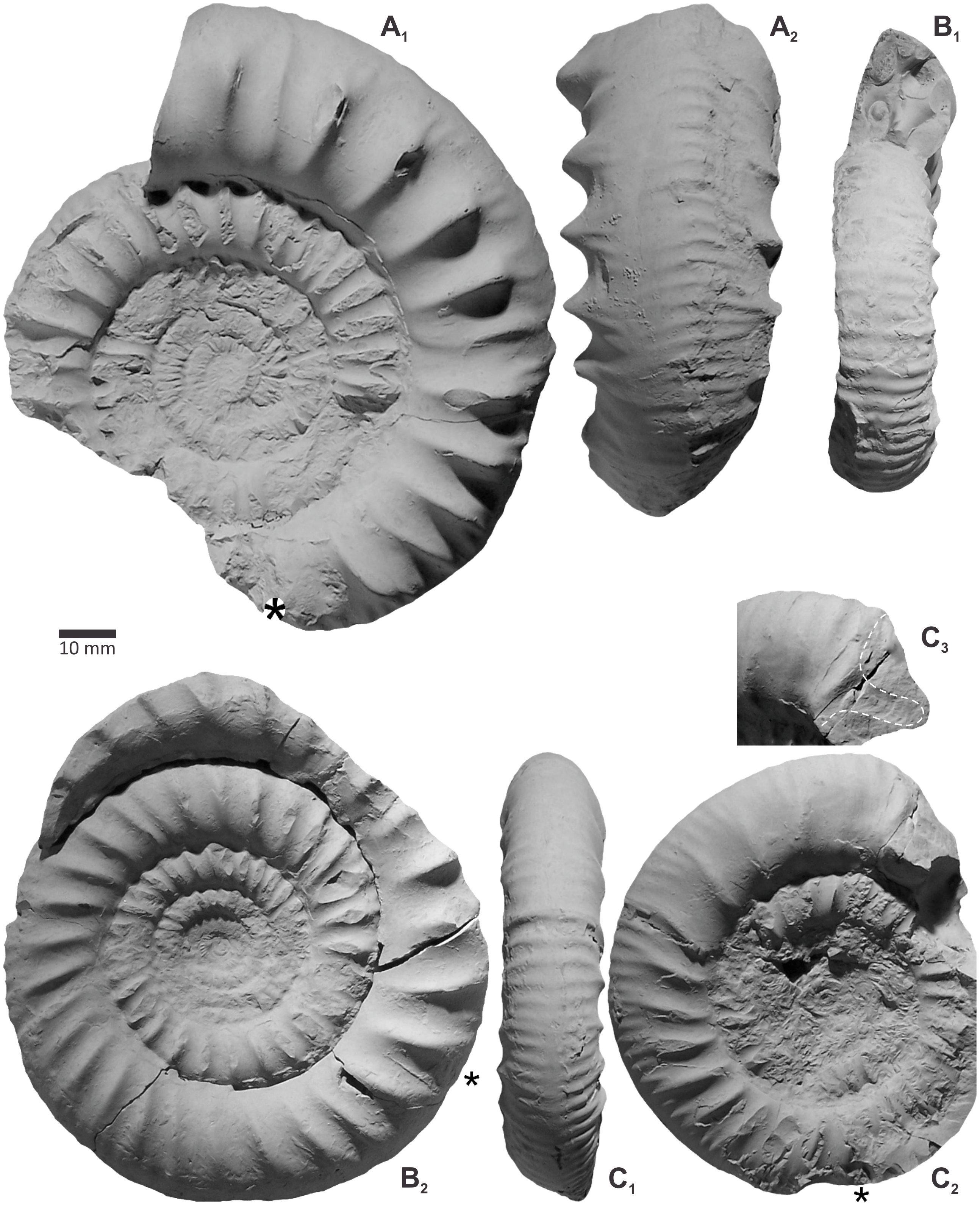


Figure 17. *Neuqueniceras steinmanni* Stehn, 1923, level CM-35, *jupiter* Hz.?, Gerthi Subzone, Steinmanni Zone. **A**: adult macroconch (MOZ-PI-7430/12), inflate morphotype. **B**: adult macroconch (MOZ-PI-7430/14), slender morphotype. **C**: adult microconch (MOZ-PI-7430/15); ventral (C_1) and lateral (C_2) standard views; C_3: lateral view of the peristome showing the lappets (different illumination than in C_2). – All natural size (x1). Asterisk at last septum.

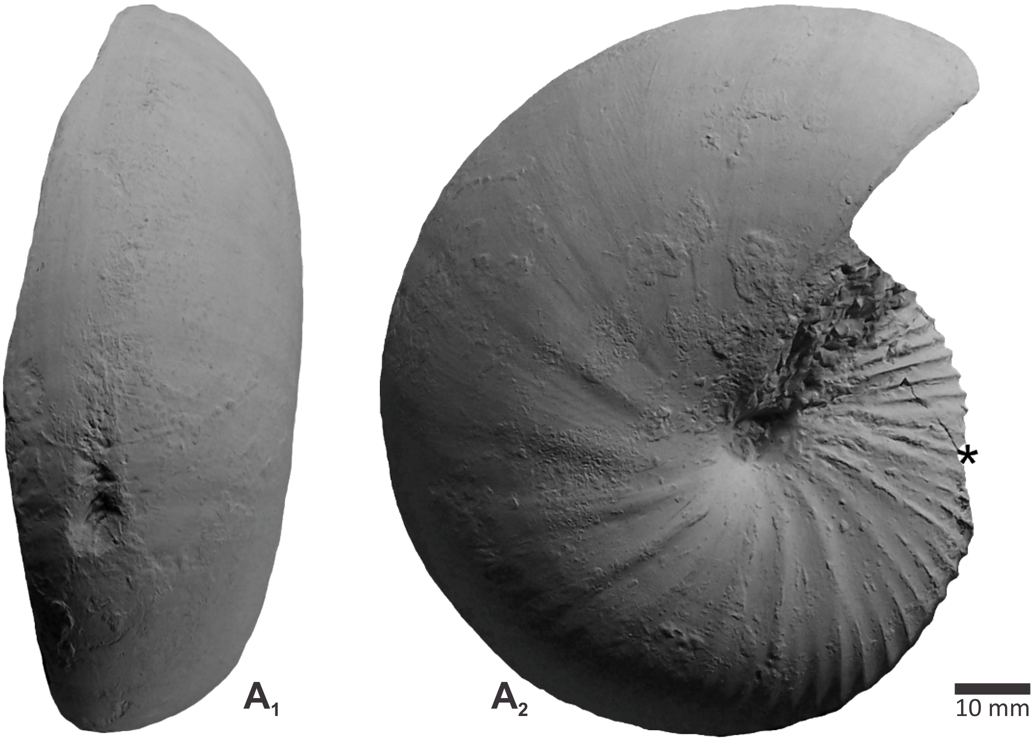


Figure 18. *Iniskinites gulisanoi* Riccardi & Westermann, 1991a, level CM-1, *gulisanoi* Hz., upper Steinmanni Subzone, Steinmanni Zone. Complete adult macroconch (MOZ-PI-7411/1). – Natural size (x1). Asterisk at last septum.

inflation of the whorl, each primary bi- or rarely trifurcates from a raised portion of the rib; the secondary ribs and some irregularly distributed intercalatories cross the venter evenly spaced.

The adult bodychamber begins at D_{ls} = 83-87 mm; the better preserved specimens have only one half-whorl preserved, but remains of the umbilical seam in the last whorl show that they were at least three-quarters whorl long. It is evolute, the section becomes more inflate and depressed. The sculpture retains the style but is reinforced, producing a moderate variocostation, especially by the raised primaries which form a tubercle from which the ribs trifurcate; there are few intercalatories. All ribs cross the widely rounded venter evenly spaced and with no modification. In fragmentary specimens the final part may be ventrally smooth, but none of them have a clearly recognizable peristome preserved.

Microconch (Fig. 17C). The only specimen available is complete and well preserved. The phragmocone is identical to that of the macroconch at comparable diameter, ending at about D_{ls} = 65 mm. The bodychamber is compressed, higher than wide, subrectangular with rather flat flanks and rounded venter. The ribbing is irregular, composed of strong sharp primaries (more rounded in the internal mold) more or less flexuous, somewhat raised on the lower flank, bi- or trifurcating on the upper third of the flanks; the secondaries are finer, sometimes rather disconnected from the parental primary or indistinctly as intercalatories; ventral ribbing is interrupted in the mid-flank forming a smooth band which vanishes towards the peristome. One constriction occurs in the middle of the bodychamber. This latter is about 210° long. The peristome has a bourrelet and bears short lappets at D_p = 78 mm.

Intraspecific variation. Our specimens compare closely with the specimens figured by Stehn (1923: pl. 4: 3) and Riccardi & Westermann (1991b: pl. 13: 1, 14: 1). In total, the known material shows a species with little variation in the macroconch/female shell. There is some variation in the whorl inflation (Fig. 17A$_2$-B$_1$), mainly in the bodychamber which may be strongly coroniform, with high and sharp tubercles in the upper flank to more perisphinctid with less prominent tubercles (Riccardi & Westermann 1991b: pl. 13: 1, 14: 1). Besides this variation in the prominence of the tubercles there is some variation in the rib density of the inner whorls (e.g. Fig. 17A$_1$, B$_2$). One of the specimens, the bodychamber of an adult macroconch, is more inflate with a wider whorl section than the remaining specimens.

Sexual dimorphism. The strongest variation within the species is manifested among the microconchs. The microconch described above is larger and strongly variocostate compared to the others known (Riccardi & Westermann 1991b: pl. 13: 2, 4). The size difference between these latter and our specimen corresponds to about one whorl, which is notoriously differentiated from the end of the phragmocone by its variocostation and compression of the section (Fig. 17C). These differences between the microconchs, assumed coeval, could be explained by (1) sex-change: a female becomes male, at least in its secondary sexual characters (somatic?), in its juvenile ontogeny, maturating earlier and developing lappets (Parent et al. 2008), or (2) great variation in the size and age, size-at-age, of maturation (Klug et al. 2015, Parent et al. 2019a). Assuming good correlation between age and size in

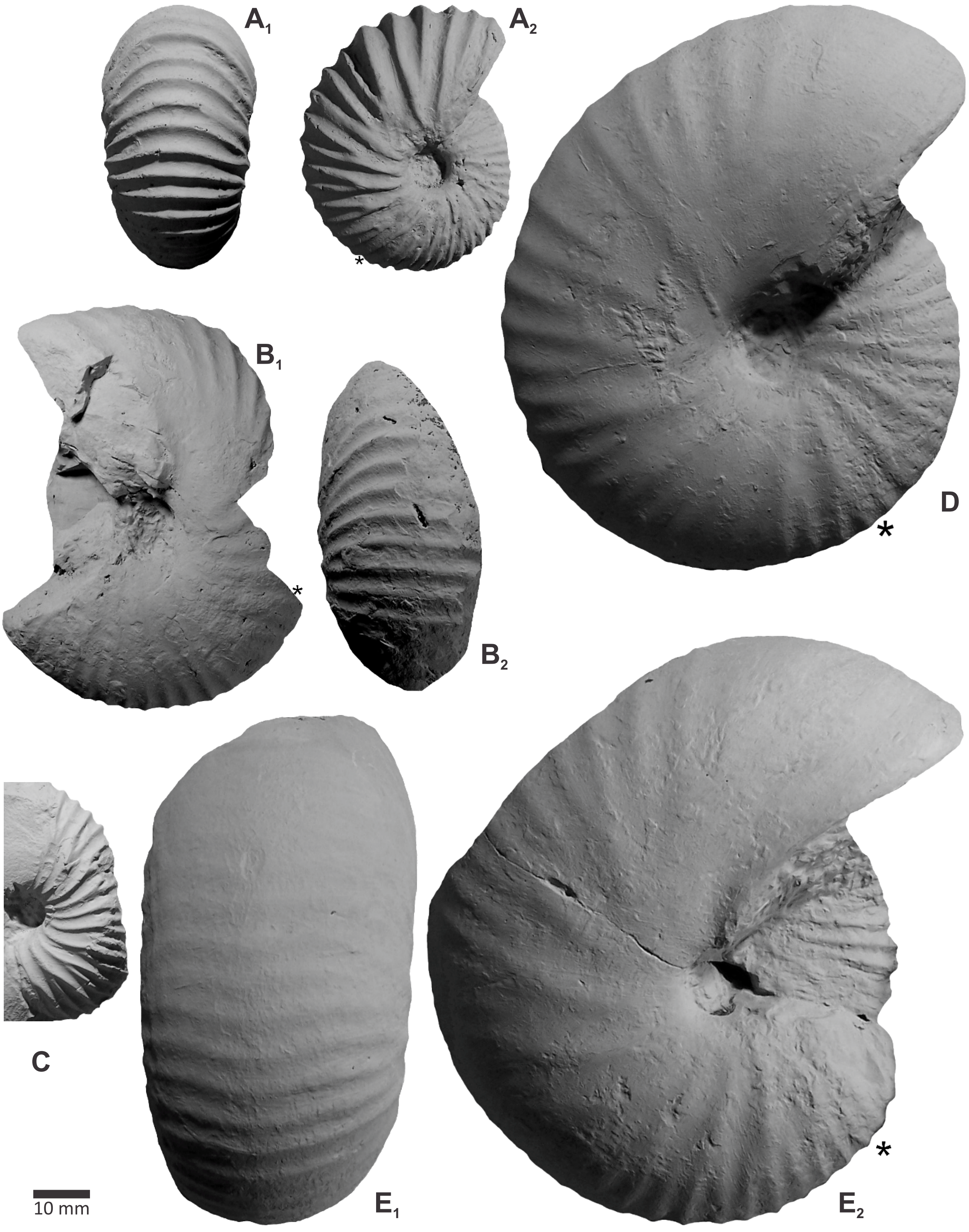


Figure 19. *Iniskinites crassus* Riccardi & Westermann, 1991a, Steinmanni Zone. **A**: adult microconch (MOZ-PI-7413/2), level CM-5, Steinmanni Subzone. **B**: adult macroconch (MOZ-PI-7413/1), level CM-5, Steinmanni Subzone. **C**: macroconch phragmocone (MOZ-PI-7413/3), level CM-6a, Gerthi Subzone. **D**-**E**: complete adult macroconchs (MOZ-PI-7415/2-3), level CM-6b, *crassus* Hz., Gerthi Subzone. – All natural size (x1). Asterisk at last septum.

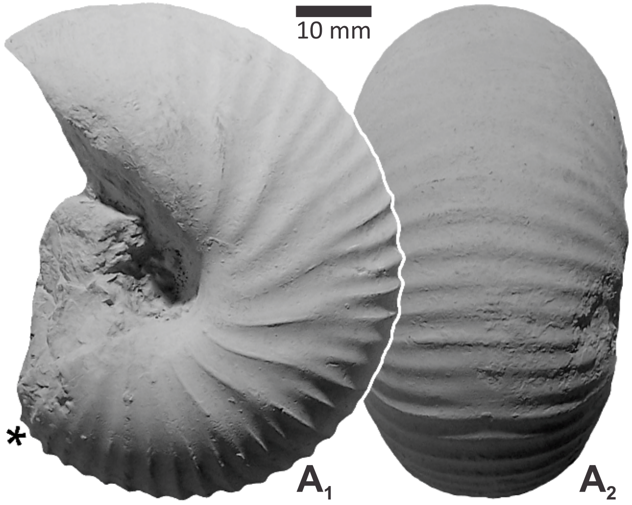


Figure 20. *Iniskinites crassus* Riccardi & Westermann, 1991a; level CM-38, basal Gottschei Zone. Complete adult macroconch (MOZ-PI-7430/16). – Natural size (x1). Asterisk at last septum.

individuals within a single species in a short time-interval, the first possibility would imply instability of the sex determination system; whereas the second possibility would indicate much flexibility in the age of starting of the maturation process which inherently leads to the halt of growth. In any case there is a common taxonomic issue to be considered, that is the importance to consider the notorious variations that the males/microconchs of a species can show. This condition leaves the criterium of identity of the inner whorls combined with the specific (adult) sexual secondary characters of each sex, as the (only?) strongest and most reliable feature for establishment of sexual dimorphic pairs, i.e. determination of the macro-microconch correspondance.

Occurrence and distribution. The present specimens come from the level CM-36, top of the Gerthi Subzone (new) in the studied section. The records of the species according to Riccardi & Westermann (1991b) range even upwards into the Gottschei Zone.

Superfamily Stephanoceratoidea Neumayr, 1875
Family Sphaeroceratidae Buckman, 1920
Subfamily Eurycephalitinae Thierry, 1978

Remarks. The scope and contents of the subfamily has been recently summarized by Howarth (2017).

Genus *Iniskinites* Imlay, 1975

Type species. *Kheraiceras magniforme* Imlay, 1953; by original designation.

Iniskinites gulisanoi Riccardi & Westermann, 1991a
Fig. 18

Synonymy. See Riccardi & Westermann (1991a).

Material. One complete adult [M] (MOZ-PI-7411/1) from the base of the studied section, level CM-1.

Description. A single, complete and well preserved macroconch, with peristome at $D_p = 101$ mm. Inner and outer whorls of the phragmocone (from $D = 15$ mm) are involute, rather compressed, subrectangular in whorl section. The ribbing consists of fine and sharp primary ribs, bi- or trifurcating in about the mid-flank. The transition to the bodychamber (from $D_{ls} = 55$ mm) shows the secondary ribbing gradually fading, then the last third of the bodychamber is smooth with a wide and shallow constriction behind the peristome. The bodychamber is three quarters of whorl long, $L_{BC} = 270°$.

Remarks. The specimen is identical to the holotype (Riccardi & Westermann 1991a: pl. 14: 6) in shell-shape, size and scultpture up to $D = 80$ mm (peristome in the holotype), from which our specimen develops a further quarter of whorl which becomes smooth. Both specimens are complete adult macroconchs as indicated by their respective preperistomatic constrictions. The difference can be attributed to a later maturation and halt of growth in the present specimen, the reasons of which, environmentally-induced and/or genetical, cannot be determined.

Occurrence and distribution. In the studied section the species occurs confined to the basal level CM-1, *gulisanoi* Hz., Steinmanni Subzone. Nevertheless, the species seems to range from somewhat lower levels of the Steinmanni Zone (Riccardi et al. 1989, Parent 1998) which are not represented in the present section.

Iniskinites crassus Riccardi & Westermann, 1991a
Figs. 19-20

Synonymy. See Riccardi & Westermann (1991a) and Parent (1998).

Material. One complete adult microconch and one macroconch from level CM-5 (MOZ-PI-7413/1-2), one fragmentary specimen from level CM-6a (MOZ-PI-7413/3), two complete adult macroconchs (MOZ-PI-7415/2-3) from level CM-6b. One complete adult macroconch (MOZ-PI-7430/16) from level CM-38.

Remarks. The species has been described in detail by Westermann & Riccardi (1991a) and Parent (1998). The macroconchs in Fig. 19D-E are typical representatives of the species, complete adults showing a preperistomatic wide, shallow constriction. The relative umbilical width of the subadult and adult stages of the ontogeny is very variable. As noted in Parent (1998: 90) there is a shift in the modal *U/D* from the older, more involute representatives (transient alpha) towards somewhat later representatives which become more widely umbilicated (transient beta). The specimens from the *crassus* Hz. match the values of *U/D* of the transient beta described in Parent (1998).

The microconch (Fig. 19A) would be included in the genus *Xenocephalites* Spath, 1928 (type species: *Macrocephalites neuquensis* Stehn, 1923; by original designation) based on purely morphologic grounds. It can be assigned to *I. crassus* because their inner whorls match from about $D = 20$ mm and it occurs associated with its corresponding macroconch in level CM-5. The phragmocone is involute, slightly inflated with suboval-subrecangular whorl section; the ribbing consists of

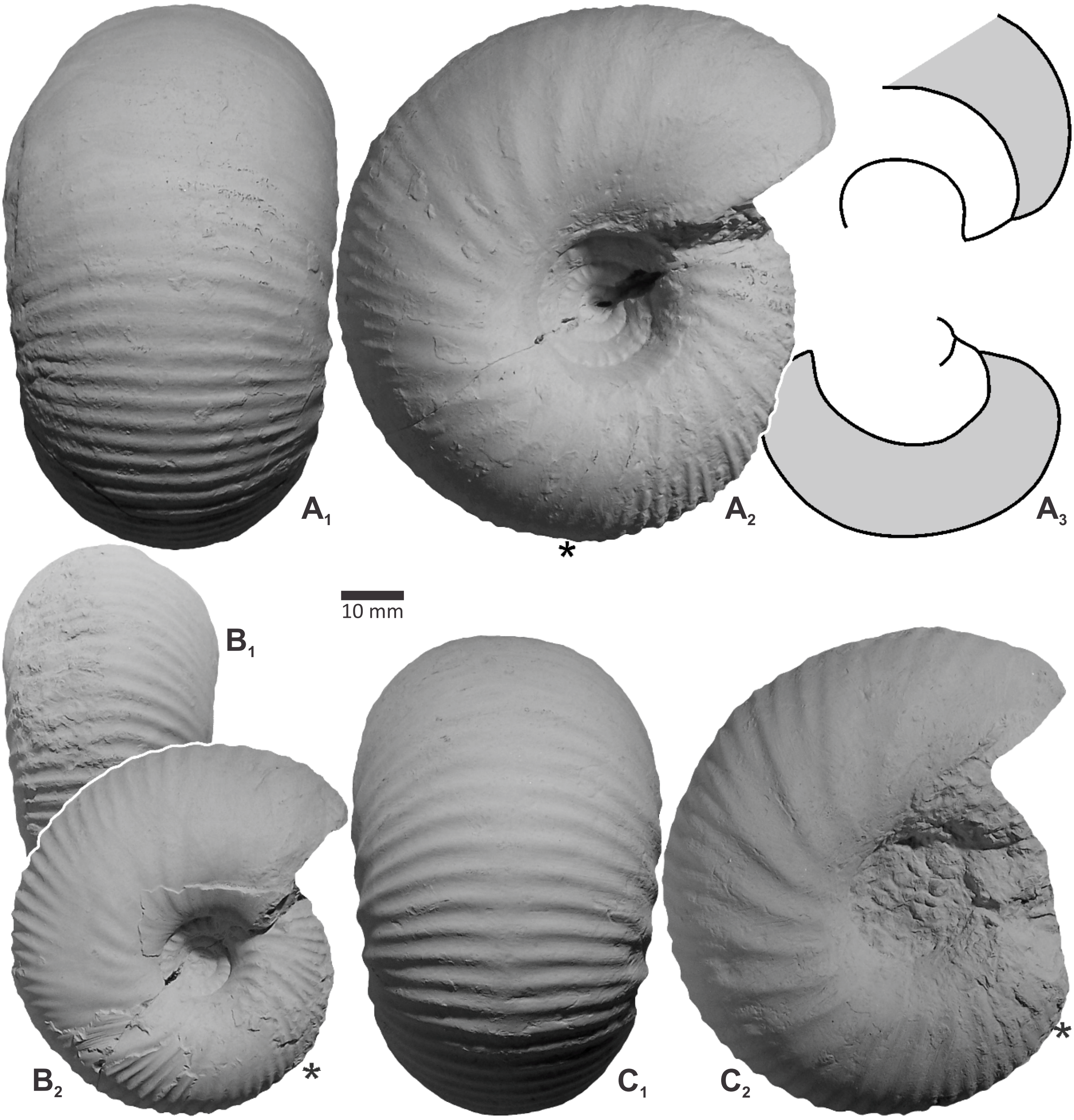


Figure 21. *Stehnocephalites gerthi* (Spath, 1928), level CM-35, *jupiter* Hz.?, upper Gerthi Subzone, Steinmanni Zone. Examples of late representatives of the species. **A**: complete adult macroconch (MOZ-PI-7430/17), large, stout, and evolute morphotype; A_3: whorl section through the peristome (bodychamber shaded). **B**: complete adult macroconch (MOZ-PI-7430/18), small, densely ribbed morphotype. **C**: complete adult macroconch (MOZ-PI-7430/19), middle-sized, coarsely ribbed morphotype. – All natural size (x1). Asterisk at last septum.

prosocline primary ribs bifurcating in the middle of the flank. In the bodychamber, which begins at D_{ls} = 35 mm and is one half-whorl long, the ribbing becomes stronger and sharp, bifurcating in middle of the flank from a slight swelling; ventral ribbing is evenly distributed, well spaced, strong and sharp, crossing the venter with a slight arching.

A small adult (bodychamber incipiently uncoiled) macroconch from level CM-38 (Fig. 20) is included in *Iniskinites* because of the combination of the following characters: (1) slightly arched ventral ribbing, (2) small umbilicus, and (3) smooth lower periumbilical area. This specmen is thus included as a late transient of *I. crassus*, for it compares closely with the holotype, only differing by its slightly smaller adult size. The relative umbilical width *U/D* = 0.10 of this specimen is comparable to the values of the early transient alpha (Parent 1998: fig. 12B). It is remarkable

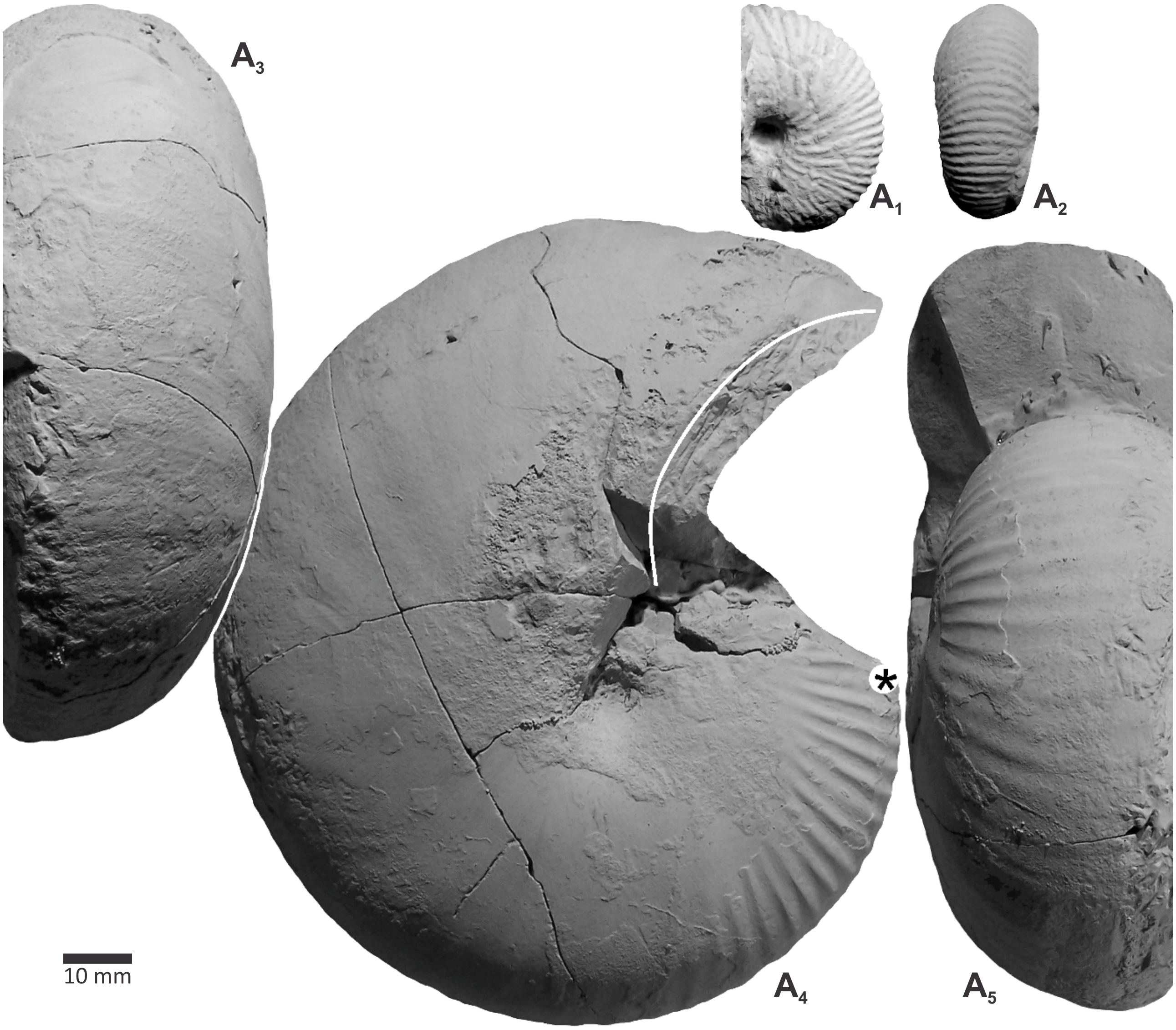


Figure 22. *Lilloettia australis* Riccardi & Westermann, 1991a, level CM-6b, *crassus* Hz., Gerthi Subzone, Steinmanni Zone. Complete adult macroconch (MOZ-PI-7416); A_1-A_2: inner whorls; A_3: ventral view of the bodychamber showing wide, blunt ribbing vanishing towards the peristome; A_4: lateral view; A_5: apertural view. – All natural size (x1). Asterisk at last septum.

to see an isolated occurrence of this species "so much" above the uppermost occurrence hithero recorded, separated by a time-gap of the duration of about one subzone. This case is a good example of the extension of the stratigraphic range of a species by subsequent sampling. A transitional form could be the specimen figured by Parent (1998: fig. 13F).

Occurrence and distribution. Levels CM-5 to CM-6a (upper Steinmanni Subzone, new), CM-6b (*crassus* Hz., Gerthi Subzone, new), and CM-38 (basal Gottschei Zone). The species is known to occur in the area of Chacay Melehué (the type locality) including Estación Rajapalo, and Rahuecó; it has been recently recorded from Quebrada Remoredo and Quebrada La Estrechura (Sierra de Reyes, Spalletti et al. 2012); in northern Chile: Quebrada El Profeta and Caracoles (Riccardi & Westermann 1991a). The stratigraphic range covers the interval upper Steinmanni Subzone to lowermost Gottschei Zone.

Genus *Stehnocephalites* Riccardi, Westermann & Elmi, 1989

Type species. *Indocephalites gerthi* Spath, 1928; by original designation.

Stehnocephalites gerthi (Spath, 1928)
Fig. 21

Remarks. This species is the most abundant in number of specimens and levels of occurrence through the studied section. The new material includes almost all the many morphotypes described by Riccardi & Westermann (1991a) and Parent (1998). However, the present collection was obtained under much finer stratigraphic control than in the cited studies, and shows that most of the extremely broad intraspecific variation described corresponds to morphologic changes through the phyletic evolution of the

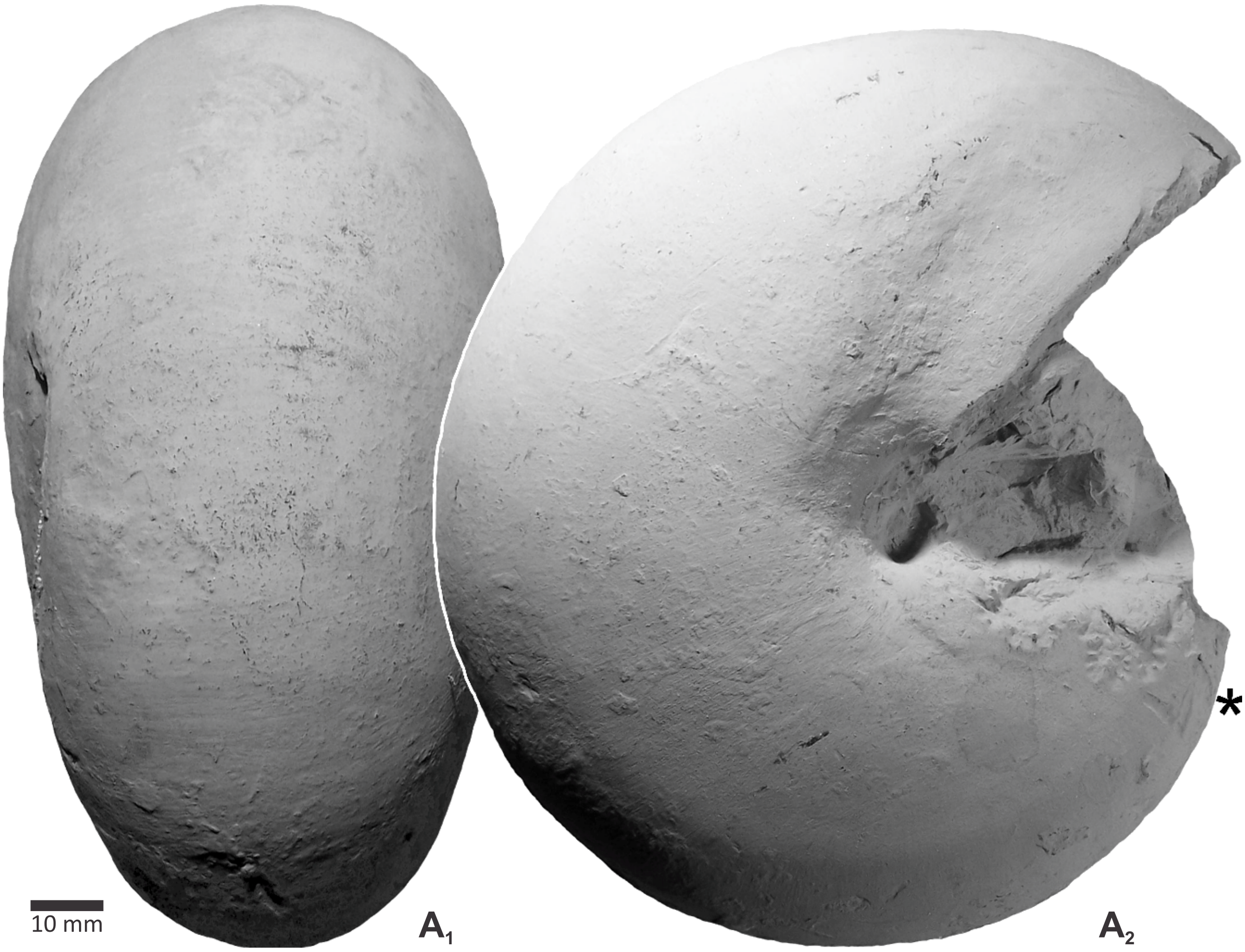


Figure 23. *Lilloettia australis* Riccardi & Westermann, 1991a, level CM-26, Gerthi Subzone, Steinmanni Zone. Complete adult macroconch (MOZ-PI-7423/1); ventral (A_1) and lateral (A_3) views showing the smooth bodychamber; note the marked preperistomatic constriction. – Natural size (x1). Asterisk at last septum.

species. The description of this material with the results of a detailed study of the complete collection of the species will be published in a separate paper.

In the studied section the species ranges from level CM-6b (*crassus* Hz., base of the Gerthi Subzone, new) up to the level CM-38 (base of the Gottschei Zone). A sample from level CM-35, showing wide variation in adult size and density of lateral ribbing, is illustrated in Fig. 21.

Genus *Lilloettia* Crickmay, 1930

Type species. *Lilloettia lilloettensis* Crickmay, 1930; by original designation.

Lilloettia australis Riccardi & Westermann, 1991a

Figs. 22-24

Synonymy. See Riccardi & Westermann (1991a).

Material. Three complete adult and one fragmentary macroconchs (MOZ-PI-7416/1-2, 7423/1-2) from levels CM-6b and CM-26.

Description. Macroconch. Inner whorls (D = 20-40 mm): rather compressed (W/D = 0.46), involute, narrowly umbilicated (U/D = 0.16), with suboval whorl section; densely ribbed (P = 12, V = 30) by moderately strong, not sharp primaries curved forward on the lowermost flank then prorsiradiate, bifurcating or rarely trifurcating from the middle of the flank; all ribs cross the venter evenly spaced and with no change.

Adult phragmocone (from about D = 40 mm to D_{ls} = 75-85 mm): somewhat more inflated (W/D = 0.50-0.60) with smaller relative umbilical width (U/D = 0.10); ribbing gradually fading away in the flanks and becoming confined to the venter.

Adult bodychamber: the whorl section becomes more compressed (W/D = 0.45) and the umbilicus slightly widens gradually with the characteristic uncoiling towards the peristome. Specimens from level CM-6b preserve some residual wide, blunt ventral ribbing in the first third part of the bodychamber, becoming smooth, whereas the specimens from level CM-26 are completely smooth from the end of the phragmocone. All the specimens have a wide well marked pre-peristomatic constriction, deeper in the lower flank, imperceptible in the venter. The bodychamber

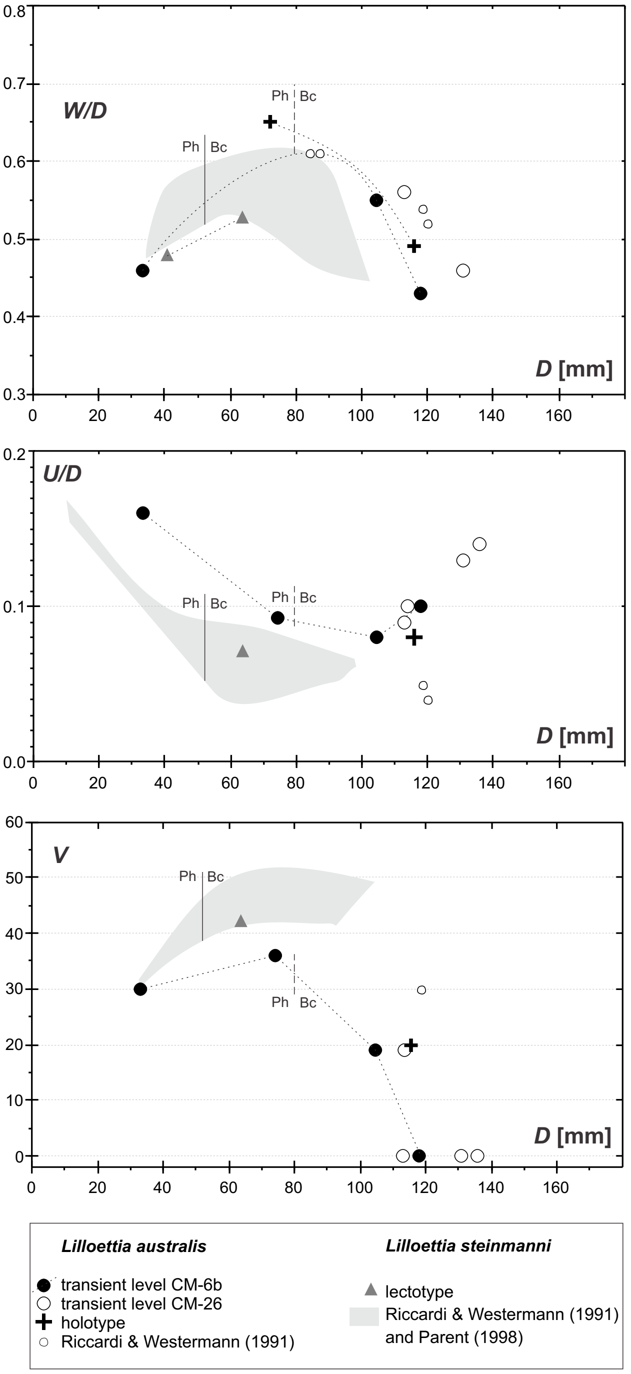


Figure 24. Ontogeny of relative whorl width (*W/D*), relative umbilical width (*U/D*), and ventral rib density (*V*) of *Lilloettia australis* and *Lilloettia steinmanni*. The thin vertical lines indicate the mean D_{ls}.

length is L_{BC} = 270°, remarkably constant in all specimens. The adult size at peristome is 118-120 mm for the level CM-6b specimens, and 131-136 mm in the level CM-26 specimens.

Remarks. The difference between the macroconchs from level CM-6b and those from level CM-26 is that these latter have a completely smooth bodychamber without the residual ventral ribbing that is retained by the older transient.

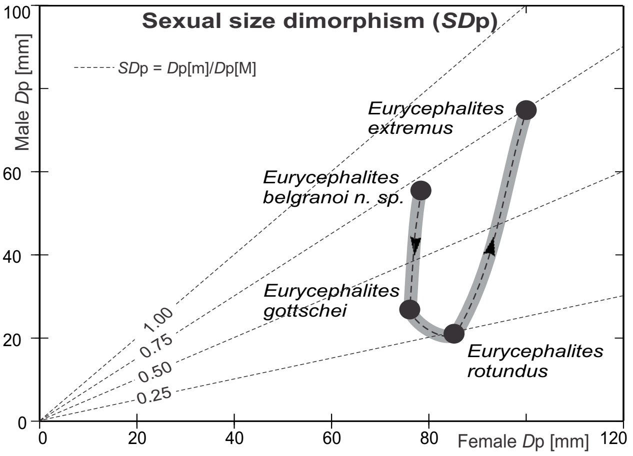


Figure 25. Sexual size dimorphism (SD_p) in *Eurycephalites* (*E. belgranoi* n. sp., *E. gottschei*, *E. rotundus*, *E. extremus*). SD_p is the ratio between the mean adult diameters at peristome of microconch males (D_p[m]) and macroconchs females (D_p[M]). Modified and updated from Klug et al. (2015: fig. 7.4).

L. australis [M] can be distinguished from *L. steinmanni* (Spath, 1928) [M] by the larger adult size (Fig. 24), the smooth adult bodychamber, and the more coarsely ribbed inner whorls, at least at *D* = 20-50 mm (cf. Fig. 22A$_1$-A$_2$ with Riccardi & Westermann 1991a: pl. 10: 3). According to Riccardi & Westermann (1991a: 52) the inner whorls of *L. steinmanni* have a subcircular to slightly compressed whorl section, but in *L. australis* it is compressed suboval and more widely umbilicated (Fig. 24). In *L. steinmanni* the D_{ls} is 39-58 mm and the D_p is 85-90 mm (data from Riccardi & Westermann 1991a), smaller than in *L. australis* (D_{ls} = 75-85 mm, D_p = 118-136 mm) what is correlated with the larger adult size at peristome of this latter (Fig. 24).

L. steinmanni is certainly recorded from the lower part of the Steinmanni Zone (Steinmanni Subzone), whereas *L. australis* occurs in the upper part (Gerthi Subzone, new). The smoothing of the bodychamber is progressive from the older representatives of *L. australis* (Fig. 22) towards the younger representatives (Fig. 23), correlated with a slight increase of D_p (Fig. 24). This pattern shown by the successive representatives or transients through the Steinmanni Zone indicate that *L. steinmanni* has changed gradually towards the completely smooth adult *L. australis*, by which this latter could be considered just the name for the later (latest?) transients of the *Lilloettia* lineage in the Andean region. However, since the name already exists it seems preferable to be preserved although *L. australis* seems to be nothing but a late transient of *L. steinmanni*.

Occurrence and distribution. Levels CM-6b and CM-26 of the studied section, indicating the species ranges at least through the Gerthi Subzone (new), Steinmanni Zone in the Upper Bathonian according to the present material. However, the holotype comes from a level W4 (in Riccardi & Westermann 1991a) which could correspond to a somewhat lower stratigraphic position. But this is unclear since the section given by Riccardi & Westermann (1991a) is rather a sketch with no details, hampering a comparison under fine stratigraphic control.

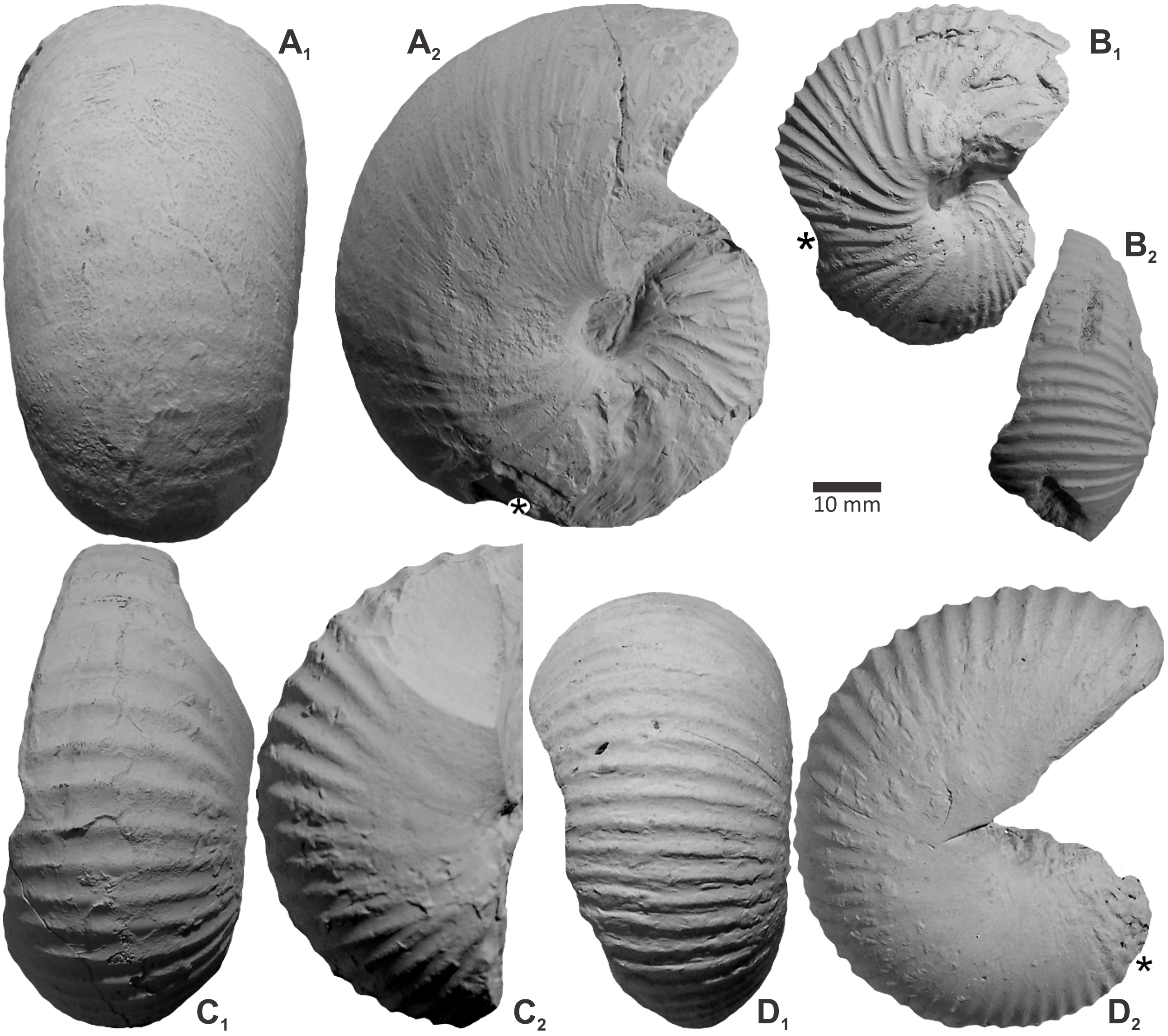


Figure 26. **A**-**B**: *Eurycephalites belgranoi* n. sp., Steinmanni Subzone, Steinmanni Zone. **A**: holotype, complete adult macroconch (MOZ-PI-7411/2), level CM-1, *gulisanoi* Hz. **B**: paratype, juvenile? macroconch with incomplete bodychamber (MOZ-PI-7413), level CM-5. **C**: *Eurycephalites* cf. *gottschei* (Tornquist, 1898), macroconch bodychamber (MOZ-PI-7414), level CM-6a. **D**: *Eurycephalites gottschei* (Tornquist, 1898), adult macroconch (MOZ-PI-7426), level CM-38, basal Gottschei Zone. – All natural size (x1). Asterisk at last septum.

Genus *Eurycephalites* Spath, 1928

Type species. *Macrocephalites vergarensis* Burckhardt, 1903; by original designation (= *Macrocephalites gottschei* Tornquist, 1898, subj.: Parent 1997).

Remarks. The genus has been studied in detail by Riccardi et al. (1989), Sandoval et al. (1990), Riccardi & Westermann (1991a), and Parent (1997, 1998). The morpho-ornamental changes developed by the lineage through its evolution in the Gottschei-Proximum zones (Lower Callovian) have been described as a succession of three species: *Eurycephalites gottschei* (Tornquist, 1898), *Eurycephalites rotundus* (Tornquist, 1898), and *Eurycephalites extremus* (Tornquist, 1898). The ontogeny and sexual dimorphism are well established, the microconchs are *Xenocephalites*-like, strongly variocostate and smaller than the macroconchs. The (sexual) dimorphic correspondence between the nominal species *Macrocephalites vergarensis* [M] and *Sphaeroceras gottschei* [m], this latter a *Xenocephalites* in morphological grounds, was demonstrated by Parent (1997). The systematic and stratigraphic nomenclatural consequences are well established, having been discussed by Parent (1998), Westermann et al. (2002), Garrido & Parent (2013), and Parent & Garrido (2015). The ontogeny of *E. rotundus* and *E. extremus* have been described by Riccardi & Westermann (1991a) and Parent (1998). The microconch of *E. rotundus* has been described and figured in Parent (1998: 112, fig. 29E-J). The corresponding microconch of *E. extremus* has been demonstrated (Parent

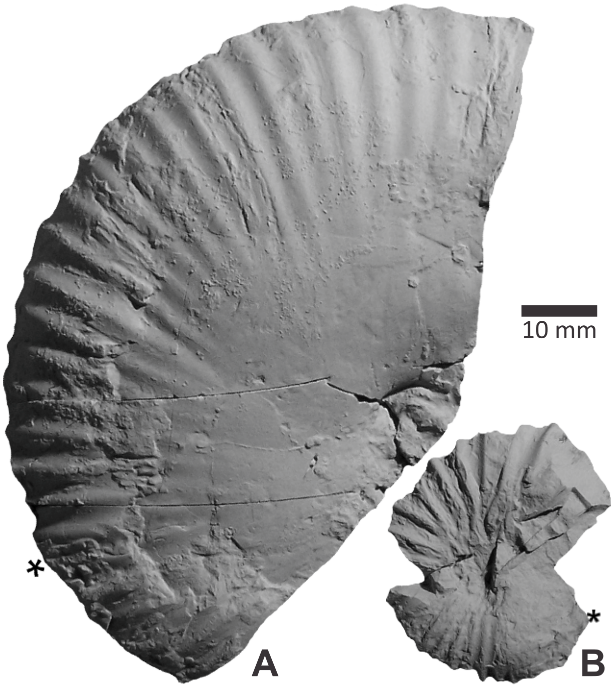


Figure 27. *Eurycephalites gottschei* (Tornquist, 1898), basal Gottschei Zone. **A**: crushed, incomplete adult macroconch (MOZ-PI-7428), level CM-42. **B**: crushed adult microconch (MOZ-PI-7430), level CM-44. – All natural size (x1). Asterisk at last septum.

1998) to be *Xenocephalites stipanicici* Riccardi, Westermann & Elmi, 1989 by identity of the inner whorls of both nominal species which co-occur in the Bodenbenderi and Proximum zones. The Upper Bathonian-Lower Callovian segment of the lineage shows imperceptible sexual size dimorphism between *E. gottschei* and *E. rotundus*, but this becomes stronger in *E. extremus* (Fig. 25); in *E. belgranoi* n. sp. seems to be strong (see below).

Eurycephalites belgranoi n. sp.

Fig. 26A-B

Etymology. After Manuel J.J.C.J. Belgrano (1770-1820), one of the founders of the República Argentina, and pioneer of the scientific research and technology as the keys for the development of the country.

Material. Holotype (Fig. 26A): a complete adult macroconch (MOZ-PI-7411/2) from level CM-1. Additional material: one juvenile? macroconch with part of bodychamber (MOZ-PI-7413) from level CM-5 (Fig. 26B).

Type locality. Chacay Melehué, northern Neuquén Province, Argentina (Figs. 1-2).

Type horizon. Bed and level CM-1 (Fig. 4), Steinmanni Subzone, Steinmanni Zone, Upper Bathonian; Los Molles Formation.

Diagnosis. Macroconch: *Eurycephalites* with a short, half-whorl bodychamber bearing only growth lines.

Description of the holotype. Macroconch. Medium size, globose macroconch (maximum D = 78 mm, probably peristome). The last whorl of the adult phragmocone is involute, depressed, subrectangular-suboval. The primary ribs are fine and sharp, subradial, slightly flexuous; they divide irregularly at about the mid-flank in secondaries of the same strength, crossing the venter with no modification.

The bodychamber begins at D_{ls} = 53 mm. Involute (U/D = 0.10). Whorl section subrectangular (W/D = 0.58) depressed with almost flat flanks, passing indistinctly into a wide rounded to flattish venter. There are few blunt ventral ribs at the beginning but these fade away leaving the flanks and venter covered only by growth lines. Short, one half whorl long (L_{BC} = 180°).

Remarks. The adult size, the stout subrectangular and depressed whorls with narrow umbilicus, densely ribbed phragmocone and smooth adult flanks indicate inclusion of the present macroconchiate specimens in *Eurycephalites*. *E. gottschei* is the most similar and closest in stratigraphic position to *E. belgranoi* n. sp. It occurs in younger levels, and differs from the new species by the persistent, strong ventral and upper flank ribbing in the bodychamber, and by the somewhat wider relative umbilicus. The smooth bodychamber as in *E. belgranoi* n. sp. reappears in extreme variants of *Eurycephalites rotundus* (Tornquist, 1898) in the Bodenbenderi Zone (e.g. Riccardi & Westermann 1991a: pl. 5: 2). *Lilloettia* has a persistent suboval to subtriangular whorl section from the inner whorls and is more finely ribbed. *Iniskinites* tends to increase coarseness of the ribbing in the bodychamber, and is more widely umbilicated at comparable diameter. *I. gulisanoi* is superficially similar, but has a higher than wide suboval whorl section, the ribbing is straight and prosocline, and the bodychamber is much longer. *Stehnocephalites gerthi* retains the ribbing in the bodychamber, is more widely umbilicated from middle whorls, and the whorl section is usually relatively wider and depressed, suboval.

The corresponding microconch seems to be represented by the specimen figured as *Xenocephalites* cf. *araucanus* (Burckhardt, 1903) in Parent (1998: fig. 32G-H); this specimen comes from levels equivalent to the type horizon of *E. belgranoi* n. sp., the ribbing at comparable diameter is the same, and the bodychamber has a similarly flattish venter.

The present species is the earliest known of the genus, showing that the origin of *Eurycephalites* is earlier than previously supposed (Riccardi & Westermann 1991a, Parent 1997, 1998) as derivative from *Lilloettia* in the uppermost Steinmanni Zone. Its co-occurrence with *I. gulisanoi* in the level CM-1 moves the earliest record of the genus down to the Steinmanni Subzone, lower part of the Steinmanni Zone.

Occurrence and distribution. The holotype comes from level CM-1 (*gulisanoi* Hz.) and the other specimen from CM-5, Steinmanni Subzone, Steinmanni Zone.

Eurycephalites gottschei (Tornquist, 1898)

Figs. 26D, 27

Synonymy. See Riccardi & Westermann (1991a), Parent (1997) and Parent (1998).

Material. Eight mostly crushed macroconchs and five microconchs (MOZ-PI-7426/1, 7428, and 7430) from levels CM-38, 42, 44 and 46. One incomplete macroconch cf.-specimen (MOZ-PI-7414) level CM-6a.

Remarks. The species is recorded from level CM-38 which is thus taken as the base of the Gottschei Zone in the studied section. The macroconchiate specimens (e.g. Figs. 26D, 27A) are rather incomplete, matching in size and shell-shape the morphotypes with smooth flanks in the bodychamber described by Riccardi & Westermann (1991a: pl. 2: 1) and Parent (1997: fig. 6.8). The microconchs are typically smaller and more coarsely ribbed, *Xenocephalites*-like ammonites (see Parent 1997, Parent 1998: fig. 29A-D).

The range of the species in the studied section is levels CM-38 to CM-47 (Fig. 4). The material from levels CM-44 and 46 consists of small juvenile unsexed specimens, macroconch phragmocones and adult microconchs. This age-structure is similarly observed in samples of *E. rotundus* from concretions of the Bodenbenderi Zone (see Parent 1998).

The fragmentary specimen figured as *E.* cf. *gottschei* [M] (Fig. 26C) comes from the level CM-6a. It is a macroconch bodychamber very similar to typical *E. gottschei* [M] but with strong ribs from the umbilical shoulder; however, its deeper stratigraphic position and the incomplete preservation hamper a closer determination.

BIOSTRATIGRAPHY AND CHRONOSTRATIGRAPHY

Biostratigraphy

The ammonite succession indicates that the levels CM-1 to CM-37 belong to the Steinmanni (standard) Zone (Fig. 4), according to the occurrence of *I. gulisanoi* (basal level), *I. crassus*, *L. australis* and *S. gerthi* (Riccardi et al. 1989, Parent 1998) as well as *N. steinmanni*, *C. jupiter* and *A.* aff. *obsoletoides*. The base of the immediately overlying Gottschei (ex Vergarensis) Zone is taken provisionally at the level CM-38 since it bears the first local occurrence of *E. gottschei*. The original definition of the Gottschei Zone (as Vergarensis Zone by Riccardi et al. 1989: 561) is defficient since no ammonite association was defined in the basal horizon, it was merely indicated as a level in a succession which unfortunately was poorly described. In this form it is not possible to identify the base of the zone out of the type section.

The studied section is located (1) about 4 km west of the section of Parent (1998) with a directly comparable ammonite succession, and (2) between the two sections studied by Riccardi & Westermann (1991a: 10-12, fig. 2A1), of which their locality 5 shows an ammonite succession closely comparable with the present one.

From the ammonite associations (Table 1, Fig. 4) three biohorizons (biostratigraphic units) can be recognized.

***gulisanoi* Hz.** (emended): level CM-1 of the studied section, characterized by the co-occurrence of *Iniskinites gulisanoi* (morphotype matching the holotype, see Fig. 18 this report, and Riccardi & Westermann 1991a: pl. 14: 5-6) and *Eurycephalites belgranoi* n. sp. (Fig. 26A).

This biohorizon was introduced in Parent (1998: 72, fig. 2) but is now restricted to the bed (or beds) containing the association of *I. gulisanoi* and *E. belgranoi* n. sp., that is the level CM-1 in the present section. It corresponds to the upper part of the bed 0 in the section of Parent (1998) and roughly to the level W3 of Riccardi & Westermann (1991a: 11).

***crassus* Hz.** (emended): level CM-6b of the studied section. The characteristic fauna consists of specific morphotypes/transients of the following ammonite species: *Lilloettia australis* (Fig. 22), *Iniskinites crassus* (Fig. 19D-E), and *Stehnocephalites gerthi* (macroconchs large and stout, depressed, with dense and strong ribbing, the secondaries with same strength as primaries).

This biohorizon was introduced in Parent (1998: 72) but is now restricted to the bed (or beds) containing the ammonite assemblage of the indicated morphotypes of *L. australis*, *I. crassus*, and *S. gerthi*, that is the level CM-6b in the present section. It corresponds to the upper part of bed 11a of Parent (1998) and roughly to the beds 4-5? of Riccardi et al. (1989: fig. 2).

In this level occur the first *L. australis* and the first *S. gerthi* in the present section. However, these first and last occurrences of single species must be taken as purely local, ecologic-taphonomic phenomena with no accurate chronostratigraphic meaning (as explained above). What matters for the definition of a recognizable marker for time-correlation is the assemblage of morphotypes of the nominal species, per se a unique event.

***jupiter* Hz.**?: the level CM-35 of the studied section seems to correspond to this biohorizon, yielding the following ammonites (see Table 1, Fig. 4): *Choffatia jupiter*, *Choffatia* aff. *subbakeriae*, *Choffatia irregularis* n. sp., *Neuqueniceras steinmanni*, *Alcidellus* n. sp. aff. *tenuitriatus*, *Oxycerites* sp. A, *Stehnocephalites gerthi*. Of these, *C. jupiter*, *N. steinmanni*, and *S. gerthi*, are abundant and very similar to those figured by Riccardi et al. (1989) and tentatively assigned to this biohorizon. The *jupiter* Hz. is typical of sections of Caracoles and Cordillera Domeyko in northern Chile (Hillebrandt 1970, Gröschke & Hillebrandt 1985), and is included in the Gerthi Subzone (new, as *gerthi* Hz. in Riccardi et al. 1989).

Chronostratigraphy

In its type locality (Chacay Melehué) the Steinmanni Zone is a time-rock unit about 110 m thick, very fossiliferous in its upper part bearing a diverse and abundant fauna (Riccardi et al. 1989, Parent 1998). In our section the interval of levels CM-6b to CM-37 represents the "*Stehnocephalites gerthi* Horizon" of Riccardi et al. (1989; see also Parent 1998). This is a thick rock unit consisting of 40-44 m of shales in the study area, that is too thick for a faunal horizon or biohorizon. Indeed, our sampling shows the fauna described above with several fossiliferous levels and differentiable assemblages with different transients of some species (mainly *S. gerthi* itself as well as *L. australis*) as described above. Thus, the "*Stehnocephalites gerthi* Horizon" includes several different biohorizons and so can be rather considered as a subdivision of the Steinmanni Zone, i.e. a chronostratigraphic subzone.

The three biohorizons considered represent time-planes in the succession that can be taken as strong markers or anchor-points. Therefore, one of them, the *crassus* Hz., is taken as the representation of a time-plane allowing the subdivision of the Steinmanni Zone in two standard subzones (Figs. 3, 4):

Steinmanni Subzone (new): the base corresponds to that of the zone as defined in Riccardi et al. (1989), and its top is below the base of the Gerthi Subzone (new), i.e., the *crassus* Hz. The fauna is described in Riccardi et al. (1989), Riccardi & Westermann (1991a, b), Parent (1997, 1998), and above (see Table 1, Fig. 4).

Gerthi Subzone (new): the base of this subzone is defined by the *crassus* Hz., level CM-6b of the studied section, and its top is below the base of the Gottschei standard Zone, thus reaching nearly 43 m in thickness (Fig. 4).

This subzone is based on the "*Stehnocephalites gerthi* Horizon" of Riccardi et al. (1989), about 40 m of shales in Chacay Melehué in the upper part of the Steinmanni Zone. The fauna of the subzone includes *Stehnocephalites gerthi* (dominant), *Lilloettia australis*, *Iniskinites crassus*, *Choffatia* aff. *neumayri* (Siemiradzki, 1899) in Parent (1998), *Choffatia* aff. *subbakeriae*, *Choffatia jupiter*, *Choffatia irregularis* n. sp., *Neuqueniceras steinmanni*, *Alcidellus* n. sp. aff. *tenuistriatus*, *Oxycerites sp.* A.

First and last occurrences should be taken as purely local, ecologic-taphonomic phenomena with restricted chronostratigraphic meaning, thus with low or provisional value for time-correlation. These punctual occurrences lose their meaning as soon as new specimens above and/or below them are recorded in the same or other section. Contrary, time-significant are assemblages or associations from a single level, whose significance is rooted in the uniqueness of the co-occurrence of specific morphotypes.

Time-correlation with the Primary Standard

Time-correlation of the Steinmanni and Gottschei zones with the Primary Standard (Fig. 3) has been discussed by Riccardi et al. (1989) and Sandoval et al. (1990). New collections from Vega de la Veranada (Fig. 1), currently under description, give strong support to an Early Callovian age for the Gottschei Zone and Late Bathonian for the Steinmanni Zone as established by Riccardi et al. (1989).

From the 60-m-thick Lajas Fm at Vega de la Veranada we have collected from scattered ammonite levels the following succession of ammonites, from below:

Faunal level I [Parkinsoni-lower Zigzag? zones, uppermost Bajocian-lowermost Bathonian]: *Lobosphinctes intersertus* Buckman, 1923; a well preserved macroconch specimen, indistinguishable from the holotype and closely comparable with a similar specimen from Chacay Melehué figured by Riccardi & Westermann (1989: pl. 1: 6). Several fragmentary specimens which could be attributed to *Caumontisphinctes*.

Faunal level II [Upper Bathonian]: *Kheraiceras* sp. A. A globose, coarsely ribbed adult phragmocone, uncoiled at the end of the last whorl, indicating a small adult size. It is closely comparable with the Late Bathonian (Bremeri Zone) specimen from Verzé N du Mâconnais figured by Martin & Mangold (2015: pl. 14: 7-8) as *Bullatimorphites* cf. *hannoveranus* (Roemer, 1911), whose adult stage seems to have been illustrated by Mangold (1971: figs. 96-97) from Boyeux-Saint-Jerome (Ain), France. Other similar is the Late Bathonian specimen from Kandern, southwestern Germany figured by Hahn (1971: pl. 8: 3) as *Bullatimorphites bullatus* (d'Orbigny, 1846). According to Courville et al. (1999) these small forms, transitional from *Bullatimorphites* to *Kheraiceras*, are characteristic of late Bathonian Discus Zone.

Faunal level III [Steinmanni Zone, Upper Bathonian]: *Lilloettia steinmanni* (phragmocones).

Faunal level IV [Steinmanni Zone, Upper Bathonian]: *Alcidellus tenuistriatus*, macroconch phragmocones very similar to, or even indistinguishable from the lectotype (Grossouvre 1888: pl. 4: 7).

Faunal level V [Gottschei Zone, Lower Callovian]: complete and well preserved macro- and microconchs of *Kheraiceras bullatum* (d'Orbigny, 1846). The macroconchs are indistinguishable from the lectotype (see Fischer 1994: pl. 56: 1). The microconchs with the peristome preserved are identical in every detail to the lectotype of the corresponding microconch morphospecies *Ammonites microstoma* d'Orbigny, 1846 (see Fischer 1994: pl. 56: 2).

The next faunal levels were recorded from the uppper part of the 21 m-thick Lotena Fm:

Faunal level VI [?Lower Callovian]: poorly preserved specimens of *Choffatia* sp. A, compressed, finely ribbed macroconch phragmocones, similar to the lectotype of *C. subbakeriae*.

Faunal level VII [*patagoniensis* Hz.?, Patagoniensis Zone, lower Upper Callovian]: *Rehmannia patagoniensis* Weaver, 1931; large complete adult macroconchs matching the specimens of the transient alpha of the species described from Picún Leufú, in the southern end of the basin (Garrido & Parent 2013).

Upwards in the succession, the Late Callovian to Early Oxfordian ammonite fauna of the La Manga Fm was already described by Parent & Garrido (2015). Some new forms are to be published elsewhere.

The ammonites are rather isolated in few levels, lacking associations for sharp time-correlation. However, we can take advantage of the succession of the several ammonite levels which, although insufficient, are an important property for chronostratigraphic assignations. This succession of ammonite levels gains significance by being taken as supplement to the successions of associations from Chacay Melehué. The occurrence of *L. steinmanni* (faunal level III) most likely indicates the Steinmanni Subzone (new) since *L. steinmanni* is known to occur in the lower part of the Steinmanni Zone (this study; see also Riccardi & Westermann 1991a). The specimens of *A. tenuistriatus* (faunal level IV) perfectly match the lectotype which is Late Bathonian. *K. bullatum* (faunal level V, Gottschei Zone) is mostly confined to the lower Herveyi (Bullatum) Zone in the Submediterranean area of the Tethys (Westermann & Callomon 1988), with some earliest occurrences in the upper Discus Zone (Upper Bathonian) in the form of the species (or older transient) *Kheraiceras* cf. *hannoveranum* (Roemer, 1911) according to Westermann et al. (1984), Courville (1988), and Courville et al. (1999). The occurrence of *Kheraiceras* sp. A in the level II gives consistence to the succession, which undoubtely would be Late Bathonian in age.

Time-correlation of the Steinmanni and Gottschei zones with the Primary Standard Zonation (Fig. 3) is rather well established (Hillebrandt 1970, Gröschke & Hillebrandt 1985, 1994, Riccardi et al. 1989). There have not been advances based on new published evidence since then, only reproductions of former results. The material described herein and the succession of Vega de la Veranada discussed above strongly support those datations.

CONCLUSION

The results of the present study describe the ammonite record of Chacay Melehué for the upper part of the Steinmanni Zone (Upper Bathonian), here established as the Gerthi (standard) Subzone (new), above the Steinmanni (standard) Subzone (new). The moderately fossiliferous Gerthi Subzone is demonstrated to be a sequence of commonly thin intervals with ammonites, separated by longer barren intervals devoid of fossils and frequent gaps in the sequence, beyond the bedding planes.

The succession is dominated by representatives of the Eurycephalitinae with intercalated, well separated levels which include perisphinctids and oppeliids. These concentrations of perisphinctids and oppeliids in discrete horizons originate from the influx of shells and/or dead animals coming from shallower eastern biocoenoses into the depocentre, the locus of formation of the studied taphocoenoses.

The recorded species are mostly already known and typical of the interval, but three taxa are new: *Choffatia irregularis* n. sp., *Eurycephalites belgranoi* n. sp., and *Alcidellus* n. sp. aff. *tenuistriatus*.

The systematics of the perisphinctids remain provisional; these ammonoids show some particular ornamental features which in combination point to a new genus or genera more or less closely related to *Choffatia* (sensu lato).

Lilloettia australis, that was so far poorly known, is well represented by large well preserved macroconchs which allow to characterize its ontogeny and to establish its stratigraphic range in the Gerthi Subzone (new). Macroconchs of *Iniskinites crassus* were recorded associated with the corresponding microconch, a *Xenocephalites*-like ammonite with stiff primary ribs. *Eurycephalites belgranoi* n. sp. and *Eurycephalites* cf. *gottschei* from the Steinmanni subzone (new) extend downwards the stratigraphic range of the genus *Eurycephalites* which was hitherto known to range from the Lower Callovian Gottschei Zone upwards. A consequence of this discovery is that *Eurycephalites* and *Lilloettia* are two independent lineages which have coexisted at least during the entire Gerthi Subzone.

The uppermost record of *I. crassus*, at the base of the Gottschei Zone, one subzone above the formerly uppermost occurrence known for the species (the precise occurrences of intermediate transients is still unknown) is a good example of the practical impossibility of knowing the full stratigraphic range of any species. The occurrence of a single species must be considered to be the consequence of many concurrent circumstancial events, and thus never be taken as a precise marker of a chronostratigraphic zone or unit, much less to define the base of a chronostratigraphic zone. This situation is solved by the use of ammonite biohorizons in establishing the base of standard chronostratgraphic subzones and zones. The association of well described morphotypes of a group of species -the ammonite assemblage- is a phenomenon really confined to a short time-interval, a time-plane for any practical purpose.

The subdivision of the Steinmanni Zone in two new standard subzones is established: the Steinmanni Subzone and the Gerthi Subzone. This latter is based on the former "*Stehnocephalites gerthi* Horizon" which includes a succession of different ammonite assemblages. The lowermost faunal horizon, the *crassus* Hz. (emended), being characterized by the association of *I. crassus*, *S. gerthi* (earliest representatives known) and *L. australis*, is taken as the base of the Gerthi Subzone. The *gulisanoi* Hz. (emended), in the upper (possibly uppermost) part of the Steinmanni Zone, is characterized by the association of *I. gulisanoi* and *E. belgranoi* n. sp. The widely accepted Late Bathonian age for the Steinmanni Zone and Early Callovian for the Gottschei Zone are strongly supported by the described fauna as well as by the new information on the ammonite succession in the Lajas Fm at Vega de la Veranada.

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