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REDESCRIPTION OF *PLEUROTOMARIA GERTHI* WEAVER, 1931 (GASTROPODA, VETIGASTROPODA), FROM THE EARLY CRETACEOUS OF ARGENTINA: NEW DATA ON ITS AGE, ASSOCIATED PALAEOENVIRONMENTS AND PALAEOBIOGEOGRAPHIC AFFINITIES

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Abstract. *Pleurotomaria gerthi* Weaver, 1931 (Gastropoda, Vetigastropoda) from the Pilmatué Member of the Agrio Formation is redescribed and reillustrated on the basis of 38 newly collected specimens from nine localities in Neuquén Province, Argentina, including its type locality. The holotype housed in the C.E. Weaver collection is also refigured. *Pleurotomaria gerthi*-bearing levels, dated using a detailed ammonoid zonation, are late Valanginian–early Hauterivian. Taphonomic and sedimentological data gathered at three of the nine studied sections indicate that *P. gerthi* dwelled in shallow marine settings above the storm-weather wave-base. Associated palaeoenvironments are interpreted as inner shelf and inner carbonate ramp settings deposited under the influence storm currents and waves. The species lived on well-oxygenated soft sandy and patchy bioclastic substrates in normal marine warm-temperate waters within the photic zone, associated with a high-diversity macrofossil assemblage. Our study shows that its preferred habitat was the middle carbonate ramp, below the fair-weather wave-base, under low to moderate energy from episodic storm waves and currents. *Pleurotomaria gerthi* is endemic to the marine Andean basins of the western margin of southern South America and its oldest record is from the Tithonian of the Aconcagua-Central Chile Basin. It bears the closest morphological resemblance to Early Cretaceous species from the Tethyan Realm. During the Berriasian–Barremian interval, *Pleurotomaria* was a pandemic genus, with records in peri-Tethyan basins of Europe and India, as well as in north and south temperate marine basins in England and the western margin of South America.

Key words. Gastropoda. *Pleurotomaria*. Lower Cretaceous. Neuquén. Argentina.

Resumen. REDESCRIPCIÓN DE *PLEUROTOMARIA GERTHI* WEAVER, 1931 (GASTROPODA, VETIGASTROPODA), DEL CRETÁCICO TEMPRANO DE ARGENTINA: NUEVOS APORTES A SU BIOCRÓN, PALEOAMBIENTES ASOCIADOS Y AFINIDADES PALEOBIOGEOGRÁFICAS. *Pleurotomaria gerthi* Weaver, 1931 (Gastropoda, Pleurotomariidae) es redescripta y reilustrada en base a 38 ejemplares inéditos colectados en nueve localidades en la provincia de Neuquén, Argentina, incluyendo su localidad tipo. El holotipo, en la colección C.E. Weaver, es también refigurado. Los niveles portadores de *P. gerthi*, datados en base a una detallada zonación de amonoideos, son valanginianos tardíos a hauterivianos tempranos. Datos tafonómicos y sedimentológicos, reunidos en tres de las nueve secciones estudiadas, indican que *P. gerthi* habitaba en ambientes marinos someros, por encima de la base de olas de tormenta. Los paleoambientes asociados se interpretan como plataforma y rampa carbonática internas, con sedimentación influenciada por tormentas, corrientes y oleaje. Esta especie ocupaba sustratos blandos arenosos a bioclásticos discontinuos, bien oxigenados, dentro de la zona fótica y bajo condiciones de salinidad marina normal y aguas templadas a cálidas, junto a una asociación de macrofósiles altamente diversa. Nuestro estudio muestra que su hábitat preferido era la rampa carbonática media, por debajo de la base de olas de tormenta, en condiciones de energía moderada a baja como consecuencia de corrientes y olas de tormentas episódicas. *Pleurotomaria gerthi* es endémica de las cuencas marinas andinas del sudoeste de América del Sur. Su registro más antiguo es del Tithoniano de la Cuenca Aconcagua-Chile Central. Muestra afinidad morfológica con las especies del Cretácico Temprano del Reino Tethyano. Durante el Berriasiano–Barremiano, *Pleurotomaria* era un género pandémico con registros en las cuencas peri-tethyanas de Europa y la India, y en cuencas marinas templadas del norte (Inglaterra) y del sur (sudoeste de América de Sur).

Palabras clave. Gastropoda. *Pleurotomaria*. Cretácico Temprano. Neuquén. Argentina.

Current knowledge on Late Jurassic and Early Cretaceous southern hemisphere gastropod faunas is drawn from relatively scarce published work on the subject. Most available data on gastropods comes from the Northern Hemisphere, especially from peri-Tethyan epicontinental seas, *e.g.*, France, Switzerland, the Caucasus region, Crimea (Ukraine), India, and also from northern temperate localities, mainly England and Germany (d’Orbigny, 1842–1843; Pictet and Roux, 1849; Pictet and Campiche, 1861–1864; Wollemann, 1896, 1900; Karakasch, 1907; Cox, 1960a; Drushchits and

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Kudryavtsev, 1960; Jaitly *et al.*, 2000; Das, 2002; Kollmann, 2005). In contrast, records from the Southern Hemisphere are few, mainly from South America and South Africa (Stanton, 1901; Kitchin, 1908; Weaver, 1931; Rennie, 1934).

Late Jurassic gastropod faunas from Argentina are known from the Neuquén Basin, lying in the west-central region of the country. These faunas have been subject of a few modern taxonomic revisions, but pleurotomariids have not been included (*e.g.*, Gründel and Parent, 2001, 2006; Gründel *et al.*, 2007). In contrast, Argentinean Early Cretaceous gastropods have been rather poorly studied despite being moderately abundant at several localities where they are associ-

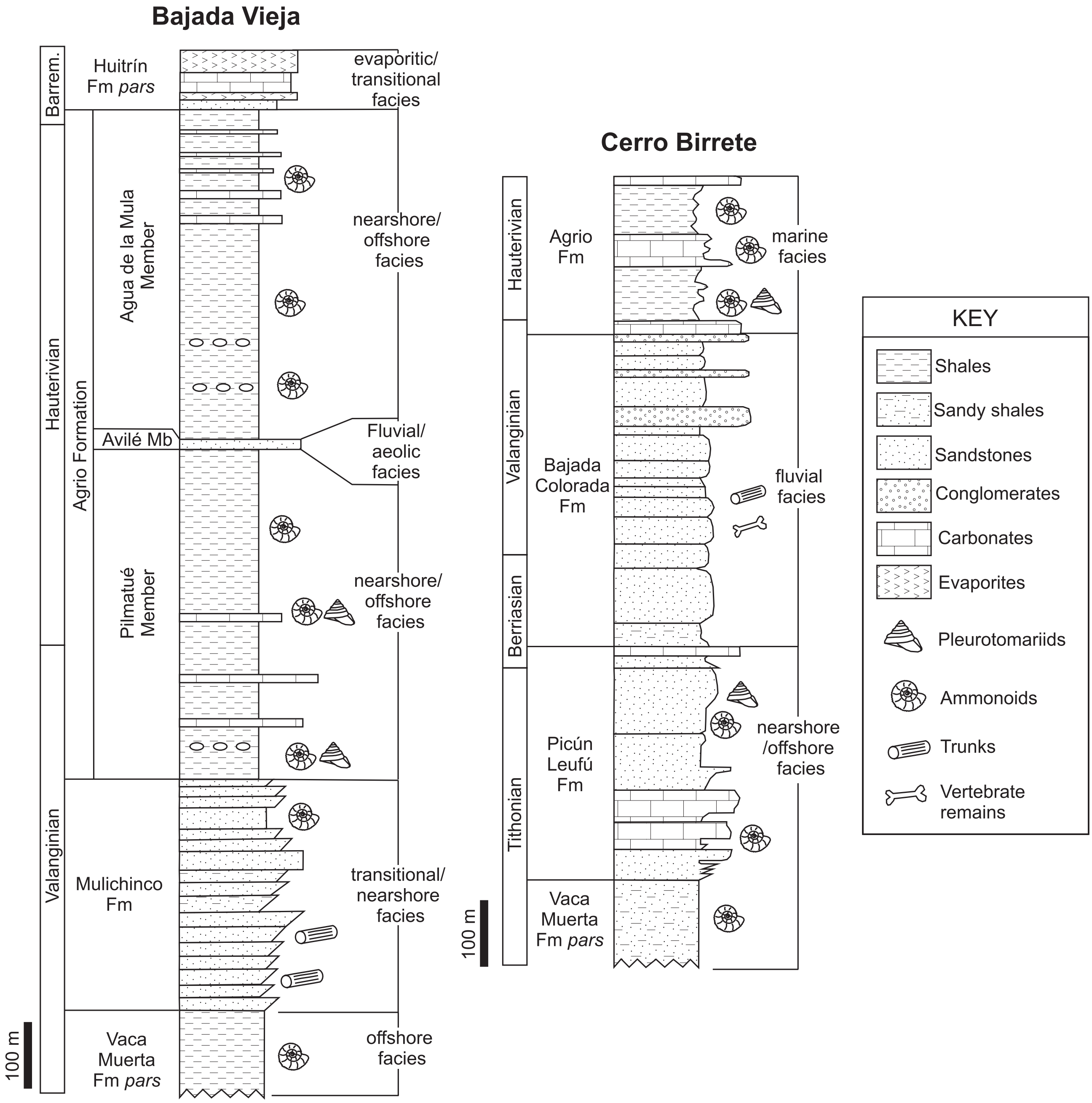


Figure 1. Stratigraphy of the upper part of the Mendoza Group at Bajada Vieja and Cerro Birrete sections showing units, lithology, facies, and pleurotomariid records. Note that the thickness of the Agrio Formation is significantly reduced at Cerro Birrete. Modified from Leanza and Hugo (1997) and Leanza *et al.* (2005)/ *Estratigrafía de la parte superior del Grupo Mendoza en las localidades de Bajada Vieja y Cerro Birrete, indicando unidades, litología, facies y registros de pleurotomáridos. Nótese que la Formación Agrio se reduce significativamente en espesor en Cerro Birrete. Modificado de Leanza y Hugo (1997) y Leanza* et al. *(2005).*

ated with cephalopods and bivalves. There are only a few works on this subject, dealing mainly with their taxonomy and stratigraphic ranges (Behrendsen, 1892; Weaver, 1931; Camacho, 1953; Damborenea *et al.*, 1979; Manceñido and Damborenea, 1984). In the particular case of Argentinean Early Cretaceous pleurotomariids, these have not been studied in detail since the work of Weaver (1931).

From the upper Middle Jurassic–Early Cretaceous interval of Argentina, six pleurotomariid species have been recorded (Tab. 1), namely (1) *P. leufuensis* Weaver, 1931; (2) *P.* cf. *provincialis* d'Orbigny, 1843; (3) *P. gerthi* Weaver, 1931; (4) *P.* cf. *jaccardi* Pictet and Campiche, 1863; (5) *P.* (*Conotomaria*?) cf. *pailleteana* d'Orbigny, 1843; and (6) *P. tardensis* Stanton, 1901. The first four were reported by Weaver (1931), the fifth by Damborenea *et al.* (1979) and the sixth by Stanton (1901). All come from the Neuquén Basin, except for *P. tardensis*, recorded in the Austral Basin (southwestern Argentina). Recently, Harasewych *et al.* (2009), in their review of the Late Cretaceous–early Paleocene pleurotomariid fauna from Antarctica, corrected the generic identification of *P. leufuensis* and *P. tardensis*, relocating them to *Leptomaria* E. Eudes-Deslongchamps, 1864.

Pleurotomariids have also been occasionally recorded in marine Upper Jurassic–Lower Cretaceous units in Chile. Most of these records were tentatively identified as *Pleurotomaria* sp. and left in open nomenclature; most of them lack illustrations. Only Biró-Bagóczky (1964) provided an illustration of the Tithonian specimen of *P. gerthi* recorded in the Lo Valdés Formation exposed in the Aconcagua-Central Chile Basin, Chile.

As part of a long term project on Early Cretaceous gastropods from Argentina, we provide herein new data on the geographic and stratigraphic distribution and palaeoecology of *Pleurotomaria gerthi* Weaver (1931). The following objectives were outlined: (1) to review the taxonomy of *P. gerthi* based on newly collected and better preserved specimens from a wide range of localities throughout the Neuquén Basin, as well as on the holotype; (2) to accurately date the

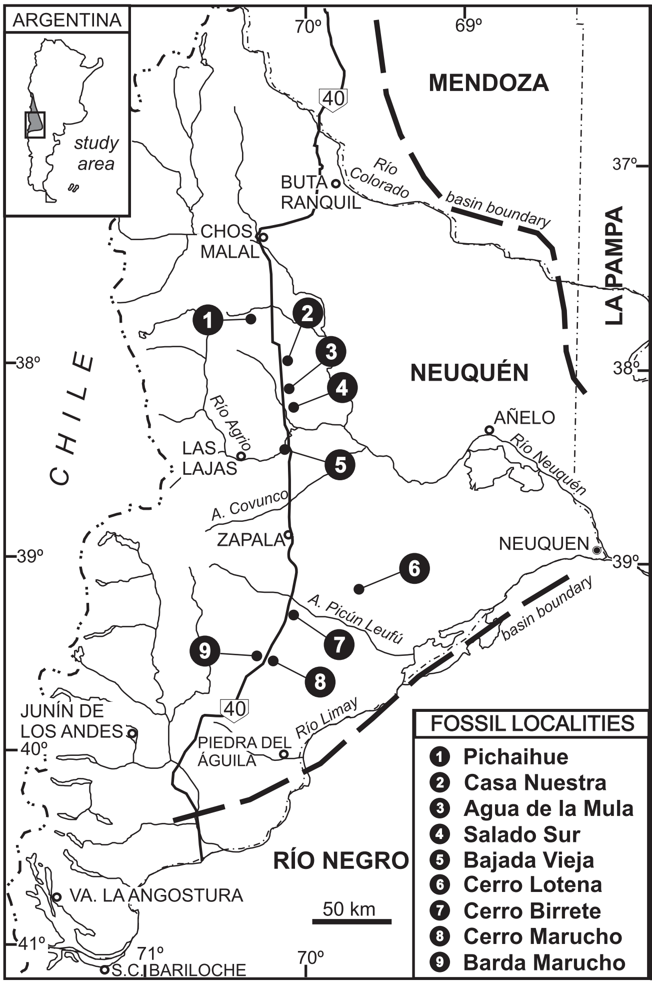
Table 1 - Stratigraphic and geographic distributions of Argentinean Jurassic–Cretaceous pleurotomariids/ **Distribución geográfica y estratigráfica de los pleurotomáridos de Argentina**

	Updated taxonomic status	*Author*	*Unit and locality*	*Ammonoid zone*	*Age*	*References*	*Notes*
Neuquen Basin	**Leptomaria leufuensis**	*(Weaver, 1931)*	*Las Lajas Fm., Cerro Picún Leufú*	*?*	*Callovian*	*Weaver (1931)*	*Originally described as* **Pleurotomaria leufuensis***. New combination by Harasewych et al. (2009).*
	Bathrotomaria *cf.* **provincialis**	*(d'Orbigny, 1843)*	*Picún Leufú Fm., Cerro Lotena*	**Windhauseniceras internispinosum** *Zone*	*Late Middle Tithonian*	*Weaver (1931), this paper*	*Originally described as* **Pleurotomaria** *cf.* **provincialis***. New combination by Kollmann (2005). Weaver's material illustrated here.*
	Pleurotomaria gerthi	*Weaver, 1931*	*Agrio Fm., Cerro Picún Leufú*	**Pseudofavrella angulatiformis-Olcostephanus laticosta** *Subzones*	*Late Valanginian-Early Hauterivian*	*Weaver (1931), this paper*	*Holotype redescribed and reillustrated here along with 38 newly collected specimens.*
	Conotomaria? *cf.* ***pailleteana***	*(d'Orbigny, 1843)*	*Chachao Fm., Puesto González and Lomas Bayas*	*?*	*Early Valanginian*	*Damborenea et al. (1979)*	*Needs revision.*
Austral Basin	**Leptomaria tardensis**	*(Stanton 1901)*	*Río Belgrano Fm., Lago Pueyrredón*	**Hatchericeras patagonense** *Zone*	*Early to Late Barremian*	*Stanton (1901), Aguirre-Urreta (2002)*	*Originally described as* **Pleurotomaria tardensis***. New combination by Harasewych et al. (2009).*

studied material based on a detailed ammonoid zonation, in order to establish the stratigraphic range of *P. gerthi*; (3) to analyse the mode of occurrence and facies relationships of the material studied and thus reconstruct the associated palaeoenvironments; and (4) to assess the palaeobiogeographic distribution of the genus *Pleurotomaria* during the Early Cretaceous and estimate possible affinities of *P. gerthi* with the pleurotomariids of other Cretaceous marine basins.

GEOGRAPHICAL AND GEOLOGICAL SETTING

The Neuquén Basin extends between 32° and 40°S along the foothills of the Andes of west-central Argentina, covering more than 120,000 km^2 and including a continuous latest Triassic–early Paleogene sedimentary column (Howell *et al.*, 2005). The basin holds one of the most complete records of Early Jurassic–Late Cretaceous marine invertebrates in South America. The Lower Cretaceous sediments consist largely of black shales and mudrocks with intercalations of limestones, sandstones and evaporites, reaching a maximum thickness of 2500 m. These strata are included in the Mendoza and Bajada del Agrio Groups (Leanza *et al.*, 2005). Gastropods for this study came from the Agrio Formation of the Mendoza Group (Fig. 1). This unit was originally defined by Weaver (1931) and reaches from southern Neuquén to northern Mendoza provinces. It overlies the Mulichinco, Chachao and Bajada Colorada formations in different parts of the basin. The stratotype has three members. The Pilmatué (lower) and Agua de la Mula (upper) members have been interpreted as mixed clastic-carbonate, storm-influenced shallow-marine settings, with warm-temperate waters as suggested by its faunal content and carbonate deposition (Spalletti *et al.*, 2001; Lazo *et al.*, 2005). The Avilé (middle) Member represents



DESCRIPTION OF FOSSIL LOCALITIES

(1) Pichaihue (37°46' S; 70°13'W)
On the west side of the Sierra de Chorriaca. Access along a track running due east off provincial road 4, 12 km east of Colipilli.

(2) Casa Nuestra (37°53' S; 70°04' W)
Immediately off national road 40, 60 km south of Chos Malal.

(3) Agua de la Mula (38°03' S; 70°03' W)
On the northern side of the Cordillera del Salado. Access from national road 40, 80 km south of Chos Malal, along a gravel road that leads to a dry oil well.

(4) Salado Sur (38°12' S; 70°03' W)
15 km south of Agua de la Mula. Access eastward from national road 40 along a track leading to the Pampa Amarga oil wells.

(5) Bajada Vieja (38°25' S; 70°02'W)
On the gravel road 10 about 7 km southwest of Bajada del Agrio village. 15 km southwest of the Agrio Fm. stratotype, located nead the junction of the Agrio and Salado rivers.

(6) Cerro Lotena (39°11' S, 69°39' W)
47 km SE of Zapala and 3 km eastward from the gravel road 34.

(7) Cerro Birrete (39°16' S, 70°04' W)
92 km south of Bajada Vieja and 7 km south of the bridge of the national road 40 over the Picún Leufú creek. Top of the Picún Leufú section of Weaver (1931).

(8) Cerro Marucho (39°25' S, 70°09' W)
18 km south of Cerro Birrete on the national road 40.

(9) Barda Marucho (39°26' S, 70°11' W)
Just in front of Cerro Marucho on the western side of the national road 40.

Figure 2. Map of the Neuquén Basin, in west-central Argentina, showing the location of fossil localities, and brief geographical description of each locality. Bed-by-bed analyses of the Pilmatué Member of the Agrio Formation were performed at Bajada Vieja, Cerro Birrete and Cerro Marucho/ *Mapa de la Cuenca Neuquina, en el centro-oeste de Argentina, mostrando la ubicación de las localidades fosilíferas y breve descripción de cada localidad. En Bajada Vieja, Cerro Birrete y Cerro Marucho fueron efectuados análisis banco por banco del Miembro Pilmatué de la Formación Agrio.*

fluvial and aeolian sediments accumulated during a middle Hauterivian regression event (Legarreta and Gulisano, 1989). This unit carries an abundant and diverse fossil content including nannofossils, microfossils, palynomorphs, and marine invertebrates and reptiles (Lazo *et al.*, 2005). The entire unit encompasses the upper early Valanginian to early Barremian interval, as indicated by a well-established ammonoid zonation (Aguirre-Urreta *et al.*, 2007).

MATERIALS AND METHODS

This paper is based on 38 newly collected specimens from the Pilmatué Member of the Agrio Formation at nine localities (Fig. 2). Thirty-six specimens were sampled by the authors and two other were collected by D. Rodriguez (Universidad de Buenos Aires). All specimens are housed in the Colección de Paleontología, Departamento de Ciencias Geo- lógicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires (**CPBA**), Argentina. Each catalogue number refers to a sample of specimens from a given section and stratigraphic position. The suffix in each **CPBA** number indicates the number of specimens within that catalogue number.

For taxonomic identification, all specimens were compared with Weaver's type specimen housed in the Burke Museum of Natural History and Culture (**BMNHC**), Seattle, USA. Additionally, a comprehensive comparison with other related species from the literature was carried out.

Morphological terminology follows Cox (1960a,b). Linear measurements were made using a 0.1 mm precision digital caliper. The following percent ratios were calculated in order to provide a useful tool for comparison among species, *i.e.*, shell-height/maximum-diameter and last-whorl height/shell-height ratios. Characters and size parameters are depicted in Figure 3. Criteria for synonymy lists and open nomenclature follow Matthews (1973) and Bengston (1988), respectively. Ammonoid zonation and age data are from Aguirre-Urreta *et al.* (2007).

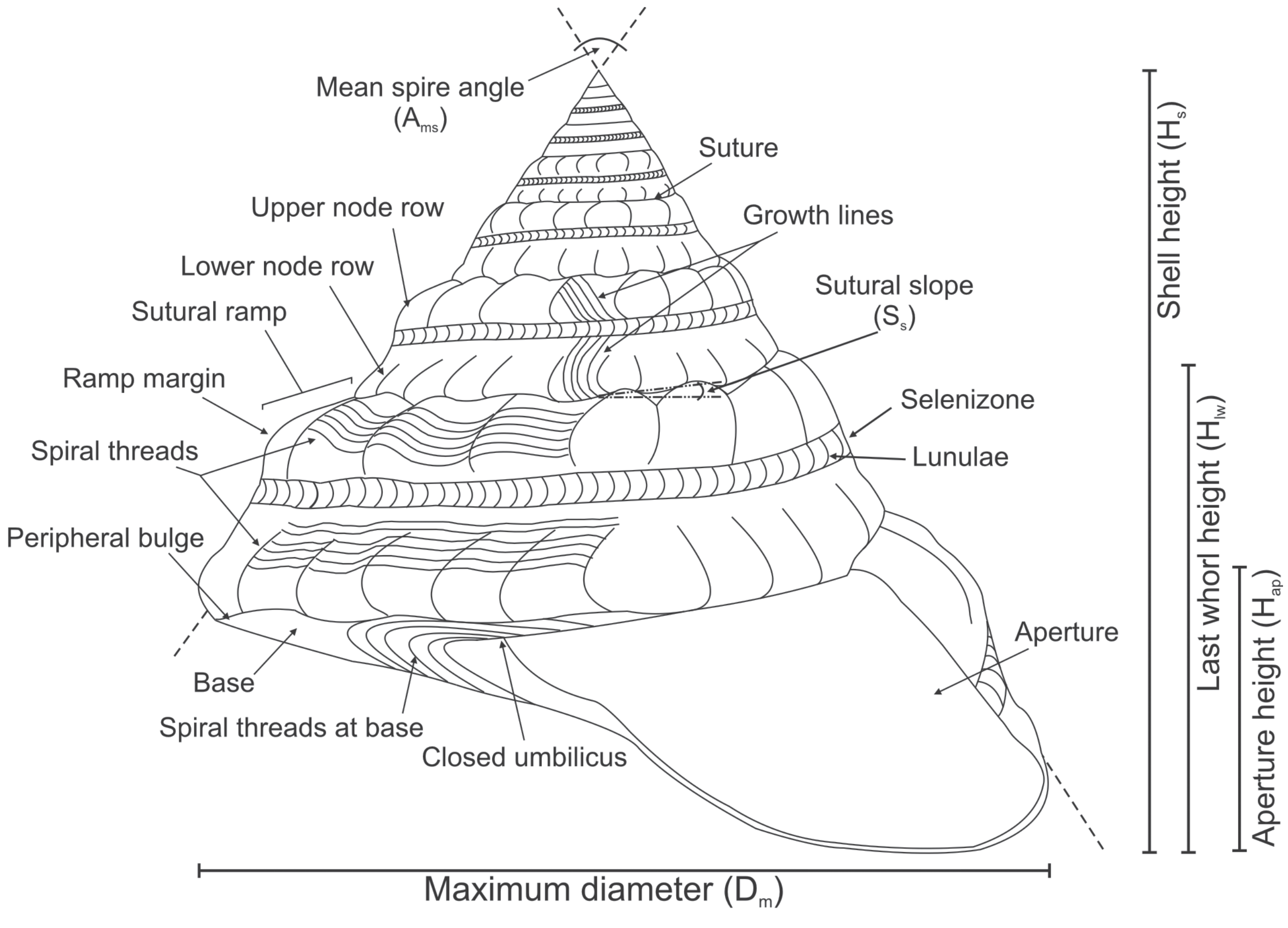


Figure 3. Schematic representation of the shell of ***Pleurotomaria gerthi*** Weaver, 1931 in apertural view showing the character distribution and measurements recorded/ *Representación esquemática de la conchilla de* **Pleurotomaria gerthi** *Weaver, 1931en vista apertural, mostrando la distribución de caracteres y las medidas tomadas.* scale bar/ *escala= 5 mm.*

Occurrence and facies relationships were assessed at three sections: Bajada Vieja, Cerro Birrete and Cerro Marucho; the Pilmatué Member was analyzed bed-by-bed at each section. Pleurotomariid-bearing facies were defined by sedimentological and taphonomic attributes including thickness, geometry, internal complexity, basal contact, primary structure, type of matrix, sorting, dominant fraction, shell-packing, orientation in cross-section, bioturbation and position in sequence. The composition of the *Pleurotomaria*-bearing levels was also analyzed in terms of taxonomy and life and feeding habits (Appendix 1). Generalized environmental interpretations are made for each facies (Tab. 2). Specimens collected were taphonomically scored in order to assess shell preservation. Scoring included mode of fossilization (original shell preserved/ recrystallized shell preserved/ internal mould), fragmentation (whole/ fragmented apex/ fragmented aperture/ fragmented apex and aperture/ fragment), external corrasion (absent/ minor/ moderate/ major), external/ internal bioerosion (absent/ present) and encrustation (absent/ present).

Institutional abbreviations. **CPBA,** Colección de Paleontología, Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina; **BMNHC,** Burke Museum of Natural History and Culture, Seattle, Washington, USA.

Abbreviations for measurements. $\mathbf{A}_{ms}$, mean spire angle; $\mathbf{D}_{m}$, maximum diameter; $\mathbf{H}_{ap}$, aperture height; $\mathbf{H}_{lw}$, last whorl height; $\mathbf{H}_{s}$, shell height; $\mathbf{S}_{s}$, sutural slope.

SYSTEMATIC PALAEONTOLOGY

The systematic classification follows the major groupings of Ponder and Lindberg (1997).

Class GASTROPODA Cuvier, 1797

Subclass ORTHOGASTROPODA Ponder and Lindberg, 1996

Order VETIGASTROPODA Salvini-Plawén, 1980

Superfamily PLEUROTOMARIOIDEA Swainson, 1840

Family PLEUROTOMARIIDAE Swainson, 1840

Diagnosis. See Knight *et al.* (1960, p. *I*219).

Stratigraphic range. Middle Triassic (late Anisian, Begg and Grant-Mackie, 2003) to Recent.

Remarks. Pleurotomariidae is the only living family of the Pleurotomarioidea. Pleurotomariids attained a widespread distribution during the Jurassic and Early Cretaceous. Their Cretaceous peak of species-level diversity was achieved during the early Late Cretaceous, when they also became more geographically restricted (Sohl, 1987). Limited to deep water (>200 m) since the early Cenozoic, members of this family are not uncommon on rocky substrates in the bathyal zone (Harasewych, 2002).

Pleurotomaria and *Bathrotomaria* have gradate shells, whilst *Stuorella*, *Pyrgotrochus*, *Leptomaria*, *Conotomaria* and *Obornella* have conical shells. *Pleurotomaria* and *Bathrotomaria* differ in that the former has nodes at the shoulder and its selenizone lies below the ramp angle.

For discussions on classification criteria, as well as on the number of pleurotomariid genera and subgenera currently recognized, see Hickman (1976), Jaitly *et al.* (2000), Das (2002) and Harasewych and Kiel (2007).

Genus *Pleurotomaria* Defrance, 1826

Type species. *Trochus anglicus* J. Sowerby, 1818; subsequent designation by Woodward (1851). Originally described from the Lower Jurassic of England.

TABLE 2 - Taphonomic, sedimentological and stratigraphic attributes of pleurotomariid-bearing beds in the Pilmatué Member of the Agrio Formation at Bajada Vieja, Cerro Birrete and Cerro Marucho sections/ **Atributos tafonómicos, sedimentológicos y estratigráficos de los niveles portadores de pleurotomariidos en el Miembro Pilmatué de la Formación Agrio en las secciones de Bajada Vieja, Cerro Birrete y Cerro Marucho.**

Facies	*Bed*	*Thickness (m)*	*Geometry*	*Internal complexity*	*Basal contact*	*Primary structure*	*Matrix*
1 SSS	*A-C*	*0,2-0,5*	*tabular*	*homogenous*	*sharp to erosive*	*horizontal lamination*	*fine to medium sandstone*
2 SSC	*I-J*	*0,25*	*tabular*	*homogenous*	*sharp*	*mottled/ concretionary*	*fine-grained*
3 CSC	*D-H*	*0,8-3,2*	*wedge shaped*	*complex*	*gradational*	*horizontal lamination/ cross-bedding/ heterolithic bedding*	*fine-grained*

Diagnosis. See Knight *et al.* (1960, p. I219).

Stratigraphic range and distribution. Middle Triassic (late Anisian, Begg and Grant-Mackie, 2003) to Early Cretaceous (Aptian according to Harasewych and Kiel, 2007). Pacaud (2004) mentioned some previous records of Danian *Pleurotomaria* species from Europe (see p. 620 and fig. 20), but those records should be revised in terms of generic assignment. Pandemic during the Early Cretaceous.

Remarks. *Pleurotomaria* is considered a 'living fossil' by many authors who have included in this taxon Mesozoic, Cenozoic and Recent forms. Following Harasewych and Kiel (2007), *Pleurotomaria* is one of the sixteen recognized Mesozoic pleurotomariid genera, and there are separate genus-level taxa for Cenozoic and Recent forms. Apart from *Pleurotomaria*, other genera present in Cretaceous units are: *Stuorella* Kittl, 1891, *Pyrgotrochus* Fischer, 1885, *Bathrotomaria* Cox, 1956, *Obornella* Cox, 1959, *Conotomaria* Cox, 1959 and *Leptomaria* E. Eudes-Deslongchamps, 1864. *Conotomaria* and *Leptomaria* have been recorded in Palaeocene rocks too (Harasewych and Kiel, 2007). The subgenus *Pleurotomaria* (*Indomaria*) Das, 2002, was recognized in the Cretaceous of India and probably also in France and England. It is characterized by a rather depressed shell with the selenizone above the periphery and lacking a nodose sculpture.

Pleurotomaria gerthi **Weaver, 1931**

Figures 4, 5.1–4 and 5.9–11

v*1931 *Pleurotomaria gerthi* n. sp.; Weaver, p. 367–368, pl. 42, fig. 281–283.
v.1931 *Pleurotomaria* cf. *jaccardi* Pictet and Campiche, 1863; Weaver, p. 368–369.

Emended diagnosis. Shell gradate-trochiform, anomphalous, with angulate spire whorls and biangulate last whorl, the lower angulation corresponding to the periphery. Upper angulation sculptured with rounded, heavy and transversely elongate nodes, forming a shoulder that delimits a wide and steeply sloping sutural ramp. Periphery with rounded nodes. Selenizone broad and flattened, just below shoulder and slightly above mid-whorl. Fine spiral cords and very thin growth lines are present. Aperture nearly oval, obliquely elongate.

Diagnosis emendada. Conchilla gradada-troquiforme, anónfala, con las vueltas de la espira anguladas y la última vuelta biangulada, la angulación inferior coincidente con la periferia. Angulación superior ornamentada con nódulos gruesos, redondeados y elongados transversalmente, formando un hombro que delimita una rampa sutural amplia y empinada. Periferia ornamentada con nódulos redondeados. Selenizona amplia y plana, ubicada justo por debajo del hombro y ligeramente por encima de la mitad de la cara de la vuelta. Cordones espirales finos y delgadas líneas de crecimiento están presentes en todas las vueltas. Abertura casi ovalada, elongada en forma oblícua al eje de enroscamiento.

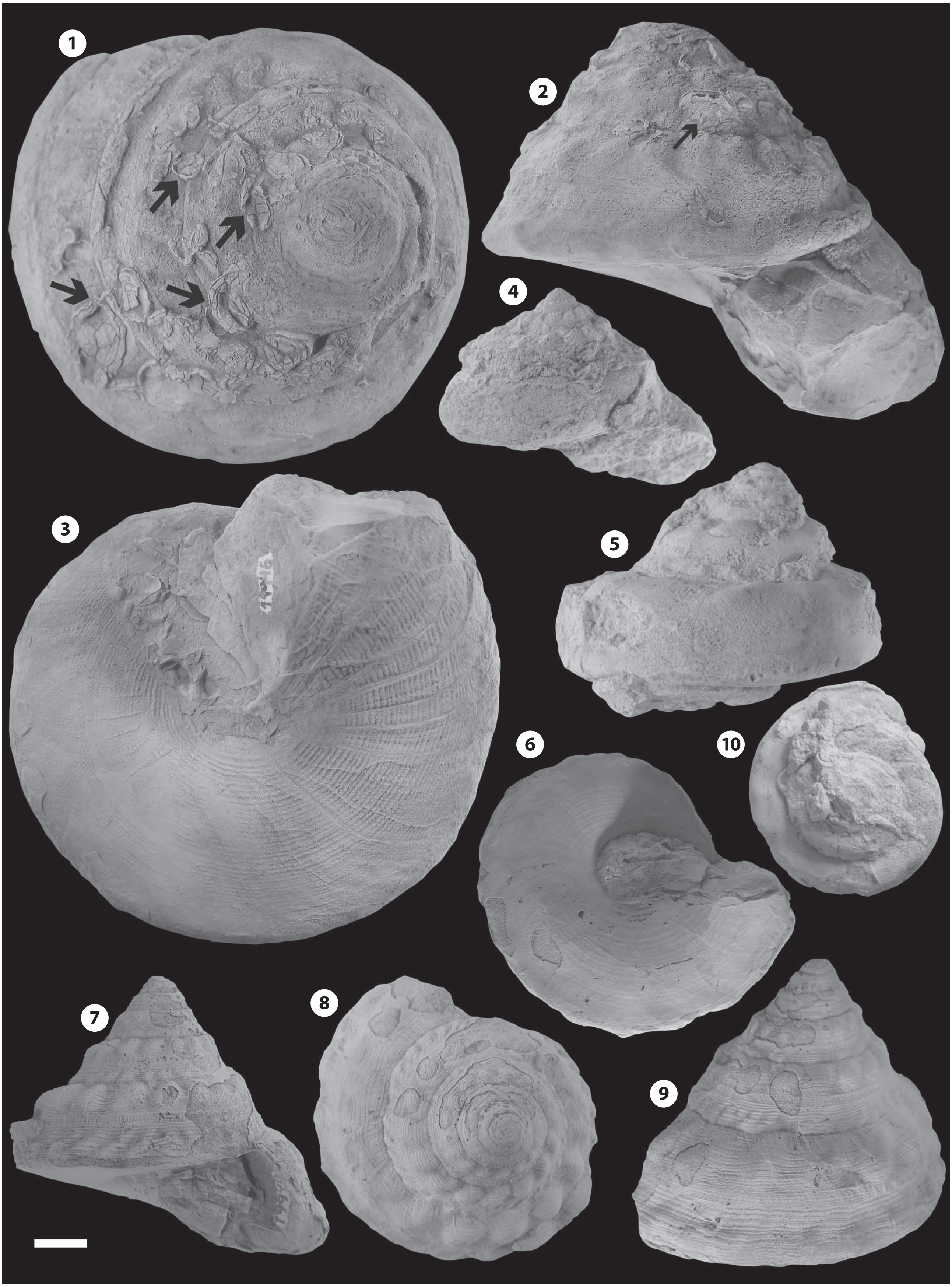
Holotype. BMNHC 266 (Fig. 5.1–4).

Material examined. Thirty-eight newly collected specimens from the Pilmatué Member of the Agrio Formation (Tab. 3) and the holotype (BMNHC 266).

Type locality and stratotype. Picún Leufú area, 10 km west from Cerro Picún Leufú (see Weaver, 1931). This locality is here referred to Cerro Birrete (S39°17.139′–W70° 4.83′), Neuquén Province, west-central Argentina. Weaver (1931) misinterpreted the age of the strata exposed at Cerro Birrete assuming that they belonged to the Agua de la Mula Member of the Agrio Formation and were of Barremian–Aptian age. Rodríguez (2007), in agreement with our field observations, stated that only part of the Pilmatué Member crops out in that area, and therefore its age is late Valanginian–early Hauterivian (see below).

Stratigraphic and geographic range. All the material studied here is of late Valanginian–early Hauterivian age —in-

Sorting	*Dominant fraction*	*Shell-packing*	*Orientation in cross-section*	*Bioturbation*	*Position in sequence*
well-sorted	*shell debris*	*poor to dense*	*high variance*	*low*	*medium*
very poorly-sorted	*valve fragments/ complete shells*	*poor to dense*	*high variance/ life position*	*high*	*medium*
very poorly-sorted	*shell debris/ complete shells*	*poor to dense*	*high variance*	*high*	*top*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9

cluding the holotype— and comes from several localities in Neuquén Province, Argentina. Two specimens of the same age collected in Lomas Bayas, Mendoza Province, Argentina, cannot be referred with certainty to *P. gerthi* because of their poor preservation. Considering the Chilean record (Biró-Bagóczky, 1964), the age range of *P. gerthi* can be extended to the latest Tithonian.

Description. Shell medium to large, wider than tall, gradate-trochiform, acute (Ams= 76°). Protoconch and first teleoconch whorls not preserved. Teleoconch with five whorls preserved. Spire low, with flat to slightly concave profile. Base flat to somewhat convex. Umbilical area narrow, umbilicus closed. Angular spire whorls and biangular last whorl, the lower angulation corresponding to the periphery. Whorls slightly overlapping, suture with moderately abutting whorls. Sutural ramp smooth and rounded in spire and last whorl, narrow in early whorls but wider in later whorls of the teleoconch; angulation ornamented with rounded nodes, separating the upper third of the whorl face from the flat, slightly concave middle third. Lower third less steep and somewhat convex given the presence of a row of rounded, obliquely elongate nodes rising from the abapical suture (or periphery). Periphery of last whorl well defined, angular, ornamented with rounded nodes. Aperture nearly oval in outline, elongate obliquely to the coiling axis. Selenizone broad, 2 mm wide on average in last whorl, immediately below shoulder and slightly above mid-whorl, bordered on each side by a spiral thread and sculptured with lunulae (*i.e.*, crescentic linear ridges concave toward aperture). Thin growth lines, prosocline-prosocyrt between selenizone and adapical suture, opisthocline-prosocyrt between selenizone and abapical suture (or periphery). Growth-rugae at base, sometimes extending adapically into the lower third of last whorl face. Spiral sculpture consisting of fine threads, thirteen between periphery and selenizone, five inside selenizone, 16 to 17 between selenizone and adapical suture, and up to 43 on base. Threads intersecting with growth lines and forming a fine reticulate pattern. On last whorl, nearly 15 rounded, obliquely elongate nodes along ramp margin, extending in an opisthocline fashion up to adapical suture. Nodes on periphery also extending adapically in an opisthocline fashion, reaching the abapical margin of selenizone.

Dimensions. See Table 4.

Discussion. The studied specimens were compared with the holotype (BMNHC 266) and found to conform in morphology, except for one specimen (CPBA 20317.10) that does not show diagnostic characters due to a very poor state of preservation.

Other species of *Pleurotomaria* have been described from the Early Cretaceous of different parts of the world. D'Orbigny (1843) recorded six species of '*Pleurotomaria*' from Lower Cretaceous strata of France, five of these have subsequently been transferred to other genera of Mesozoic pleurotomariids (Kollmann, 2005). The remaining species, *P. astieriana* d'Orbigny, 1850, differs from *P. gerthi* mainly by lacking nodose sculpture.

Pictet and Campiche (1861–1864) recorded five species as similar to *P. gerthi* because of the presence of one or two rows of nodes in their shells, parallel to the sutures, *i.e.*, *P. defrancii* Matheron (Pictet and Campiche, 1861–1864, p. 416, pl. 77, fig. 2), *P. villersensis* Pictet and Campiche, 1863 (p. 418, pl. 77, fig. 3), *P. lardyi* Pictet and Campiche, 1863 (p. 419, pl. 77, fig. 4, 5), *P. aubersonensis* Pictet and Campiche, 1863 (p. 420, pl. 77, fig. 6), and *P. renevieri* Pictet and Campiche, 1863 (p. 431, pl. 79, fig. 5). *Pleurotomaria defrancii* bears two uneven rows of nodes in each whorl, and differs from *P. gerthi* by being almost as tall as wide and by having a broader, almost horizontal sutural ramp and a steeper outer whorl face. Nonetheless, as the original description of this species was based on internal moulds, information on shell surface sculpture and position and appearance of the selenizone is lacking. In *P. villersensis* the sutural ramp is also broader than in *P. gerthi* but slightly steeper than in *P. defrancii*, and shell outline is somewhat more gradate than in the Argentinean species. Moreover, only one row of nodes occurs along the ramp margin, and the shell is slightly taller than wide. Shell sculpture consists of spiral and colabral threads placed between the selenizone and the abapical suture (or periphery), and absent in the area between the selenizone and the adapical suture. In contrast,

Figure 4. *Pleurotomaria gerthi* Weaver, 1931. **1–3,** CPBA 19946 (late Valanginian, Salado Sur) in (**1**) apical, (**2**) apertural and (**3**) basal views; arrows point to articulated and disarticulated oysters encrusting shell surface. **4,** CPBA 20317.1 (late Valanginian, Cerro Birrete) in apertural view. **5**, CPBA 20317.9 (Late Valanginian, Cerro Birrete) in abapertural view. **6–9**, CPBA 19948.1 (early Hauterivian, Bajada Vieja) in (**6**) basal, (**7**) apertural, (**8**) apical and (**9**) abapertural views; **10,** CPBA 20317.11 (late Valanginian, Cerro Birrete) in apical view/ **Pleurotomaria gerthi** *Weaver, 1931;* ***1–3,*** *CPBA 19946 (Valanginiano tardío, Salado Sur) en vistas (**1**) apical, (**2**) apertural y (**3**) basal; las flechas señalan ostreidos articulados y desarticulados incrustando la superficie de la conchilla.* ***4,*** *CPBA 20317.1 (Valanginiano tardío, Cerro Birrete) en vista apertural.* ***5****, CPBA 20317.9 (Valanginiano tardío, Cerro Birrete) en vista abapertural.* ***6-9****, CPBA 19948.1 (Hauteriviano temprano, Bajada Vieja) en vistas (**6**) basal, (**7**) apertural, (**8**) apical y (**9**) abapertural;* ***10,*** *CPBA 20317.11 (Valanginiano tardío, Cerro Birrete) en vista apical.* Scale bar/ *escala= 10 mm*

P. gerthi has spiral threads and growth lines superimposed to the nodes and sutural ramp. *Pleurotomaria lardyi* differs from *P. gerthi* by having a conical non-gradate shell outline that is as tall as wide, with two weakly developed rows of nodes, forming a slightly protruding angulation only at the abapical margin of the whorl surface. *Pleurotomaria aubersonensis* has a much more depressed gradate shell, with a sutural ramp almost horizontal and a smooth carina near the periphery. Nonetheless, its H_s/D_{max} ratio is close to that of *P. gerthi*. Finally, *P. renevieri* resembles *P. gerthi* in terms of shell outline and H_s/D_{max} ratio, but its sutural ramp is less steep, its shoulder is slightly sharper —forming an almost right angle—, and it has only a single row of nodes along its ramp margin.

Cox (1960a) recorded several species of Pleurotomariidae from the British Cretaceous. Four of them are worth mentioning as they show a nodose sculpture. These are (1) *P. toulmini* Cox, 1960a (p. 392, pl. 46, fig. 5), (2) *P. plicata* (J. Sowerby) (see Cox, 1960a: p. 394, pl. 49, fig. 5–7), (3) *P. vectensis* Cox, 1960a (p. 394, pl. 50, fig. 8–10), and (4) *P. rockenensis* Cox, 1960a (p. 395, pl. 51, fig. 2–4). *Pleu-*

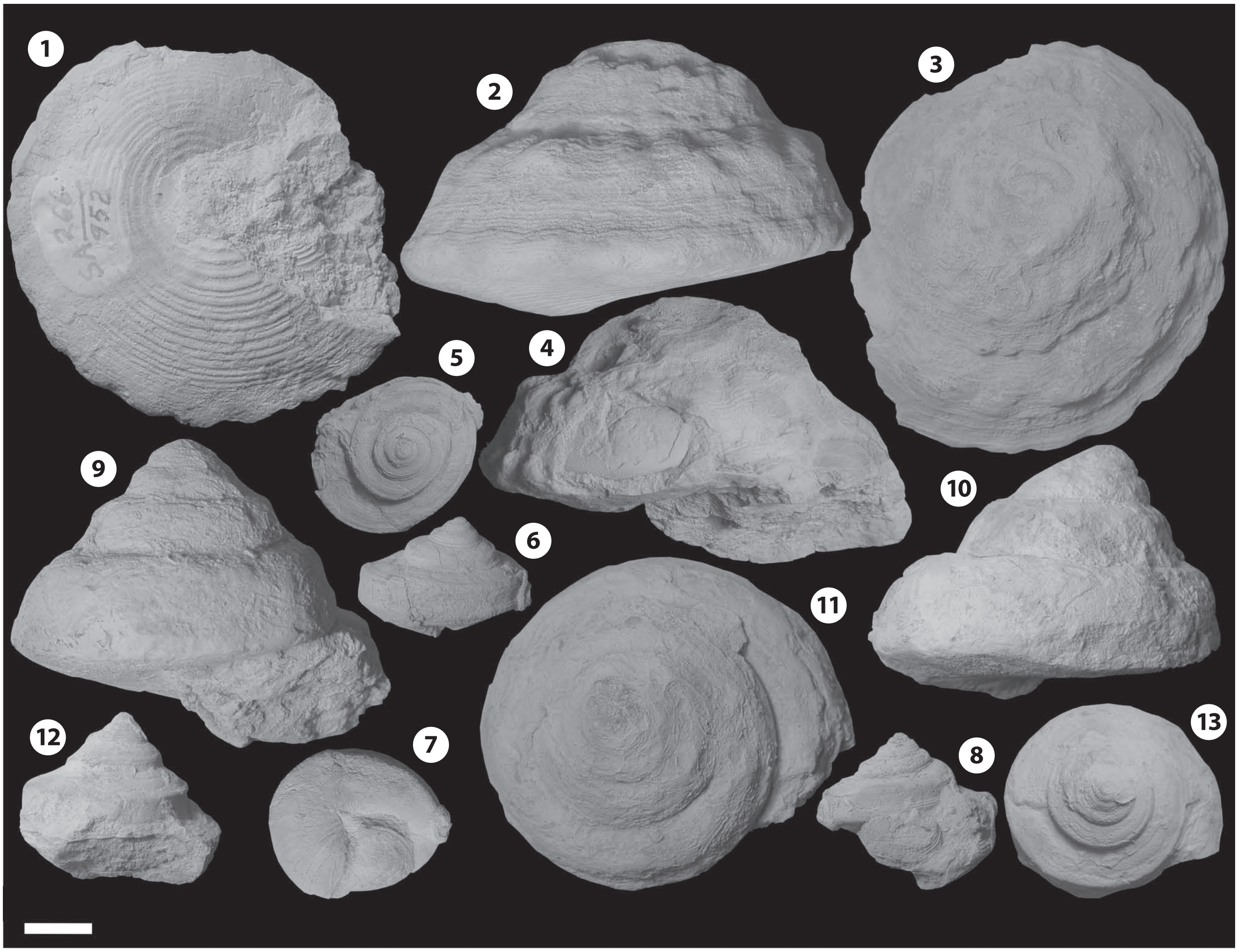


Figure 5. Pleurotomariid gastropods from the Neuquén Basin published in Weaver (1931). **1–4,** BMNHC 266 (Valanginian–early Hauterivian, Cerro Birrete) holotype of ***Pleurotomaria gerthi*** Weaver, 1931 (p. 367–368, pl. 42, fig. 281–283) in (**1**) basal, (**2**) abapertural, (**3**) apical and (**4**) apertural views; **5–8,** BMNHC 49007 (middle Tithonian, Cerro Granito) "***Pleurotomaria*** cf. ***provincialis***" in the collection of the Burke Museum in (**5**) apical, (**6**) abapertural, (**7**) basal and (**8**) apertural views; **9–11**, BMNHC 267 (Valanginian–early Hauterivian, Cerro Birrete) referred to as "***Pleurotomaria*** cf. ***jaccardi***" in Weaver (1931, p. 368–369), re-identified here as *P. gerthi*, in (**9**) apertural, (**10**) abapertural and (**11**) apical views; **12–13,** BMNHC 265 (middle Tithonian, Cerro Granito), "***Pleurotomaria*** cf. ***provincialis***" (see Weaver, 1931, p. 366–367), reinterpreted as ***Bathrotomaria*** cf. ***provincialis***, in (**12**) apertural and (**13**) apical views/ *Gastrópodos pleurotomáridos de la Cuenca Neuquina publicados en Weaver (1931). **1–4,** BMNHC 266 (Valanginiano–Hauteriviano temprano, Cerro Birrete) holotipo de* **Pleurotomaria gerthi** *Weaver, 1931 (p. 367–368, pl. 42, fig. 281–283) en vistas (**1**) basal, (**2**) abapertural, (**3**) apical y (**4**) apertural; **5–8,** BMNHC 49007 (Tithoniano medio, Cerro Granito) "***Pleurotomaria** cf.* **provincialis** *"en la colección del Burke Museum en vistas (**5**) apical, (**6**) abapertural, (**7**) basal y (**8**) apertural; **9–11,** BMNHC 267 (Valanginiano–Hauteriviano temprano, Cerro Birrete) bajo "***Pleurotomaria** cf.* **jaccardi**" *en Weaver (1931, p. 368–369), reidentificado aquí como* **P. gerthi**, *en vistas (**9**) apertural, (**10**) abapertural y (**11**) apical; **12–13,** BMNHC 265 (Tithoniano medio, Cerro Granito) 'plesiotipo' de "***Pleurotomaria** cf.* **provincialis**" *(Weaver, 1931, p. 366–367), reinterpretado como* **Bathrotomaria** *cf.* **provincialis**, *en vistas (**12**) apertural y (**13**) apical.* Scale bar/ *escala= 10mm.*

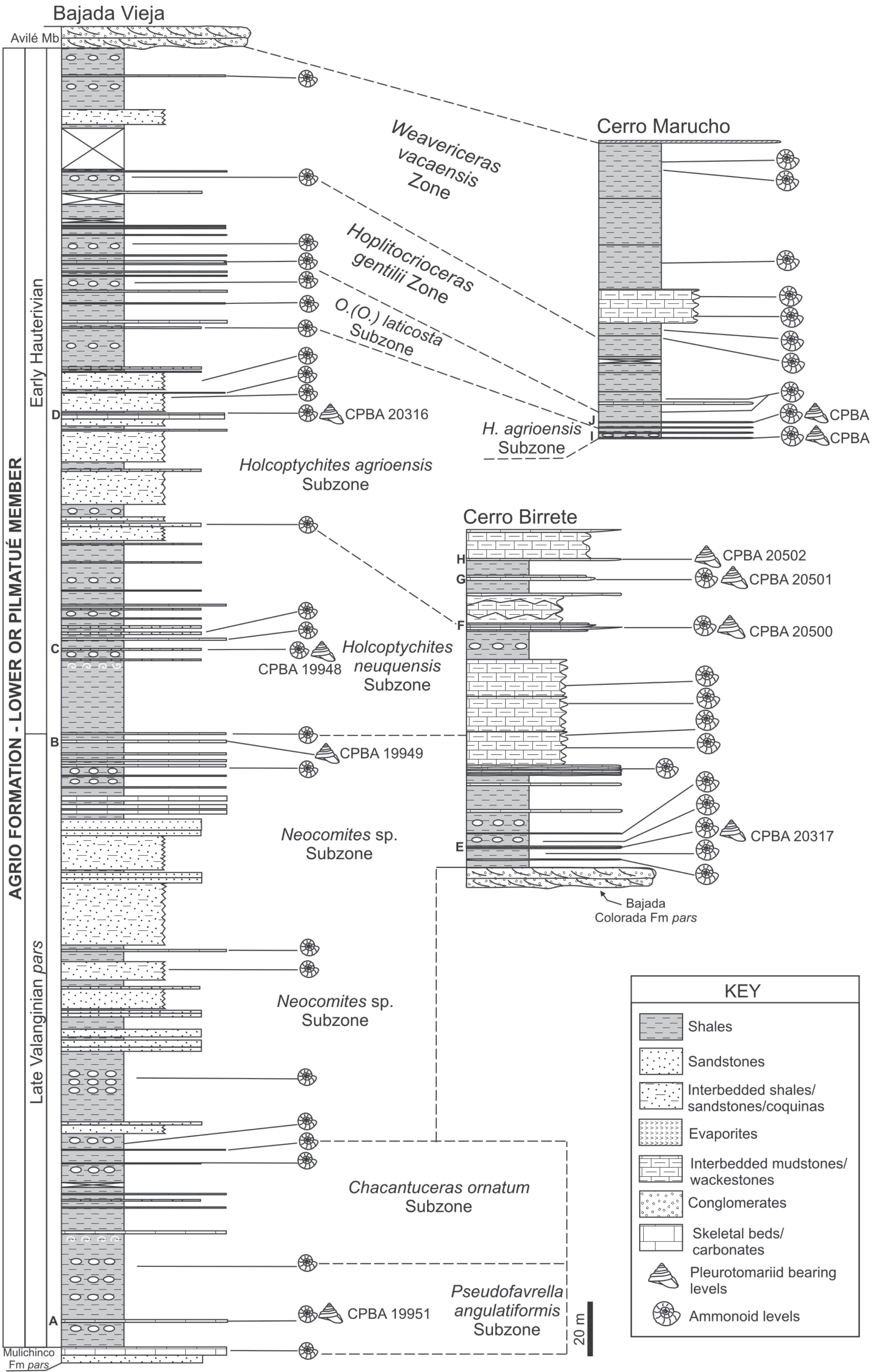
rotomaria toulmini is similar to *P. gerthi* in having two rows of nodes per whorl, one at ramp angle and a second one near the abapical suture. However, a rather conical, higher-spire outline, a shell equally tall as wide, and a slightly more acute spiral angle readily distinguishes this species from *P. gerthi*. *Pleurotomaria plicata* shows H_s/D_{max} ratio and sculpture similar to that of *P. gerthi*; however, the ornament of *P. plicata* is composed of broad colabral (prosocline) ribs on the ramp surface, while *P. gerthi* has elongate and gently opisthocline nodes there. *Pleurotomaria vectensis* bears a row of transversely elongate nodes on the narrow ramp, but it can be easily distinguished from *P. gerthi* by its depressed-conical outline and almost flat whorl face. Lastly, *P. rockenensis* shows a complex pattern of nodose sculpture, which includes a row of rounded nodes on the ramp and small, transversely elongate nodes crossed by spiral threads on the periphery. Nevertheless, a very depressed shell, twice as wide as tall, with a markedly cyrtoconoidal outline and a rounded peripheral bulge differentiates this species from *P. gerthi*.

Das (2002) described the subgenus *Indomaria* based on the species *Pleurotomaria* (*Indomaria*) *umiensis* Das, 2002, from the Berriasian of India. This author also suggested other European species that could belong in this subgenus (Appendix 1). The species of *Indomaria* show a depressed shell and lack nodose sculpture.

As stated before, few publications document the occur-

Table 3 - Fossil material studied. See stratigraphic distribution of ammonoid biozones in the Agrio Formation sections of Figure 6/ **Material fósil estudiado. Ver Figura 6 para la distribución estratigráfica de las biozonas de ammonoideos en la Formación Agrio.**

Locality	*Collection Nº (CPBA)*	*Ammonite biozone*	*P. gerthi-bearing levels*	*Age*	*Nº of specimens*
Pichaihue	*19950*	**Olcostephanus (Olcostephanus) laticosta** *Subzone*		*Early Hauterivian*	*1*
Casa Nuestra	*20323*	**Hoplitocrioceras gentilii** *Subzone*		*Early Hauterivian*	*1*
Agua de la Mula	*19945*	**Olcostephanus (Olcostephanus) laticosta** *Subzone*		*Early Hauterivian*	*1*
	20498	**Holcoptychites neuquensis** *Subzone*		*Early Hauterivian*	*1*
Salado Sur	*19947*	**Holcoptychites neuquensis** *Subzone*		*Early Hauterivian*	*1*
	19946	**Neocomites** *sp. Subzone*		*Late Valanginian*	*1*
Bajada Vieja	*20316.1-2*	**Holcoptychites agrioensis** *Subzone*	*D*	*Early Hauterivian*	*2*
	19948.1-2	**Holcoptychites neuquensis** *Subzone*	*C*	*Early Hauterivian*	*2*
	19949.1-2	**Neocomites** *sp. Subzone*	*B*	*Late Valanginian*	*2*
	19951	**Pseudofavrella angulatiformis** *Subzone*	*A*	*Late Valanginian*	*1*
Cerro Lotena	*20319*	**Olcostephanus (Olcostephanus) laticosta** *Subzone*		*Early Hauterivian*	*1*
Cerro Birrete	*20502*	**Holcoptychites agrioensis** *Subzone*	*H*	*Early Hauterivian*	*1*
	20501.1-2	**Holcoptychites agrioensis** *Subzone*	*G*	*Early Hauterivian*	*2*
	20500.1-2	**Holcoptychites agrioensis** *Subzone*	*F*	*Early Hauterivian*	*2*
	20317.1-14	**Neocomites** *sp. Subzone*	*E*	*Late Valanginian*	*14*
Cerro Marucho + Barda Marucho	*20504.1-2*	**Olcostephanus (Olcostephanus) laticosta** *Subzone*	*J*	*Early Hauterivian*	*2*
	20503	**Holcoptychites agrioensis** *Subzone*	*I*	*Early Hauterivian*	*1*
	20505.1-2	**Neocomites** *sp. Subzone*		*Late Valanginian*	*2*
					TOTAL = 38


Bajada Vieja
Avilé Mb
AGRIO FORMATION - LOWER OR PILMATUÉ MEMBER
Early Hauterivian
Late Valanginian *pars*
Mulichinco Fm *pars*
A
B
C
D
CPBA 20316
CPBA 19948
CPBA 19949
CPBA 19951
Weavericeras vacaensis Zone
Hoplitocrioceras gentilii Zone
O.(O.) laticosta Subzone
H. agrioensis Subzone
Holcoptychites agrioensis Subzone
Holcoptychites neuquensis Subzone
Neocomites sp. Subzone
Neocomites sp. Subzone
Chacantuceras ornatum Subzone
Pseudofavrella angulatiformis Subzone
20 m
Cerro Marucho
J
I
CPBA 20504
CPBA 20503
Cerro Birrete
H
G
F
E
CPBA 20502
CPBA 20501
CPBA 20500
CPBA 20317
Bajada Colorada Fm *pars*
KEY
Shales
Sandstones
Interbedded shales/ sandstones/coquinas
Evaporites
Interbedded mudstones/ wackestones
Conglomerates
Skeletal beds/ carbonates
Pleurotomariid bearing levels
Ammonoid levels

rence of this genus in Argentina. Weaver (1931, p. 368) recorded *Pleurotomaria* cf. *jaccardi* Pictet and Campiche, 1863 in the Agrio Formation at the Cerro Birrete section. *Pleurotomaria jaccardi* was originally described from the Valanginian of Sainte-Croix, Switzerland (Pictet and Campiche 1863, p. 423, pl. 78, fig. 3), and Weaver tentatively referred his specimens to this species on the basis of similarities in general shape, sculpture and dimensions. According to Weaver, the Argentinean specimen is characterized by somewhat angulated whorls, a spiral angle of nearly 90° and sculpture consisting of regularly spaced spiral threads and growth lines. Weaver's specimen BMNHC 267 was re-examined and a series of observations are formulated. This specimen is mostly an internal mould on which the spiral elements of the sculpture are discernible only on a small fragment of shell on the base. These spiral threads are identical to those on the base of *P. gerthi*. The overall description of the form as well as H_s/D_{max} and H_{lw}/H_s ratios seem to agree well with that of *P. gerthi*, and the internal moulds studied here are almost exactly the same as the specimens depicted by Weaver under *Pleurotomaria* cf. *jaccardi*. It is also worth noting that no specimens bearing the sculpture mentioned in the original description by Pictet and Campiche have yet been found at any of Weaver's localities, nor in any of the other studied localities of the Agrio Formation. Therefore, we conclude that the specimen identified as *P.* cf. *jaccardi* by Weaver is referable to *P. gerthi*.

The specimen identified by Weaver as *Pleurotomaria* cf. *provincialis* d'Orbigny was collected from the Picún Leufú Formation at Cerro Granito, southern Neuquén, *i.e.*, BMNHC 265 (Fig. 5.12–13). There is another specimen collected by Weaver from the same locality (BMNHC 49007; Fig. 5.5–8). These records are referable to the *Windhauseniceras internispinosum* Zone of late middle Tithonian age (Riccardi, 2008). Kollmann (2005) transferred *P. provincialis* to *Bathrotomaria*. Weaver's "*P.* cf. *provincialis*" is characterized by a trochiform shell that is wider than tall, gradate and slightly obtuse (A_{ms}= 91º), with a small umbilicus and biangular last whorl and outer lip; the selenizone is placed on the mid-whorl angulation, and sculpture consists of spiral threads and growth lines. This record clearly represents a species of the genus *Bathrotomaria*, so further comparison with *P. gerthi* is irrelevant.

'Pleurotomaria' tardensis Stanton, 1901 (p. 29, pl. 7, fig. 1, 2) comes from the Río Belgrano Formation (early Barremian) in the Lago Pueyrredón area, Santa Cruz Province (Austral Basin, southwestern Argentina). Shell features in *P. tardensis* (*e.g.*, convex whorls, rounded periphery, non-nodose sculpture) do not match the generic diagnosis of *Pleurotomaria.* In fact, Harasewych *et al.* (2009) transferred *P. tardensis* to the genus *Leptomaria*.

STRATIGRAPHY, FACIES RELATIONSHIPS AND PALAEOECOLOGY

Stratigraphy and sedimentology of the studied localities

Three sections of the Pilmatué Member were analyzed in detail, *i.e.*, Bajada Vieja, Cerro Birrete and Cerro Marucho (Fig. 2). They occur along a 110 km long, approximately N–S straight line; they were laterally correlated using ammonoid first occurrences (Fig. 6). General description of facies of the Agrio Formation and interpretation of associated palaeoenvironments can be found in Brinkmann (1994), Spalletti (1992) and Lazo (2003).

Cerro Birrete and Cerro Marucho are located near the southern boundary of the Neuquén Basin and are more proximal than Bajada Vieja. This accounts for the reduced thickness in comparison to that section. Also, they are located far south from areas of siliciclastic input located on the eastern sector of the basin. This situation probably enhanced carbonate deposition as indicated by previous lithofacies and microfacies studies (Marchese, 1971; Di Paola, 1990). Both sections are composed mainly of carbonate shales alternating with coquinas, skeletal sandstones, packstones and grainstones. Microfacies indicate a range of environments from high energy neritic shoals to tidal flats and channels deposited on a shallow homoclinal carbonate-siliciclastic ramp (Di Paola, 1990).

MODE OF OCCURRENCE

Most of the studied specimens retain an incompletely preserved recrystallized shell, generally with apical and apertural regions chipped and showing a high degree of corrasion, meaning that shell sculpture is poorly or infrequently preserved. Both bioerosion and encrustation were identified. Bioerosion, present in a very low number of specimens, was

Figure 6. Detailed stratigraphic sections of the Pilmatué Member of the Agrio Formation at Bajada Vieja, Cerro Birrete and Cerro Marucho, Neuquén Basin, west-central Argentina. The stratigraphic positions of beds containing *Pleurotomaria gerthi* Weaver, 1931 are indicated (A–J). Ammonoid zonation and ages are based on Aguirre-Urreta *et al.* (2007)/ *Perfiles sedimentológicos de detalle del Miembro Pilmatué de la Formación Agrio en Bajada Vieja, Cerro Birrete and Cerro Marucho, Cuenca Neuquina, centro-oeste de Argentina. La posición estratigráfica de las capas con* Pleurotomaria gerthi *Weaver, 1931 está indicada (A–H). Zonación de amonoideos y edades basados en Aguirre-Urreta* et al. *(2007).*

Table 4 - Measurements (in mm) of the studied specimens of **Pleurotomaria gerthi** ***Weaver, 1931. For details see Materials and Methods and Figure 3/*** **Medidas (en mm) de los especímenes de *Pleurotomaria gerthi* Weaver, 1931, estudiados. Ver detalles en Materiales y Métodos y Figura 6.**

Specimen (CPBA)	***Linear measurements (mm)***				***Angular measurements (º)***		***Rates***	
	Hs	*Hlw*	*Hap*	*Dmax*	*Ams*	*Ss*	*(Hs/Dmax)*100*	*(Hlw/Hs)*100*
19945	*86,10*	*60,40*	*40,60*	*112,00*	*72,92*	*9,23*	*76,875*	*70,150*
20498	*-*	*27,00*	*19,00*	*49,00*	*-*	*-*	*-*	*-*
19946	*76,70*	*53,10*	*31,40*	*91,00*	*72,57*	*-*	*84,290*	*69,230*
19947	*96,10*	*66,80*	*36,50*	*125,00*	*70,48*	*5,63*	*76,880*	*69,510*
19948.1	*46,50*	*30,30*	*19,00*	*55,00*	*64,86*	*5,66*	*84,545*	*65,160*
19948.2	*-*	*-*	*-*	*113,00*	*-*	*-*	*-*	*-*
19949.1	*-*	*-*	*-*	*73,50*	*-*	*-*	*-*	*-*
19949.2	*56,80*	*-*	*-*	*-*	*-*	*-*	*-*	*-*
19950	*-*	*55,30*	*33,70*	*100,40*	*69,20*	*10,72*	*-*	*-*
19951	*15,30*	*13,30*	*-*	*30,00*	*-*	*-*	*-*	*-*
20316.1	*93,2*	*58,70*	*31,70*	*113,40*	*65,55*	*5,39*	*82,190*	*62,980*
20316.2	*79,80*	*54,50*	*32,70*	*97,50*	*65,77*	*-*	*81,850*	*68,295*
20323	*72,30*	*53,50*	*35,50*	*94,10*	*71,17*	*9,76*	*76,830*	*74,000*
20319	*19,50*	*13,30*	*7,60*	*21,80*	*66,00*	*-*	*89,450*	*68,200*
20317.1	*47,10*	*33,70*	*21,50*	*61,60*	*84,66*	*-*	*76,460*	*71,550*
20317.2	*45,50*	*30,10*	*19,60*	*57,40*	*72,98*	*10,24*	*79,270*	*66,150*
20317.3	*40,50*	*32,00*	*21,50*	*56,50*	*78,36*	*2,90*	*71,680*	*79,010*
20317.4	*-*	*27,80*	*19,00*	*53,00*	*84,14*	*4,78*	*65,090*	*80,600*
20317.5	*-*	*20,60*	*14,20*	*36,40*	*69,47*	*9,08*	*67,310*	*84,080*
20317.6	*-*	*14,40*	*6,50*	*26,90*	*91,82*	*6,57*	*66,910*	*80,000*
20317.7	*-*	*15,90*	*10,40*	*28,20*	*94,19*	*-*	*-*	*-*
20317.8	*15,30*	*11,40*	*8,50*	*25,00*	*91,21*	*2,73*	*61,200*	*74,500*
20317.9	*44,30*	*35,90*	*25,50*	*54,90*	*74,57*	*-*	*80,690*	*81,030*
20317.11	*29,80*	*19,70*	*12,80*	*39,70*	*87,09*	*3,21*	*75,060*	*66,110*
20317.12	*12,60*	*10,20*	*7,30*	*18,70*	*86,93*	*-*	*67,380*	*80,950*
20317.13	*35,80*	*25,70*	*-*	*46,30*	*64,00*	*5,14*	*77,320*	*71,790*
20317.14	*-*	*-*	*-*	*-*	*-*	*-*	*-*	*-*
20500.1	*-*	*25,90*	*-*	*45,30*	*-*	*-*	*-*	*-*
20500.2	*46,50*	*33,70*	*20,40*	*57,10*	*76,10*	*0,00*	*81,430*	*72,470*
20501.1	*91,20*	*-*	*41,50*	*114,30*	*-*	*-*	*79,790*	*-*
20501.2	*-*	*16,10*	*10,80*	*31,40*	*-*	*-*		
20502	*-*	*22,10*	*14,50*	*43,00*	*-*	*-*	*-*	*-*
20503	*92,30*	*58,30*	*38,20*	*100,20*	*67,50*	*3,48*	*92,115*	*63,160*
20504.2	*21,80*	*-*	*-*	*26,60*	*72,48*	*-*	*81,950*	*-*
20505.1	*38,80*	*31,30*	*19,60*	*50,00*	*79,00*	*11,00*	*77,600*	*80,670*
20505.2	*-*	*-*	*-*	*72,00*	*-*	*-*	*-*	*-*
Average	*52,34*	*32,80*	*22,20*	*62,07*	*75,72*	*6,21*	*77,260*	*72,710*
Standard deviation	*28,00*	*17,22*	*11,05*	*32,45*	*9,24*	*3,28*	*7,590*	*6,510*
CV%	*53,50*	*52,50*	*49,77*	*57,28*	*12,20*	*52,82*	*9,820*	*8,950*
HOLOTYPE	*45,00*	*21,00*	*-*	*58,00*	*70,00*	*-*	*77,580*	*46,660*

detected as microborings, probably as a result of the activity of microendolithic algae, fungi and/or clionid sponges. In contrast, external encrustation was observed on more than half of the specimens, although internal encrustation was quite infrequent. Three different encrusting organisms were found, *i.e.*, articulated and disarticulated oysters, serpulids and cyclostome bryozoans. The sedimentary infill of shells and the lithology of internal moulds match the host matrix meaning that shells were not reworked after final burial. The overall degree of taphonomic modification shown by the studied specimens accounts for reworking and substantial exposure time of the shells on the sea floor, but not necessarily a high degree of lateral transport.

FACIES RELATIONSHIPS OF PLEUROTOMARIID-BEARING LEVELS

Pleurotomaria gerthi is less common in the Pilmatué Member than other gastropods, for instance the aporrhaid *Protohemichenopus neuquensis* Camacho. Specimens of *P. gerthi* occur in discrete levels throughout the unit (see levels in Tab. 3 and Fig. 6). Generally, only one or two specimens were found in each horizon at most of the studied localities, even though each bed was searched for hundreds of meters along strike (Tab. 3). However, level E at Cerro Birrete is an exception because it yielded 12 specimens. The macrofossil assemblages of the Pilmatué Member have a maximum time-averaging of 0.5 My approximately, based on the chronology of the ammonoid zonation (see Lazo, 2007). Associated macrofossils are listed in Appendix 1. Facies containing *P. gerthi* are summarized in Table 2. Palaeoenvironmental interpretations are made for each facies.

Facies 1: Simple skeletal sandstones. This facies is represented by tabular skeletal sandstones ranging from 0.2 to 0.5 m in thickness. Individual beds have sharp to erosive bases sometimes including a basal lag of small calcareous nodules. The dominant matrix is fine-grained sandstone mixed with other fine-grained sediments. Generally, they are homogenous in cross-section. Highly fragmented shell debris and well-sorted bivalve valves are the most abundant component. However, there are isolated complete shells of cephalopods and bivalves. Reworked clusters of large oysters are recorded. There is no preferred orientation of complete shells in cross-section, but shell debris may be concordant reflecting horizontal lamination. A rich assemblage of 17 taxa is associated to this facies, including bivalves, nautilids, ammonoids and serpulids (see Appendix 1). Suspension-feeders dominate. Bioturbation is not very common even though some bivalve shells show macrobioerosion by *Lithophaga* sp. This facies occurs intercalated in thicker beds of shales (beds A–C) at Bajada Vieja section.

Interpretation. These sandy beds seem to have been deposited under the influence of moderate- to high-energy conditions, as suggested by erosive basal contacts and the presence of reworked bioclasts, especially cemented oysters and serpulids. Shell concentration was largely due to physical processes. Sandy sediments and shell debris were most probably transported by storm-currents and waves from shallow areas located close to clastic input from the continent. Beds were finally deposited on muddy deposits of the inner shelf below fair-weather wave base. Shell debris is significantly transported and may be regarded as parautochtonous while complete and articulated shells were probably eroded and slightly transported within the inner shelf and thus may be regarded as slightly parautochtonous. The associated macrofauna belongs to the '*Cucullaea-Mimachlamys-Panopea*' biofacies defined by Lazo (2007). It is characterized by a well-oxygenated soft sandy and patchy bioclastic substrate, normal marine salinity, and warm-temperate waters. This biofacies is generally recorded in shallow marine settings (less than 5 m deep) of the Agrio Formation. Dominance of suspension-feeders suggests that suspension-nutrients were available, probably due to the high-energy conditions. The record of macrobioerosion suggests a shallow sea-bottom placed within the photic zone and colonized by benthic algae (Bromley, 1992).

Facies 2: Simple skeletal carbonates. This facies forms tabular wackestones and packstones up to 0.25 m thick. These are internally homogenous due to the high degree of bioturbation, and concretionary due to high carbonate content. Bases are sharp. The dominant fraction is composed of valve fragments and complete shells, but no shell debris. They range from matrix- to bioclast-supported and have a highly variable orientation of bioclasts in cross section. Deep infaunal bivalves are usually in life position. The associated macrofauna is composed of nine taxa including bivalves, nautilids, ammonoids, gastropods and serpulids (Appendix 1). The assemblage of bivalves has a lower diversity in comparison to Facies 1. This facies occurs intercalated within thicker shale beds at Cerro Marucho section (Fig. 6 beds I–J; Fig. 7.1).

Interpretation. These fine-grained carbonate beds suggest a subtidal, low- to moderate-energy environment below fair-weather wave base that would correspond to a semi-protected inner shelf affected by episodic wave and current activity. High carbonate content suggests that clastics did not reach this environment. Concentration of bioclasts has a mixed physical and biological origin. Erosion was low, as deep infaunal bivalves are usually recorded in life position. Whole mollusc shells have not been significantly transported and thus are deemed parautochtonous.

The presence of a low-richness bivalve assemblage suggests that there were ecological constraints on settlement and proliferation on the carbonate substrate possibly by a combination of factors including oxygen level and substrate consistency. The presence of ammonoids and nautilids suggests normal marine conditions.

Facies 3: Composite skeletal carbonates. This facies is represented by wedge shaped amalgamated skeletal wackestones and packstones reaching 3.2 m of maximum thickness. Basal contact is usually gradational from wavy-bedding to flaser-bedding deposits. Top contact is either a hardground or firmground or gradational to wavy- and lenticular-bedding deposits. Simple beds are elongated lenses tens of meters wide. They are loosely to densely packed and range in thickness from 0.2 to 0.8 m. They may show internal horizontal lamination, gross cross-bedding or heterolithic bedding. Single beds have sharp to erosional bases often overlain by small calcareous nodules.

Simple beds are lenses tens of meters maximum width. These are loosely to densely packed and 0.2–0.8 m thick. Thickness may taper laterally. Basal contacts are either sharp or erosive, especially in lenses interpreted as channel facies. The dominant fraction is composed of shell debris mixed with whole shells. Matrix is fine-grained. Bioturbation is very common only towards the top. Bioclasts are concordant in cross-section (shells convex-down and convex-up). However, deep infaunal bivalves are usually in life position.

The macrofossil assemblage is characterized by its high richness and includes 32 taxa of nautilids, ammonoids, gastropods, bivalves, echinoids, serpulids and corals (Appendix 1). Suspension-feeders dominate. Some bivalve shells show macrobioerosion by *Lithophaga* sp.. This facies occurs on top of sequences intercalated in thicker shale beds at Bajada Vieja and Cerro Birrete sections (Fig. 6, beds D–H; Fig. 7.2). It includes level E with a high abundance of *P. gerthi*.

Interpretation. This facies records the amalgamation of skeletal banks deposited under the influence of episodic high-energy waves, currents and tides. Wedge shaped skeletal banks were defined as fringing banks of carbonates ramps (Read, 1985). They are complex linear accumulations of shoals and bars that parallel the shoreline cut by interbar tidal channels. They overlie deep ramp facies and underlie sublittoral sand sheets and tidal/supratidal complexes. High carbonate content suggests that clastics did not reach this environment. Bioclast concentration is due mainly to physical processes, but deep infaunal organisms remained in life position. Whole shells have not been significantly transported and are thus deemed to be parautochtonous. The associated macrofauna belongs to the '*Cucullaea-Mimachlamys-Panopea*' biofacies in association with the 'coral colonies' biofacies as defined by Lazo (2007). As stated above these biofacies point to

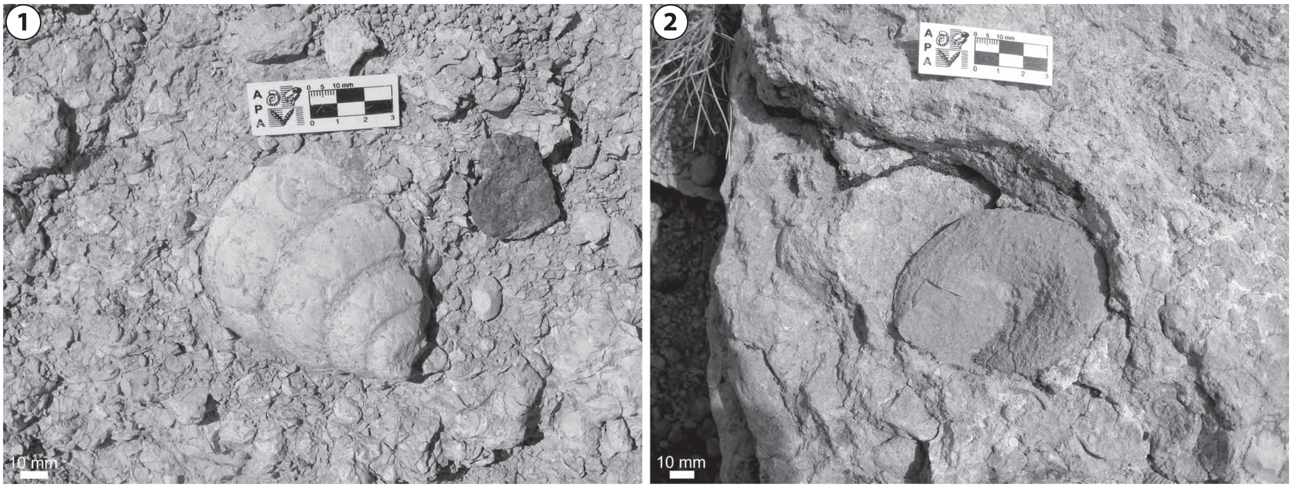


Figure 7. Mode of occurrence of *Pleurotomaria gerthi* Weaver, 1931, in the field. **1,** lateral view of internal mould recorded in level I, simple skeletal carbonates facies, *Holcoptychites agrioensis* Subzone, Pilmatué Member, Cerro Marucho. Note chipped apical region; **2,** upside down specimen on top of level G, composite skeletal carbonates facies, *H. agrioensis* Subzone, Pilmatué Member, Cerro Birrete/*Modo de ocurrencia de* Pleurotomaria gerthi *Weaver, 1931 en el campo.* ***1,*** *vista lateral de molde interno perteneciente al nivel I, facies de areniscas esqueletales simples, Subzona de* H. agrioensis, *Miembro Pilmatué, Cerro Marucho. Nótese ápice roto;* ***2,*** *espécimen invertido en el tope del nivel G, facies de carbonatos esqueletales compuestos, Subzona de* H. agrioensis, *Miembro Pilmatué, Cerro Birrete.*

a very shallow-marine setting. Low coral meadows developed on fringing banks without coral overgrowth or lateral coalescence probably due to unsuitable substrate conditions and relatively high sedimentation rates. Biofacies point towards a well-oxygenated substrate, normal marine conditions and warm-temperate waters. The record of macrobioerosion suggests a shallow sea bottom placed entirely within the photic zone and colonized by benthic algae.

P. gerthi is abundantly recorded in this facies, suggesting that it inhabited the middle carbonate ramp below the fair-weather wave-base under normal marine conditions and within the photic zone. However, it was probably a generalist regarding substrate preference, as it is recorded in a variety of substrates ranging from sandy to fine carbonate and patchy bioclastic substrates.

PALAEOECOLOGICAL REMARKS

Recent pleurotomariids are epifaunal mobile gastropods found mainly on islands with rocky substrates at bathyal depths exceeding 200 m (Hickman, 1976, 1984, 1998; Harasewych and Kiel, 2007). A number of extant species, including *Entemnotrochus adansonianus* (Crosse and Fischer), *Perotrochus charlestonensis* Askew, *Perotrochus midas* Bayer, *Perotrochus amabilis* (Bayer) and *Mikadotrochus beyrichii* (Hilgendorf) have been recovered from hard-substrate habitats below 100 m. Cenozoic pleurotomariids were present in shallow-water environments and also in deeper settings. According to Hickman (1976), shallow-water forms may have been progressively eliminated instead of shifting to deeper waters.

Facies relationships of *Pleurotomaria gerthi* in the Pilmatué Member show that this species inhabited shallow marine settings above storm-weather wave- base, which are interpreted as inner shelf and middle carbonate ramp deposits under the influence of storm currents and waves. *Pleurotomaria gerthi* lived on well-oxygenated soft sandy fine carbonate and patchy bioclastic substrates, under warm-temperate waters of normal marine salinity. It was part of a high diversity macrofaunal assemblage including cephalopods, bivalves, other gastropods, serpulids, echinoids and coral colonies. As it was found related to a variety of lithologies, we infer that *P. gerthi* was not substrate-controlled.

Work by other authors revealed similar environmental findings for *Pleurotomaria*. Begg and Grant-Mackie (2003) recorded six species of *Pleurotomaria* in the Middle to Late Triassic of New Zealand; the fossils were recovered from lithologies dominated by sandstones, suggesting mid- to inner shelf depositional environments; preliminary palaeoecological analysis suggests that the species lived in shallow waters. From the Middle Jurassic (Callovian) of Kutch, western India, Jaitly *et al.* (2000) recorded *Pleurotomaria* in the Chari Formation, deposited under shallow marine conditions. Das (2002) described new *Pleurotomaria* species from shoal-lagoonal facies of the Berriasian stage of western India. Finally, Kiel and Bandel (2004) showed that *Pleurotomaria* still inhabited rocky-shore environments during the Cenomanian of the Kassenberg Quarry (Mülheim, Germany).

EARLY CRETACEOUS PALAEOBIOGEOGRAPHIC DISTRIBUTION OF *PLEUROTOMARIA*

Published work on palaeobiogeographic distribution of Cretaceous gastropods has focused on differences between the Tethyan and the Northern Temperate Realms (*e.g.,* Sohl, 1987). This is due to the fact that palaeobiogeographic data available is biased towards northern faunas, revealing a lack of detailed knowledge on southern associations. According to Sohl (1987), Cretaceous gastropods might fit the general patterns of bivalve distribution studied by Kauffman (1973). The latitudinal boundaries of the Tethyan Realm, although variable over time, are linked to the maximum geographical distribution of reef-building associations of rudists, corals and algae. Within this tropical belt, the highest gastropod diversity is recorded in shallow water carbonate platforms. North and south of the Tethyan Realm boundaries, there are transitional zones that grade into distinctly temperate faunas. However, Kiel (2002) published a different view, proposing that the Tethyan *vs.* Temperate provinces division is not appropriate for the palaeobiogeographic treatment of Late Cretaceous gastropods, due to the fact that typical temperate forms have been recorded in tethyan localities. Instead, he proposed a different scheme of faunal provinces. Kiel (2002) also emphasized the importance of distinguishing between the latitudinal limits of reef communities and the distribution of tropical forms of gastropods and other marine groups.

During the Early Cretaceous, *Pleurotomaria* was a moderately diverse and widely distributed genus. Appendix 2 shows a list of those Early Cretaceous records of *Pleurotomaria* which leave little or no doubt regarding their generic affinity. Therefore, it does not include records lacking illustrations or those of which generic affinity is doubtful. Records from Appendix 2 were plotted in a Berriasian-Barremian palaeogeographic reconstruction (Fig. 8).

P. gerthi is endemic to the marine Andean basins of the western margin of southern South America and occurs in the Neuquén Basin (west-central Argentina), the Aconcagua-Central Chile and the Chañarcillo (northern Chile) basins (Biró-Bagóczky, 1964; Pérez and Reyes, 2000). These three areas were connected by shallow water during the early Valanginian–late Hauterivian interval (Mourgues, 2004; see Aguirre-Urreta, 1993, for a general account of their Early Cretaceous geography and stratigraphy). The distribution patterns of other invertebrate taxa support this connection (Cichowolski *et al.*, 2004; Aguirre-Urreta *et al.*, 2007, 2008).

The oldest record of *P. gerthi* is from the Tithonian of the Aconcagua-Central Chile Basin, whilst in Neuquén and Chañarcillo it appeared during the late Valanginian and Hauterivian, respectively. Therefore, it seems that this species differentiated first in populations inhabiting central Chile, and later migrated northwards into Chañarcillo and south-eastwards into Neuquén. The absence of *P. gerthi* earlier in the Neuquén Basin (during the Tithonian–Barremian interval) was probably caused by the development of very different facies there in comparison to those present in central Chile. Whilst clastics and carbonates accumulated in littoral and sub-littoral settings in the Aconcagua-Central Chile area, deep neritic shales and marls predominated in central Neuquén Province and southern Mendoza Province (Hallam *et al.*, 1986). This environmental condition must have precluded the development of pleurotomariid faunas in this area until the early Valanginian. A shallow-water carbonate depositional system developed during the Tithonian–early Barremian interval in the southern part of Neuquén Province. In this area, other pleurotomariid species have been recorded in Tithonian strata, *i.e.*, *Bathrotomaria* cf. *provincialis* and an internal mould of Pleurotomariidae gen. et sp. indet. (pers. obs.). Despite its endemism, the species showing the closest morphological resemblance to *P. gerthi* are those from the Tethys. This is also true for other benthic elements of the Neuquén fauna, especially bivalves (see Aguirre-Urreta *et al.*, 2008).

Pleurotomaria dispersion routes between the basins along the western margin of southern Gondwana and other basins of the world cannot be presently ascertained. The reasons for this are the endemism of its species and the lack of a good level of taxonomic understanding regarding many Early Cretaceous records of the genus, especially those from Chile (Tavera, 1956; Corvalán, 1973; Pérez and Reyes, 2000) and South Africa (Kitchin, 1908; Rennie, 1934). Gründel (2001) could not confirm Early Jurassic faunistic relationships between gastropods of Andean and European basins because of the high endemism and poor state of preservation of the South American material.

After the early Barremian, marine sedimentation in the Neuquén Basin was replaced by mainly continental and mar-

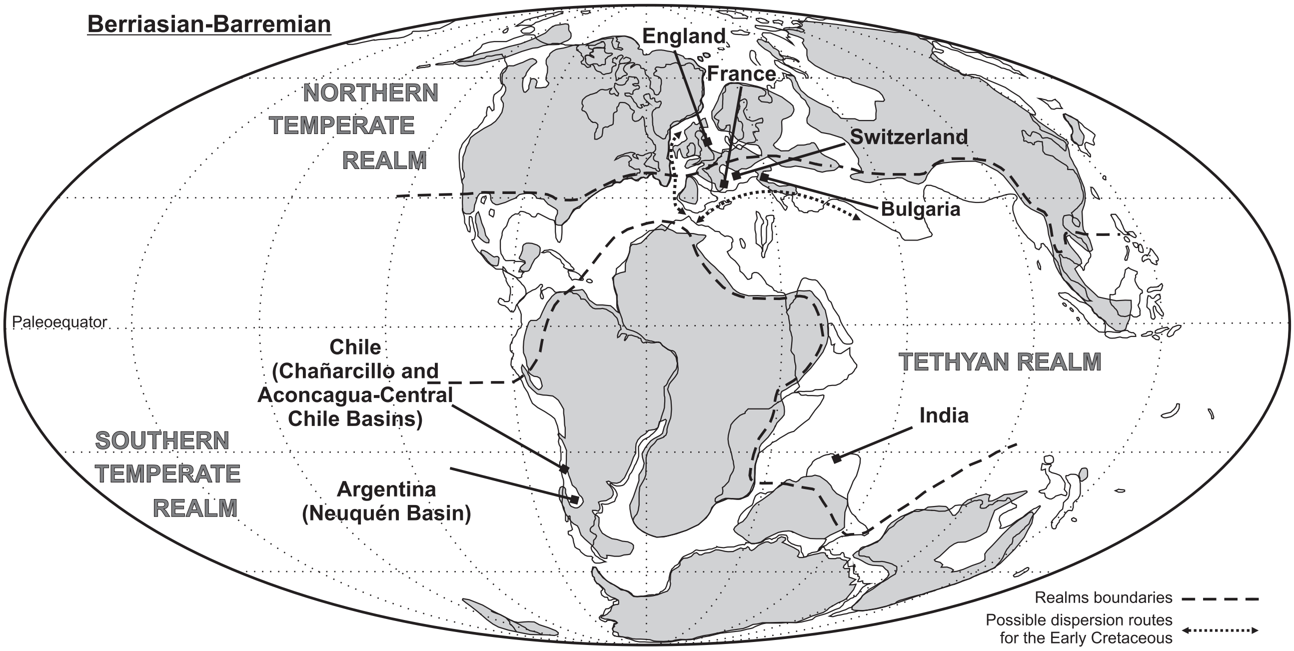


Figure 8. Distribution of the genus ***Pleurotomaria*** Defrance, 1826 during the Berriasian–Barremian interval. Realm boundaries follow Kauffman (1973). Palaeocoastline reconstruction from Smith *et al.* (1994). Records of ***Pleurotomaria*** compiled in Appendix 2/ *Distribución del género* **Pleurotomaria** *Defrance, 1826 durante el intervalo Berriasiano–Barremiano. Límites de reinos según Kauffmann (1973). Reconstrucción de paleo-líneas de costa de Smith* et al. *(1994). Registros de* **Pleurotomaria** *compilados en Apéndice 2.*

ginal-marine deposits, whilst in the Aconcagua-Central Chile Basin marine sedimentation stopped in the late Hauterivian (see Mourgues, 2004 and references therein). Only in the Chañarcillo Basin there was a second marine cycle beginning in the early Barremian, although pleurotomariids have not been yet reported from this basin. A late Barremian–early Aptian connection between the Austral (south-western Argentina and Chile) and the Chañarcillo basins was hypothesized by Mourgues (2004). As *Leptomaria tardensis* (Stanton) is recorded in the Barremian of the Austral Basin, it is highly possible that pleurotomariids inhabited the Chañarcillo area too.

CONCLUSIONS

At least two species of pleurotomariids occur in Early Cretaceous rocks of Argentina, *i.e.*, *Pleurotomaria gerthi* and *Leptomaria tardensis.* A third record, '*P.* cf. *jaccardi*', was herein synonymyzed with *P. gerthi*, and a fourth, *Conotomaria*? cf. *pailleteana,* is a record that has yet to be confirmed.

In the Agrio Formation of the Neuquén Basin, the family Pleurotomariidae is represented only by *P. gerthi*, which is endemic to the Andean basins of Argentina and Chile. Within the Agrio Formation, *P. gerthi* ranges from late Valanginian to early Hauterivian, as indicated by the associated ammonoids. Its earliest record is from the Tithonian of the Lo Valdés Formation, Aconcagua-Central Chile Basin.

The study of facies relationships and occurrence carried out at three of the nine sections studied in the Neuquén Basin showed that *P. gerthi* inhabited shallow marine settings interpreted as inner shelf and middle carbonate ramp deposits influenced by storm-currents and waves. The preferred habitat of *P. gerthi* was the middle carbonate ramp, although it was probably a generalist regarding substrate composition, as it has been recorded in a variety of substrates ranging from sandy to fine carbonate and patchy bioclastic substrates.

The genus *Pleurotomaria* was widely distributed during the Early Cretaceous, and was recorded in the Tethyan, Northern Temperate and Southern Temperate Realms. Despite its endemism, *P. gerthi* shows the closest morphological resemblance to contemporary *Pleurotomaria* species of the Tethyan Realm.

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