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A new Early Cretaceous nerineoid gastropod from Argentina and its palaeobiogeographic and palaeoecological implications

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ABSTRACT

A new species of nerineoid gastropod, *Eunerinea mendozana*, is described from the top of the Agrio Formation, Lower Cretaceous, at Lomas Bayas, Mendoza Province, west-central Argentina. The significance of this record lies in that it extends the Early Cretaceous distribution of the genus to the Southern Hemisphere and also may point to the occurrence of subtropical conditions in the northern part of the Neuquén Basin close to the Hauterivian/Barremian boundary. Individuals of *E. mendozana* are found forming large monospecific assemblages immersed in carbonate sediments. The relationships of *E. mendozana* with other South American Early Cretaceous nerineoids are considered, together with a re-evaluation of some of those records.

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1. Introduction

Nerineoids are rather scarce elements in Jurassic and Cretaceous faunas of South America, in comparison with European or Mexican faunas. Jurassic records in South America are restricted so far to the Early and Middle Jurassic (Bayle and Coquand, 1851; Jaworski, 1925; Weaver, 1931; Cox, 1956; Gründel, 2001; Ferrari 2011). Recently, Ferrari (2011) provided a revision of several Early and Middle Jurassic South American records. Early Cretaceous nerineoids from the western margin of South America include the following species: *Eunerinea dianae* (Von der Osten, 1957), *Eunerinea hicoriensis* (Cragin, 1893), *Nerinea pseudoconvexa* Stanton, 1947, *Nerinea riverae* Stanton, 1947, *Eunerinea aquilina* (Stanton, 1947, reported by Von der Osten, 1957 as *Nerinea roemeri* Whitney, 1952, which is a junior synonym; see Kollmann et al., 2003) and *Nerinea trishae* Von der Osten, 1957, all from the Aptian Taguarumo Member of the Barranquín Formation at Bahía de Santa Fé, Venezuela (Von der Osten, 1957, pp. 587, 588, pl. 65, figs. 4, 5, 16, 17, 19, 25, pl. 66, fig. 21); *Nerinea* cf. *pseudoconvexa* Stanton, 1947 from Lower Cretaceous deposits at Sierra Nevada el Cocuy, Colombia (Etayo-Serna, 1985); *Teleoptyxis peruviana* Olsson, 1934 (p. 65, pl. 10, figs. 1, 3), from the Upper Aptian–Lower Albian of the Amotape region, Peru; *Eunerinea* cf. *gigantea* (d'Hombres-Firmas, 1838) from the Barremian–Aptian Pabellón Formation at Copiapó, Chile (Tavera, 1956); and *Nerinea* sp. from the Barremian–Aptian Pabellón Formation at Quebrada Las Breas, Chile (Aguirre-Maturana, 2001). Additionally, Paulcke (1903) reported the presence of a nerineoid in Albian strata from Peru; however, this record possibly belongs to the Campaniloidea (see Section 3, "Comparisons").

Up to now, the only previous unequivocal record of an Argentinean nerineoid is that of Damborenea et al. (1979), who reported a late Valanginian–late Hauterivian record from the Chachao and Agrio formations in Mendoza Province. Although Weaver (1931) reported nerineoid remains from the top of the Agrio Formation in Neuquén Province, this is a record that is questioned here (see Section 3, "Comparisons").

This overview of the presence of the Nerineoidea in Lower Cretaceous deposits of South America points to the relative scarcity of records and to the necessity, in most cases, of a comprehensive taxonomic revision.

The aim of this paper is to report a new species of nerineoid gastropod of the genus *Eunerinea* from well-dated nerineoid-dominated shell beds at the top of the Agrio Formation at Lomas Bayas, Mendoza Province, west-central Argentina. This record is of importance to the Neuquén Basin and also to the western margin of southern South America mainly because nerineoids are regarded as key benthic elements of Jurassic and Cretaceous carbonate palaeoenvironments (Sohl, 1987; Wieczorek, 1988), especially in the ramps and platforms of the tropical Tethys Sea where they were so markedly abundant and even dominant. For these reasons they are considered to be evidence of subtropical to tropical marine conditions (e.g., Saul and Squires, 2002). This finding makes a significant contribution to the distribution of *Eunerinea* during the Early

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Cretaceous, extending its southern boundary to the south-eastern Pacific.

2. Geological context, material and methods

Lomas Bayas is located in southern Mendoza Province (34°39′S, 69°31′W), about 110 km west of San Rafael city (Fig. 1A). The outcrops lie adjacent to the southern bank of the River Diamante near the settlement of Las Aucas and close to the eastern boundary of the Neuquén Basin. At Lomas Bayas, the lowermost levels of the Agrio Formation (Upper Valanginian–Lower Barremian) rest with an angular unconformity over localised, discontinuous Mesozoic red beds and Permo-Triassic volcanics (Aguirre-Urreta et al., 2011) (Fig. 1B). In this locality the section of the Agrio Formation is only 105 m thick. The lower half is mainly siliciclastic, whereas carbonates prevail in the upper part. The top of the Agrio Formation is overlain by siliciclastic, mixed carbonate-siliciclastic and dolomitic rocks of the Huitrín Formation (Barremian–Aptian).

The specimens of the new species described herein come from relatively thin, lensoid patches (maximum thickness of each is approximately 14 cm) of *E. mendozana*-dominated shell beds (Fig. 2) which in turn are within the highest 50 cm of a bioclastic grainstone 1.5 m thick. These beds lie near the top of the Agrio Formation within the *Sabaudiella riverorum* ammonoid Zone (Aguirre-Urreta and Rawson, 2012), of late Hauterivian–early Barremian age. In these shell beds, a high number of specimens of *E. mendozana* appear embedded in an oolitic matrix. For this reason, their study was somewhat difficult as the shells could hardly be removed from the rock matrix and were visible mostly in longitudinal and oblique sections. However, a few three-dimensional specimens preserving part of the shell were obtained, some of which are designated as the holotype and the paratypes of the new species described here. *Eunerinea mendozana* specimens are preserved mostly as calcitic recrystallised shells with a rather low proportion of apex and aperture fragmentation. Recrystallisation left no traces of the original shell structure.

Study of the type specimens of *E. mendozana* was complemented by the description and measurement of ten well-preserved selected specimens that could not be removed from the rock matrix but showed a high number of whorls available for analysis. These field-studied specimens offered a longitudinal section through the spire, i.e., more or less parallel to the shell axis throughout the columella showing internal folds. This allowed key angular measurements to be made such as the mean spire and pleural angles, thickness of shell wall and columella, and diameter and height of folds. Additionally, previously collected material housed in the collections of the Museo de La Plata, Argentina, was included in the analysis.

3. Systematic palaeontology

Systematic categories adopted here observe the classification scheme of Bouchet and Rocroi (2005). The morphological terminology employed follows Cox (1960) and the modifications introduced by Wieczorek (1979). Criteria for the preparation of the synonymy list are in line with Matthews (1973).

Measured parameters conform to those depicted by Cox (1960) and also those listed by Wieczorek (1979): PA, pleural angle; SS, sutural slope; Hn, total height of n whorls; D, maximum shell diameter; h, height of the penultimate preserved whorl; d, maximum diameter of the penultimate preserved whorl; h/d, height to diameter ratio of the penultimate preserved whorl; dmin/dmax, whorl concavity index; hf, fold height; dfb, diameter of fold base.

Institutional abbreviations. MCNAM-PI, Colección de Paleoinvertebrados, Museo de Ciencias Naturales y Antropológicas Juan

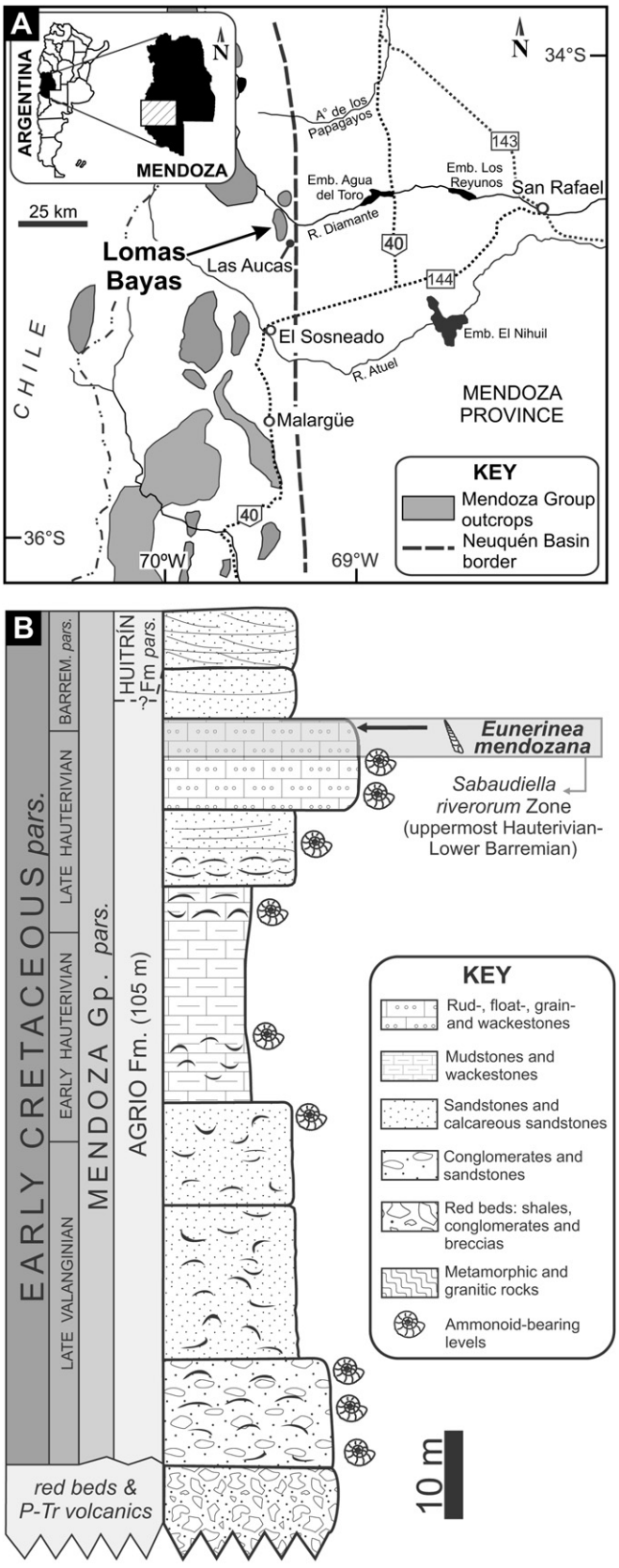

Fig. 1. Geographical and geological context of *Eunerinea mendozana*. A, map showing the location of Lomas Bayas, the type locality of *E. mendozana*, in Mendoza Province, Neuquén Basin, west-central Argentina. B, general stratigraphic column at Lomas Bayas showing position of *E. mendozana* stratotype. Ammonoid biostratigraphy and ages from Aguirre-Urreta et al. (2007) and Aguirre-Urreta and Rawson (2012).

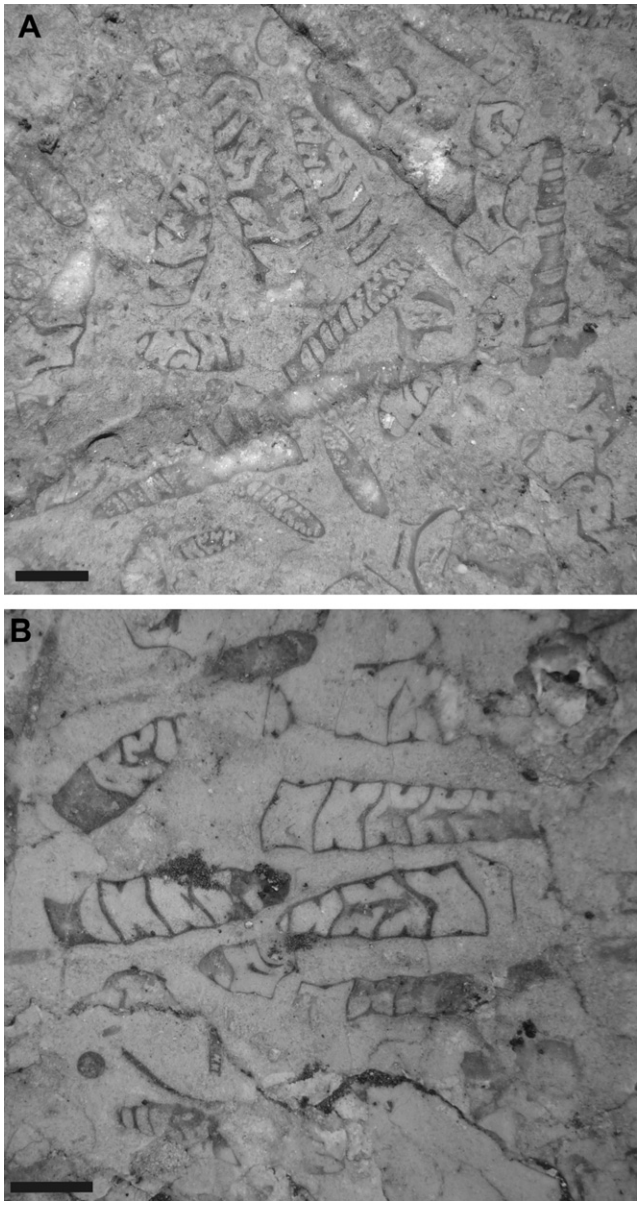

Fig. 2. *Eunerinea mendozana*-dominated shell beds in close up. A, B, plan view of *E. mendozana* stratotype showing high abundance of shells in longitudinal cut. Scale bar represents 10 mm.

Cornelio Moyano (Mendoza Capital, Mendoza, Argentina); MLP, Museo de La Plata (La Plata, Buenos Aires, Argentina); BMNHC, Burke Museum of Natural History and Culture, University of Washington (Seattle, Washington, USA).

Order Heterobranchia Haszprunar, 1988
Suborder Allogastropoda Haszprunar, 1988
Superfamily Nerineoidea Zittel, 1873
Family Nerinellidae Pchelintsev, 1960
Subfamily Diptyxinae Pchelintsev, 1960

Remarks. Kollmann (2005, pp. 28, 32, 235) included *Eunerinea* in a new subfamily within the Nerinellidae, based on that genus: Eunerineinae. Soon afterwards, Bouchet and Rocroi (2005, pp. 257, 258, 278, 279) presented a conservative classification scheme, following a personal communication of H.A. Kollmann, in which *Eunerinea* was placed in the Subfamily Diptyxinae, Family Nerinellidae. Additionally, they discussed extensively the nomenclatural history of *Nerinea* and *Eunerinea*. In light of the instability brought about by the change of the type species of *Nerinea* from *N. tuberculosa* Deshayes to *N. mosae* Defrance, Kollmann and Bouchet (fide Kollmann, 2006) proposed the following to the ICZN: to abandon usage of the family Nerineidae, to erect a new family-level taxon based on *Eunerinea* and to employ Ptygmatididae for the family containing true *Nerinea*. Here, the conservative scheme in Bouchet and Rocroi (2005) is adopted since the ICZN has not yet pronounced on the matter.

Genus *Eunerinea* Cox, 1949

Type species. *Nerinea castor* d'Orbigny, 1850 (by original designation), Late Jurassic (late Oxfordian), France.

Stratigraphic range and distribution. Middle Jurassic (Bajocian)–Late Cretaceous (Cenomanian): southern and central Europe, Britain, northern Africa, south-western Asia, Caribbean, Gulf of Mexico, Tibet, Japan and south-western South America.

Diagnosis (from Cox, 1949). Shell moderately acute, with strongly concave whorls and a convex, protruding sutural region. Aperture rhomboidal, anterior canal long and oblique, and with three internal folds: a labial fold, a columellar fold and a parietal fold.

Remarks. The genus *Eunerinea* was described by Cox (1949) to replace *Nerinea* Defrance, 1825 (= "*Nerinea sensu stricto*" of Cossmann, 1896). Originally, Cox (1949) proposed *Eunerinea* as a subgenus of *Cossmannea* Pchelintsev, 1927, on the basis of their identical external morphology and the priority of the name *Cossmannea*. However, Wieczorek (1975) and Kollmann (2005, following Vaughan, 1988) preferred to keep *Eunerinea* as a separate genus; Wieczorek (1975) pointed out different internal morphology and ontogenetic development, while Kollmann (2005) referred to the fact that *Eunerinea* has a long and oblique anterior canal, absent in the type species of *Cossmannea*, *Nerinea desvoidyi* d'Orbigny, 1850. Many external characters of *Eunerinea* are identical to those of *Cosmannea*; nevertheless, they can be readily separated when seen in longitudinal section given the presence of three internal folds in *Eunerinea* in contrast with the two present in *Cossmannea*, which lacks a parietal fold. *Eunerinea* species are similar to species of other genera which also show three internal folds, which is the case of *Nerinella* Sharpe, 1850. *Nerinella* shells are characteristically acicular, fairly high to high, of relatively small diameter and with a very low mean spire angle. In this genus whorls are usually concave and have a rounded sutural region, with suture placed between spiral cords. Granular spiral threads are common. Internally, *Nerinella* shows a labial fold, one or two columellar folds and a parietal fold either slightly developed or absent (Saul and Squires, 1998). In general, shells in *Nerinella* are rather taller, more slender and more cylindrical than those of *Eunerinea*. Moreover, the presence of an external sculpture of spiral, sometimes granular threads, is more frequent in *Nerinella* than in *Eunerinea*.

Eunerinea mendozana sp. nov.
Fig. 3

v.1979
Cossmannea (*Eunerinea*) sp. Damborenea et al., p. 73, pl. 11, fig. 1.

Derivation of name. After Mendoza Province, Argentina, where the type locality is situated.

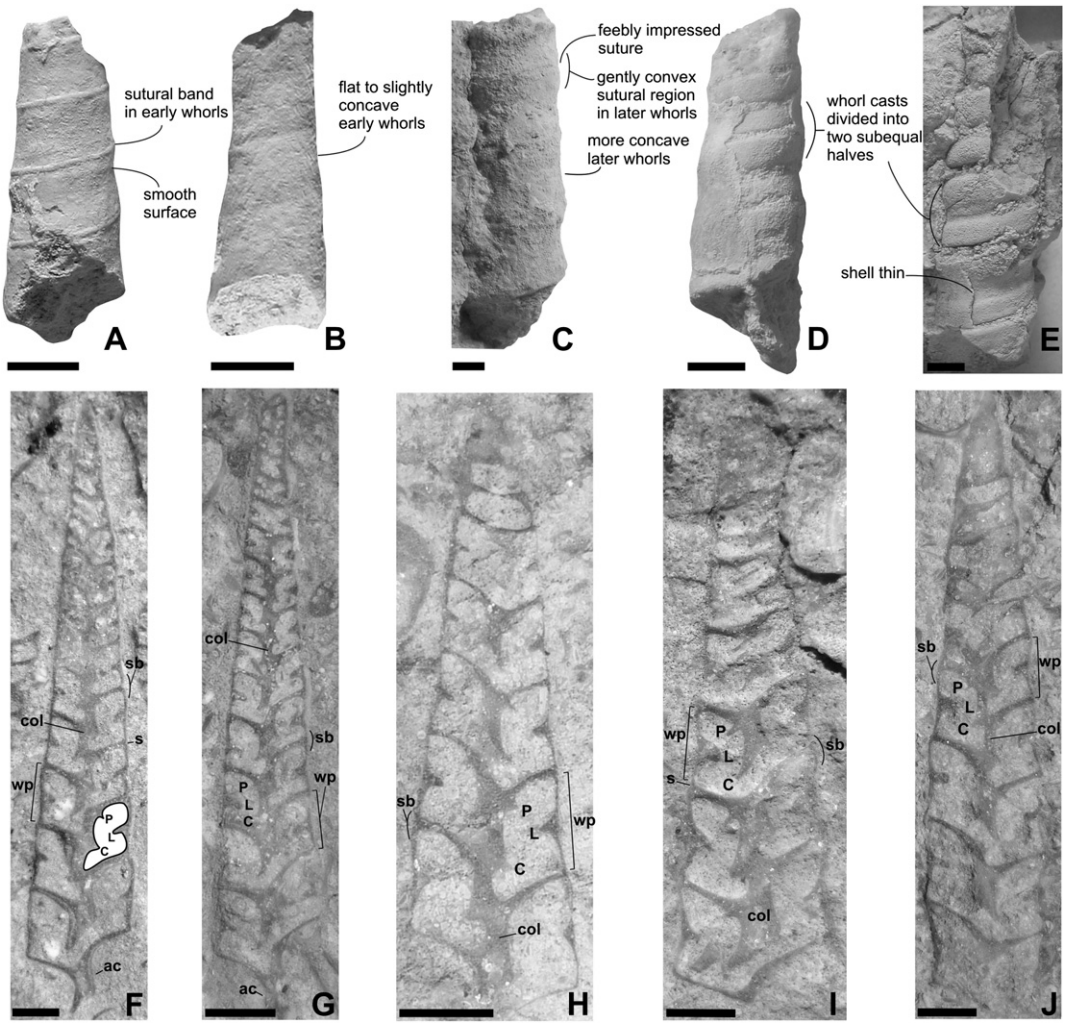

Fig. 3. *Eunerinea mendozana* sp. nov. A, MCNAM-PI 24473, holotype. B, MCNAM-PI 24474.1, paratype. C, MCNAM-PI 24474.2, paratype. D, MCNAM-PI 24474.3, paratype. E, MCNAM-PI 24474.4, paratype. F–J, longitudinal sections of field-studied specimens depicting different morphological features: P, parietal fold; L, labial fold; C, columellar fold; ac, short anterior canal; col., massive columella; wp, slightly concave whorl profile; s, feebly impressed suture; sb, slightly swollen sutural band. A–E, coated with ammonium chloride. All from Lomas Bayas, Mendoza Province; Agrio Formation, *Sabaudiella riverorum* Zone (uppermost Hauterivian–Lower Barremian). Scale bar represents 5 mm.

Material. Holotype, MCNAM-PI 24473; paratypes, MCNAM-PI 24474.1–4. All from the Agrio Formation at Lomas Bayas, Mendoza Province.

Additional material. MCNAM-PI 24474.5–6, MLP 14891, Lomas Bayas (Mendoza Province), Agrio Formation, uppermost Hauterivian–Lower Barremian. MLP 14965, Los Pirilos (Mendoza Province), Chachao Formation (Upper Valanginian).

Type locality and stratotype. Lomas Bayas, Mendoza Province; Agrio Formation, *Sabaudiella riverorum* Zone (uppermost Hauterivian–Lower Barremian).

Stratigraphic range and distribution. Upper Valanginian (Chachao Formation); uppermost Hauterivian–Lower Barremian (Agrio Formation).

Diagnosis. Shell thin, slightly cyrtoconoid. Whorls with slightly concave walls, sutural region gently convex, suture feebly impressed. Smooth surface. Rhomboidal aperture. Well-developed, triangular labial fold; wide, slightly curved adapically columellar fold; short, spiniform parietal fold.

Description. Shell thin (less than 0.6 mm), conical to subcylindrical (PA 6°–8.5°, as measured in the last two preserved whorls of several specimens), elongate, with slightly convex to flat sides, i.e., slightly cyrtoconical. Protoconch not preserved. Teleoconch usually with high number of whorls, frequently exceeding 12. Base flat to slightly concave, periphery angular and well defined. Whorls relatively tall (h/d 0.57–0.67, as measured in the penultimate preserved whorl of several specimens), only slightly overlapping, i.e., imbricate. Whorls with slightly concave to flat walls (dmin/dmax 0.82–0.92), with the maximum concavity near mid-whorl. Concavity of whorls increases towards the last whorl. Suture feebly marked and concurrent with periphery of preceding whorl (SS 17–20°). Surface of whorls adjacent to the suture slightly swollen forming a gently rounded raised band; the swelling located abapical to the suture is slightly more prominent than the adapical one. Last whorl not different from those preceding it. Umbilicus closed. Massive, relatively thick columella (diameter in longitudinal section between 1.6 and 2.8 mm). Anterior canal apparently not taller than last whorl. Aperture rhomboidal. Whorl surface smooth, sometimes with a very fine spiral thread abapical to the suture in early whorls. Growth-lines not preserved. Longitudinal section of shell shows three internal folds, its fold formula being 1.1.1.0. Labral

fold well-developed, being the most conspicuous of the three internal folds, located near mid-whorl and concurrent with the maximum concavity of whorl face; in early whorls it is triangular in shape, thick, generally symmetrical, with a wide base and round top; in later whorls it becomes slightly assymetrical and gently curving abapically and in the last whorls it changes to a lower triangular shape and is more or less sharply pointed (dfb 1.62 mm; hf 1.07 mm, measured in the penultimate whorl of a specimen of H12+ 63.15 mm). Columellar fold also conspicuous, low-triangular in shape, asymmetrical, with a wide base and a sharp point, and slightly curved adapically; in the last whorls it becomes less sharply pointed (dfb 2.98 mm; hf 1.2 mm, same specimen); it is located slightly abapical to the mid-whorl. Parietal fold poorly developed, spiniform, slightly hook-shaped to straight and sharply pointed, located very close to the columella (dfb 0.43 mm; hf 0.46 mm, same specimen). Proportional relationships of known fragments suggest a total shell height for *E. mendozana* of over 120 mm and D reaching 15 mm.

Dimensions. Holotype MCNAM-PI 24473: PA, 5.78°; SS, 11.36°; n, 4.5; H4.5, 20.42 mm; D, 7.36 mm; h, 4.28 mm; d, 7.03 mm; h/d. 0.6; dmin/dmax, 0.94.

Remarks. The holotype of *E. mendozana* (Fig. 3A) is a small fragment, slightly more than 20 mm high, of four and a half whorls, preserving shell material. This specimen was chosen given the scarce representation of shell material among the known specimens of *E. mendozana*, which are mainly internal moulds. MCNAM-PI 24473 is slightly worn and recrystallisation of original shell material into calcite has left no trace of growth lines.

The material described herein fits the diagnosis of *Eunerinea* as given by Cox (1949), especially in the distinctiveness of the fold pattern shown by the members of this genus. *Eunerinea mendozana* is distinguished from many *Eunerinea* species (Table 1), including the type species, *E. castor* (d'Orbigny, 1850, p. 109, pl. 262, figs. 3, 4; see also the revision of this species in Fischer and Weber, 1997), by the presence of smooth and slightly concave whorls. *Eunerinea castor* is also more conical, i.e., shorter and wider, than *E. mendozana*. However, in the Argentinean species the whorls become slightly more concave towards the last whorl (see Fig. 3C), but the sutural region does not form a prominent narrow band as in *E. castor*, and instead is subtly rounded to sub-angular.

Comparisons. Von der Osten (1957) reported six nerineoid species from the Aptian Taguarumo Member of the Barranquín Formation at Bahía de Santa Fé, Venezuela. Among them, three belong to *Eunerinea*: *E. dianae* (Von der Osten, 1957), *E. hicoriensis* (Cragin, 1893) and *E. aquilina* (Stanton, 1947). *Eunerinea dianae* is similar to *E. mendozana* in its gently concave whorls, but differs in having a narrow subangular ridge adjacent to the adapical suture of each whorl, an external sculpture of fine spiral threads and a much less developed columellar fold. *Eunerinea hicoriensis* is most common in the lower part of the Travis Peak Formation in Texas, USA (Aptian–Albian; Cragin, 1893; Adkins, 1928; Stanton, 1947) and was also recorded in several Aptian–Albian units in Mexico (see Alencáster, 1956; Buitrón and Barceló-Duarte, 1980; Buitrón-Sánchez and Pantoja-Alor, 1994; Buitrón-Sánchez and López-Tinajero, 1995). It features a very large shell, with a maximum diameter of 30 mm in 5-whorl-high specimens (Stanton, 1947). It is very similar in general outline to *E. mendozana*, especially with respect to its gently concave, relatively tall whorls with faintly impressed sutures and smooth outer surface, but differs in having a more prominent, narrow subangular sutural band with a thicker ridge adapical to the suture. Besides these differences, the labial fold in *E. hicoriensis* is located slightly abapical to the mid-whorl, unlike in *E. mendozana*, and as a result the adapical lobe is slightly taller than the abapical one, dividing internal moulds of whorls into two asymmetrical parts. This is also the case in *E. aquilina*, which similarly has strongly concave whorls and a protruding, rounded sutural band with impressed sutures. Von der Osten (1957) attributed the specimens of *E. aquilina* from the Barranquín Formation to *Nerinea roemeri* Whitney, 1952, which is actually a junior synonym (see Kollmann et al., 2003). *Eunerinea aquilina* was originally described from the Aptian–Albian Trinity Group of Texas (Stanton, 1947; Whitney, 1952; Kollmann et al., 2003). The other nerineoids from the Lower Cretaceous of Venezuela mentioned by Von der Osten (1957) as well as the Colombian record published by Etayo-Serna (1985) do not match the diagnosis of *Eunerinea* and, therefore, are not relevant for further comparison with *E. mendozana*. However, it is worth mentioning that although *Nerinea riverae* Von der Osten (1957) has two internal folds (1.0.1.0), this could be owing to the fact that this species is known from a few late whorls of an incomplete shell where the number of folds is usually reduced; its concave-convex whorl outline agrees with the diagnosis of *Cossmannea* Pchelintsev, 1931.

Eunerinea poblana (Buitrón and Barceló-Duarte, 1980, p. 53, fig. 8a–d), from the Upper Barremian Agua del Burro Formation, north of San Juan Raya, Mexico, is characterised by a very large, cylindrical shell, and can be readily separated from *E. mendozana* on the basis of its deeply concave whorls and very broad, rounded, bulging sutural band.

Eunerinea occidentalis (Stanton, 1947, p. 86, pl. 62, figs. 11, 17), from the Aptian–Albian of Texas, USA (see also Kollmann et al., 2003), has a nearly cylindrical shell and its whorls have a characteristic profile with an almost flat adapical half and a slightly convex abapical half. The labial fold, which is thinner than in *E. mendozana*, divides whorls into two unequal parts in internal moulds.

Alencáster (1956, p. 40, pl. 7, fig. 1) recorded *Eunerinea* cf. *aptiensis* (Pictet and Campiche, 1863) from the Aptian San Juan Raya Formation at San Juan Raya, Mexico. His specimens are quite similar to *E. mendozana* in general outline, smooth surface and slightly concave whorl outline, but their suture is deeply impressed and limited adapically by a prominent sutural ridge. *Eunerinea aptiensis* was originally described from the Lower Aptian at Sainte-Croix, Switzerland (see Pictet and Campiche, 1863, p. 244, pl. 69, fig. 3), and is very similar to *Nerinea gaultina* Pictet and Campiche, op. cit. (p. 246, pl. 69, fig. 5) and *Nerinea etalloni* Pictet and Campiche, op. cit. (p. 232, pl. 66, figs. 5–7), also from the Lower Cretaceous of Switzerland. These two species could be allocated to *Eunerinea* on the basis of shell outline and the number of internal folds. Also both have a broad conical shell and a labial fold that is located well below the mid-whorl. Pchelintsev (1965) described a new genus, *Etallonea*, based on *N. etalloni*.

Eunerinea gigantea (d'Hombres-Firmas, 1838; see also d'Orbigny, 1843; Cossmann in Pellat and Cossmann, 1907, p. 9, pl. 1, figs. 1–5; Kollmann, 2005, p. 27, pl. 3, fig. 6a, b), known from the Upper Barremian of France, is exceptionally large for the genus and is characterised by deeply concave whorls, twice as wide as high, with a grooved suture and salient sutural band. In this species the last whorls are less strongly concave and the shell becomes nearly cylindroid; the columellar fold is tall, symmetrical and round-topped; there are weakly developed nodes along the sutural bands.

Among the Early Cretaceous *Eunerinea* species recorded from Spain, *E. mendozana* is most similar in morphology to *Eunerinea cazorlensis* (Termier and Termier in Foucault et al., 1975, p. 248, pl. 1, figs. 3–5; pl. 2, fig. 1), from the Berriasian–Lower Valanginian of Cazorla. *Eunerinea cazorlensis*, especially "form C", shares with *E. mendozana* the nearly flat, slightly concave whorls. It differs from *E. mendozana* by its variable external sculpture, sometimes with nodose spiral threads. The fold morphology in *E. cazorlensis* is very

Table 1
Diagnostic features of *Eunerinea mendozana* sp. nov. and other *Eunerinea* species mentioned in the text. See section 3, "Comparisons" for full references and occurrences of each species. C, columellar fold; P, parietal fold; L, labial fold.

Species	Shell outline	Whorl profile	Maximum concavity	External sculpture	Sutural region	Whorl section
E. mendozana sp. nov.	Elongate, conical, slightly cyrtoconical	Flat to slightly concave	At mid-whorl	Smooth	Gently rounded band	
E. castor (d'Orbigny)[a]	Broadly conical	Moderately concave	At mid-whorl	Smooth	Narrow band	
E. dianae (von der Osten)[b]	Elongate, conical	Slightly concave	At mid-whorl	Fine spiral threads	Narrow sub-angular adapical ridge	–
E. hicoriensis (Cragin)[c]	Large, cylindrical	Slightly concave	Slightly below mid-whorl	Smooth	Narrow sub-angular band	
E. aquilina (Stanton)[d]	Large, slender, cylindrical	Strongly concave	Below mid-whorl	Smooth	Broad rounded band	
E. occidentalis (Stanton)[e]	Large, cylindrical	Moderately concave	Below mid-whorl	Smooth?	Gently rounded band	
E. poblana (Buitrón & B. Duarte)[f]	Large, cylindrical	Strongly concave	At mid-whorl	Smooth?	Prominent rounded band	
E. cf. *aptiensis* (Pictet & Campiche)[g]	Large, cylindrical	Slightly concave	Below mid-whorl?	Smooth	Prominent adapical ridge	–
E. gigantea (d'Hombres-Firmas)[h]	Large, cylindrical	Strongly concave	At mid-whorl	Smooth (feeble sutural nodes)	Prominent rounded band	
E. *cazorlensis* (Termier & Termier)[i]	Large, cylindrical	Flat to slightly concave	At mid-whorl	Nodose spiral threads	Gently convex band	
E. cf. *chloris* (Coquand)[j]	Broadly conical	Moderately concave	At mid-whorl?	Smooth	Narrow ridges?	
E. zumoffeni (Delpey)[k]	Sub-cylindrical	Strongly concave	Below mid-whorl	Smooth?	Broad sub-angular band	
E. lopezi Calzada & Urquiola[l]	Elongate conical to sub-cylindrical	Moderately concave	Below mid-whorl	Smooth?	Broad sub-angular/ rounded band	

Table 1 (*continued*)

Species	Shell outline	Whorl profile	Maximum concavity	External sculpture	Sutural region	Whorl section
E. nepomuceni Calzada & Urquiola[m]	Elongate conical to sub-cylindrical	Moderately to strongly concave	At mid-whorl	Smooth	Narrow rounded band	
E. pauli (Coquand)[n]	Elongate conical to sub-cylindrical	Strongly concave	At mid-whorl	Smooth	Narrow sub-angular band	

[a,c–f,h–n]drawings after: a, d'Orbigny, 1850, pl. 262, fig. 3; c, Stanton, 1947, pl. 58, fig. 3; d, Stanton, 1947, pl. 58, fig. 9; e, Stanton, 1947, pl. 62, fig. 11; f, Buitrón and Barceló-Duarte, 1980, fig. 8d; h, Kollmann, 2005, pl. 3, fig. 6b; i, Termier and Termier in Foucault et al., 1975, pl. 1, fig. 5; j, Calzada and Carrasco, 2011, fig. 3; k, Calzada, 1986, pl. 3, fig. 5; l, Calzada and Urquiola, 1995, fig. 1.E; m, Calzada and Urquiola, 1995, fig. 1.N; n, Calzada, 2008, fig. 3.9. [b,g] longitudinal sections not illustrated in the references.

similar to that of *E. mendozana* although the parietal fold is slightly more developed, taller and curved abaxially in the Spanish species.

Eunerinea cf. *chloris* (Coquand, 1865), recorded by Calzada and Carrasco (2011) from the Aptian of Huesca, has a broad conical shape and tall whorls. Its labial fold is strong and wide.

Eunerinea zumoffeni (Delpey, 1939), originally described from the Aptian of Lebanon and also recorded from Algeria, Tibet and Spain (see Calzada, 1986), has a characteristic morphology of thin, projecting, slightly curved folds. Its whorls are also deeply concave and with an angular profile.

Eunerinea lopezi Calzada and Urquiola, 1995, from the Upper Aptian of Castellón, Spain, has moderately concave whorls in which the maximum concavity is displaced abapically. The abapical half of the whorl face is short and slightly convex. Internal folds are blunt, and the labial fold is located well below mid-whorl.

In *Eunerinea nepomuceni* Calzada and Urquiola, 1995, also from the Upper Aptian of Castellón, Spain, the sutural band forms a rather acute edge, the labial fold is rather narrow and the columellar fold is broad and with an acute distal end directed adapically.

Eunerinea pauli (Coquand, 1862, p. 177, pl. 4, fig. 3) was originally described from the Upper Aptian of Lebanon and Tunisia, and from the Barremian of Algeria, but it was subsequently recorded from several other localities within Theia (see revision of the species in Calzada, 1993). It typically shows tall whorls and bears some resemblance to *E. mendozana* in general outline, smooth surface and weak sutural bands; but in *E. pauli* the whorls are deeply concave and its columellar fold is sharp and acute whereas in *E. mendozana* it is broad and triangular.

Nerinea sp. (Kase, 1984, p. 173, fig. 22-a) is a very badly preserved nerineoid from the Upper Hauterivian of north-eastern Japan that shows smooth, slightly concave whorls with a thin, projecting labial fold, a less developed, triangular columellar fold and a small, acute parietal fold. The morphology of the labial fold is quite different from that in *E. mendozana*. Although Kase (1984) stated that this morphology could justify the assignment to *Nerinea*, it is also close to the diagnosis of *Eunerinea*. However, the few preserved shell features are unfortunately not conclusive.

A previous record of an alleged nerineoid gastropod from the upper Agrio Formation in Neuquén Province is Weaver's (1931, p. 383) identification of "*Nerinea* cf. *nerinaeformis* (Coquand, 1862)". Coquand's species was included in the genus *Mrhilaia* by Pervinquière (1912), a fact that Weaver did not seem to acknowledge. According to Kollmann and Peza (1997), *Mrhilaia* belongs to the Campanilidae. Weaver also linked his record with the "*Nerinea* cf. *nerinaeformis*" reported by Paulcke (1903) from the Upper Albian–Lower Cenomanian of north-western Peru. Weaver's specimen (BMNHC 289) is mostly an internal mould with patches of recrystallised shell, which compared to the original description and illustration of *M. nerinaeformis* (Coquand, 1862), shows much shorter whorls and lacks the medium spiral groove which in internal moulds is indicative of the presence of a labial fold. Thus, it follows from these differences that the initial comparison of Weaver's specimen with *M. nerinaeformis* is not satisfactory. Furthermore, although Weaver mentioned the presence of an inner and an outer fold in the aperture of his specimen, there are no signs of such folds and the aperture is actually not preserved. A longitudinal section through the spire shows no development of internal folds either. Although the details of its external morphology are not well known, the general features of Weaver's specimen fits the diagnosis of the Family Campanilidae as given in Kiel et al. (2000): elongate and turreted shell with flat to slightly convex whorls; more or less incised sutures; narrow, fusiform aperture; columella projecting anteriorly as if it formed an anterior canal; columella smooth; recrystallised shell patches suggesting the presence of sub-sutural cords. However, there are not enough features to ensure an unambiguous generic assignation of specimen BMNHC 289.

On the other hand, Paulcke's (1903) Peruvian material of "*Nerinea* cf. *nerinaeformis*" consists of poorly preserved internal moulds in which the apertural details are not preserved. Since this author did not describe properly or illustrate the specimens, no comparison is possible with *E. mendozana* or with Weaver's (1931) record. Paulcke only mentioned the presence of a constriction in the middle of each whorl mould and a general resemblance to *M. nerinaeformis* (Coquand, 1862). However, Olsson (1934) stated that Paulcke's record may possibly belong to *Teleoptyxis peruviana* Olsson (1934, p. 65, pl. 10, figs. 1, 3), a fact that remains unclear due to its very poor preservation. *Teleoptyxis peruviana*, known from the Upper Aptian–Lower Albian of Paita, north-western Peru, shows four characteristic internal folds: two columellar, one parietal and one labial; its shell is tall and has a large maximum diameter, and the whorls are concave and twice as wide as tall.

There are two nerineoid records from the Barremian–Aptian Pabellón Formation, Chile, but unfortunately neither was adequately described or figured; therefore, no inferences can be drawn as to their relationship with *E. mendozana* or their reference to the genus *Eunerinea*. These are *Eunerinea* cf. *gigantea* (d'Hombres-Firmas, 1838), reported by Tavera (1956, p. 28) and *Nerinea* sp., mentioned by Aguirre-Maturana (2001).

It is worth noting that the *Nerinea* sp. recorded by Fritzsche (1924, p. 11, fig. 3) from the Upper Cretaceous (?Cenomanian) of Miraflores, Bolivia, bears some resemblance to *E. mendozana* in general outline and proportions. In addition, it has weakly convex whorls somewhat swollen next to the sutures and three internal folds of simple morphology similar to those of *E. mendozana*. However, the only specimen recorded is poorly preserved and is

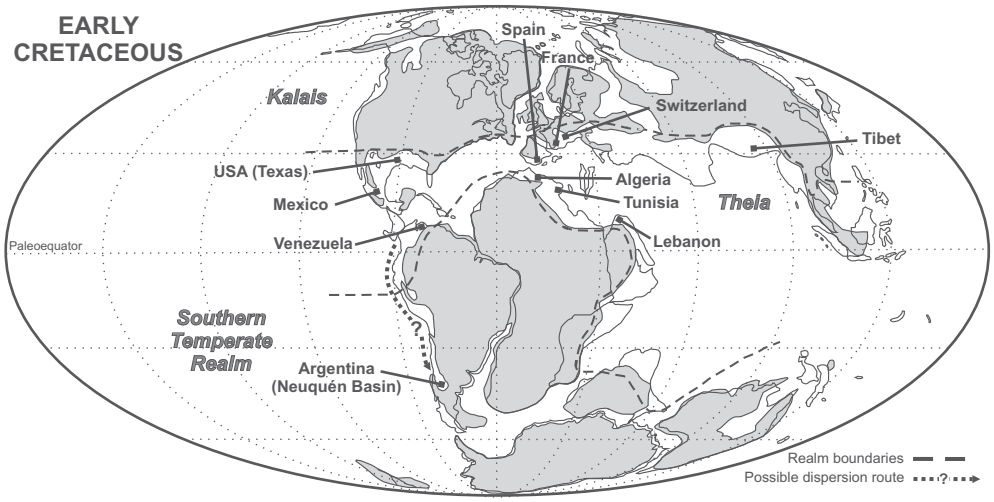

Fig. 4. Distribution of *Eunerinea* during the Early Cretaceous. Theian boundaries from the equivalent "Tethyan Realm" of Kauffman (1973). Palaeocoastline reconstruction redrawn from Smith et al. (1994).

seen only longitudinal section; hence, the details of its external morphology are not known. *Eunerinea mendozana* and Fritzche's record may be related, but a further revision of this latter would be necessary to confirm.

4. Palaeobiogeographic and palaeoecological implications

During the Early Cretaceous the genus *Eunerinea* was moderately diverse and the records so far reported point to a distribution restricted to Theia (sensu Kollmann, 2002; formerly the Tethyan Realm sensu Kauffman, 1973). Records come from south and central Europe (Spain, France, Switzerland, the Carpathian–Balkan area and the Dinarides), south-western Asia (Lebanon), northern Africa (Tunisia, Algeria), the Caribbean (Venezuela), the Gulf of Mexico (Mexico, Texas) and Tibet (e.g., Pictet and Campiche, 1863; Delpey, 1939; Stanton, 1947; Von der Osten, 1957; Buitrón and Barcelo-Duarte, 1980; Yu and Xia, 1985; Calzada and Urquiola, 1995; Sirna, 1999; Kollmann, 2005) (Fig. 4). The Mediterranean and the Gulf of Mexico show similar species diversity. *Eunerinea pauli* and *E. zumoffeni* show a broad distribution in the Mediterranean area during the Early Cretaceous, as does *E. hicoriensis* in the Caribbean-Gulf of Mexico area. The species described herein, *E. mendozana*, expands the Early Cretaceous distribution of the genus to the south-eastern Pacific, which is much farther south than previously reported, to the "Southern Temperate Realm" (sensu Kauffman, 1973).

In South America, *Eunerinea* was present, during the Early Cretaceous, solely in Venezuela and Argentina. If the possible Chilean record is confirmed to belong to *Eunerinea*, this would mean that *E. mendozana* does not represent an isolated, exceptional record of the genus in southern South America. *Eunerinea* must have reached the Neuquén Basin through shallow-water platform connections along the Andean basins of the western margin of the South American plate. Such connections are necessary in the case of benthic fauna with short-lived planctotrophic larvae. The existence of long-lived, open marine connections between the basins along the western margin of South America and the Tethys Sea is well-documented through the palaeobiogeographic affinities of other invertebrate taxa that inhabited the Neuquén Basin during the Early Cretaceous, e.g., ammonoids, bivalves and echinoids (see Aguirre-Urreta et al., 2008). The latter authors suggested that the east–west equatorial oceanic current (sensu Gordon, 1973) may have been one of the mechanisms that aided faunal exchange between the Tethys and the Andean basins.

Eunerinea mendozana formed large monospecific populations that dwelt in the Lomas Bayas area. Deposits in the Agrio Formation where individuals accumulated have been interpreted as reflecting an inner carbonate-ramp setting (Cataldo et al., in press). Both facies and associated fauna suggest that the individuals inhabited a soft substrate in a very shallow marine setting, and in these conditions, *E. mendozana* may have had an infaunal or semi-infaunal habit (Cataldo et al., in press). Nerineoid mass-accumulations have been signalled as evidence of the opportunistic character of these gastropods (Wieczorek, 1979), because of their considerable abundance when ecologic conditions were optimal (Levinton, 1970). Therefore, the record of *E. mendozana* in relatively high-density populations in Lomas Bayas may point to subtropical conditions in the northern part of the Neuquén Basin, close to the Hauterivian/Barremian boundary.

5. Conclusions

Eunerinea mendozana is characterised by a rather thin, moderately conical, smooth shell with weakly concave whorls, only slightly swollen sutural bands and barely impressed sutures. Its internal fold morphology consists of a well-developed, triangular labial fold, a wide, somewhat curved adapically columellar fold, and a short, spiniform parietal fold. Total shell height of adult specimens may have reached 120 mm with a maximum diameter of 15 mm. Whorl concavity increases slightly towards the last whorl of adult shells.

The new species is reported from the top of the Agrio Formation at Lomas Bayas, Mendoza Province, within the *S. riverorum* Zone (uppermost Hauterivian–Lower Barremian), where it forms high-density accumulations.

Weaver's (1931) "*Nerinea* cf. *nerinaeformis* (Coquand, 1862)" does not belong to the Nerineoidea. It could be included in the Campanilidae, although an unequivocal generic assignation is not possible.

During the Early Cretaceous *Eunerinea* was widespread in Theia, and the record of *E. mendozana* extends the Early Cretaceous distribution of the genus to the south-eastern Pacific, within the "Southern Temperate Realm". During this interval *Eunerinea* was present also in Venezuela, while a possible Chilean record remains

to be confirmed. The record of *E. mendozana* in relatively high-density populations in Lomas Bayas may point to subtropical conditions in the northern part of the Neuquén Basin, close to the Hauterivian/Barremian boundary.

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