



Taphonomy and palaeoecology of Hauterivian–Barremian nerineoid shell beds from the Neuquén Basin, west-central Argentina

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Nerineoid shell beds are described for the first time from Lower Cretaceous deposits of southern South America. These come from carbonates near the top of the Agrio Formation in southern Mendoza Province, west-central Argentina. To envisage the origin of the nerineoid shell beds, a taphonomic study was carried out, which indicated that these represent within-habitat time-averaged, primary sedimentological concentrations with a secondary biogenic imprint related to a relatively high local production of nerineoid shells. The associated palaeoenvironments were studied through a facies analysis of the carbonate succession including the shell beds. The carbonates were deposited in a homoclinal ramp system and depict a shallowing upward trend from mid to inner ramp. The individuals lived and accumulated in oolitic shoals within the inner ramp, in a shallow, well-lit, high-energy setting above fair-weather wave base. Substrate was oxygenated and loose. The nerineoids are shown to belong to one species of the genus *Eunerinea*, and through the functional morphology of the shells they are tentatively interpreted as infaunal or semi-infaunal. It is suggested that the recorded monospecific nerineoid shell beds indicate that the palaeoenvironmental conditions may have been favourable for the development of abundant populations of these gastropods in the northern part of the Neuquén Basin during a short time interval in the Hauterivian–Barremian boundary. This could have been related to a brief warming episode, but other factors may have also been involved. □ *Argentina, Early Cretaceous, Gastropods, nerineoids, Neuquén Basin, shell beds, taphonomy.*

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In this article, we present precisely-dated taphonomic and palaeoecological data regarding the occurrence of nerineoid shell beds in Lower Cretaceous deposits of the Neuquén Basin. This basin is presently located between 32° and 40° S in the Andean foothills of west-central Argentina and central Chile (Howell *et al.* 2005). During the Early Cretaceous, it had a mid-latitudinal location not far from its current position, approximately between 28°–36°S, based on reliable palaeomagnetic data from South America (Somoza 2011). Thus, its fossil record may be considered a key link between the Tethyan and South Temperate realms faunas (*sensu* Kauffman 1973; see also Aguirre-Urreta *et al.* 2008).

Nerineoids are readily recognized in Jurassic–Cretaceous shell beds due to the presence, in most representatives, of their most distinctive feature: the internal spiral folds. They have been traditionally considered

as a key benthic element of Jurassic and Cretaceous carbonate reefal facies, especially in the Tethys Sea (Sohl 1987; Wieczorek 1988), where they formed large mass accumulations several metres thick in warm shallow euhaline waters (Wieczorek 1988; Buitrón-Sánchez & Pantoja-Alor 1994). In some cases, they attained gigantic thick shells up to 60-cm long (Whitney 1952; Buitrón & Barceló-Duarte 1980).

During the Early Cretaceous, nerineoids were abundant in the Tethyan Realm (*sensu* Kauffman 1973), from Portugal through most of Europe to southern China, the northern coast of Africa from Algeria to Egypt, northern India and the Caribbean Province. On the contrary, they have been less recorded outside the Tethyan Realm and the only findings so far come from Japan and California in the North Temperate Realm (Shikama & Yui 1973; Saul & Squires 1998)

and Argentina and Chile in the South Temperate Realm (Tavera 1956; Damborenea *et al.* 1979; Mouragues *et al.* 2010). A record from Peru (Olsson 1934) would fall within the Tethyan Realm, or very close to the boundary with the South Temperate Realm, according to Kauffman (1973, Fig. 1).

Tethyan records of nerineoids appear usually in the form of complex mass accumulations of high generic and specific diversity embedded in thick carbonate platform or ramp deposits, commonly associated with rudists and corals (e.g., Sohl 1987; Barker 1990; Waite *et al.* 2008). This type of accumulation has been extensively studied (e.g. Dauwalder & Remane 1979; Wieczorek 1979; Waite *et al.* 2008). However, less common, mid- to high-latitude nerineoid occurrences are of special palaeoecological and palaeoclimatic interest as they lie outside the Cretaceous carbonate platform belt (see Simo *et al.* 1993).

In this paper, we characterize in detail an Early Cretaceous record of nerineoid shell beds located near the top of the Agrio Formation at Lomas Bayas, Mendoza Province. Based on a section logged in detail, a comprehensive taphonomic scoring of the shell beds and a sedimentary facies analysis of the associated carbonates, we intend to interpret the palaeoecological clues and the palaeoenvironmental scenario where these gastropods thrived in mid latitudes outside the aforementioned Cretaceous carbonate platform belt.

Geological setting

The Neuquén Basin, located at west-central Argentina, has a nearly continuous sedimentary record from the

Late Triassic to the Late Cretaceous, and probably represents the most complete Mesozoic basin of the Southern Hemisphere. The outcrops form a narrow belt along the Andes in the north, covering part of the Principal Cordillera and extend eastward in the south to form the Neuquén Embayment. The basin is bounded by the Sierra Pintada Massif to the east, by the North Patagonian Massif to the southeast, whereas towards the west it was communicated with the Palaeo-Pacific Ocean through an active volcanic arc. Thick, mostly marine rocks of the Mendoza Group (Groeber 1953) accumulated in a retro-arc setting during Late Jurassic to Early Cretaceous times.

Lomas Bayas is a classic locality of the easternmost margin of the Neuquén Basin in southern Mendoza Province (Fig. 1A, B). It is in the vicinity of the southern bank of the Diamante river near Las Aucas settlement ($34^{\circ}39' S$, $69^{\circ}31' W$). The geology of the region has been known since the early pioneer work of Gerth (1925, 1931), which was followed by several expeditions of the national geological survey (Groeber 1947; Volkheimer 1978; Sruoga *et al.* 2000) and more recently by numerous regional and structural studies (Schwarz *et al.* 2002; Tunik *et al.* 2005; Turienzo 2009; among others). The regional basement corresponds to Ordovician sedimentary and metamorphic rocks intruded by granitoids, both covered by Permo-Triassic volcanics. The studied sedimentary succession of the Agrio Formation rests with an angular unconformity over the basement and localized red beds and is conformably covered by clastics and dolomites of the Barremian–Aptian Huitrín Formation (Fig. 2).

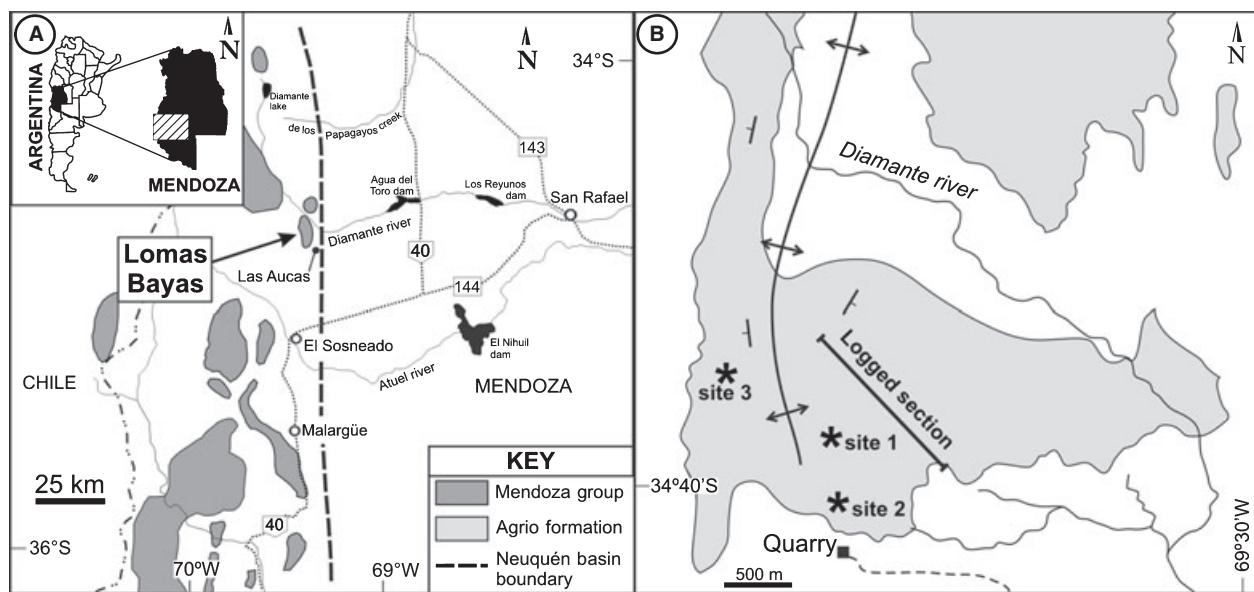


Fig. 1. A, location map of Lomas Bayas locality in the Mendoza Province, Neuquén Basin, west-central Argentina. B, studied fossil sites and logged section on outcrops of the Agrio Formation at Lomas Bayas.

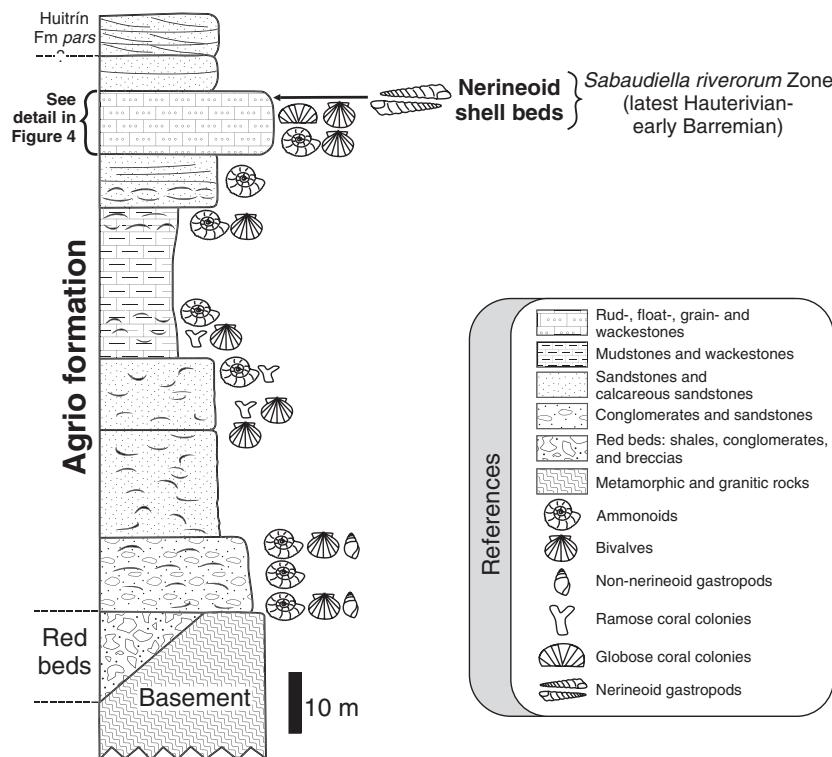


Fig. 2. General stratigraphical column at Lomas Bayas locality and position of the nerineoid shell beds near the top of the Agrio Formation.

The total thickness of the Agrio Formation reaches only 105 m in Lomas Bayas (Fig. 3A), compared to more than 1200 m in the basinal area (Weaver 1931). The facies are condensed, denoting a palaeogeographical position very close to the basin margin and it is difficult to recognize the three-fold member division of this unit as in the embayment area. However, this condensation is not biostratigraphical, as all the ammonoid zones of the Agrio Formation are clearly recognized in Lomas Bayas, but with a much thinner development.

The nerineoid shell beds described here lie slightly above beds with *?Hamulinites* sp. and *Sabaudiella?* sp. indet., small heteromorphs ammonoids that characterize the new *Sabaudiella riverorum* biozone dated as latest Hauterivian to early Barremian (Fig. 2; Aguirre-Urreta & Rawson 2012).

Material and methods

A general stratigraphical section from the basement through the Agrio Formation to the base of the Huitrín Formation was measured at Lomas Bayas locality (Fig. 2). The nerineoid shell beds were recorded near the top of the Agrio Formation, specifically in the *Sabaudiella riverorum* ammonoid zone. A detailed section (1:50) of the carbonate succession including the

nerineoid shell beds was measured, taking into account stratigraphical and sedimentological features such as geometry, thickness, lithology, contacts, sedimentary and biogenic structures and macrofossil content (Fig. 4). Several rock samples were collected while logging the detailed section to prepare thin and polished sections for petrographic studies to precisely define lithofacies and interpret palaeoenvironments. We followed Dunham (1962) and Flügel (2004) for this purpose. The analysed carbonate interval is bounded on base and top by thick carbonate-siliciclastic mixed beds that are excluded from this study.

The nerineoid shell beds are thin lensoid patches that were recorded at three different sites, named here as 1, 2 and 3, at Lomas Bayas locality (Fig. 1B). These sites are located on a NW-SE transect, approximately 1.14-km long. The lensoid patches are included within the uppermost 0.50 m of a grainstone bed 1.5-m thick and are easily correlated laterally by the presence of distinct ammonoid levels. Only one of these, i.e. site 1, could be studied in detail as a large bedding surface at the top of the shell beds was available for description. All measurements come from this site and from one lensoid patch. The other two, i.e. sites 2–3, were used for qualitative descriptions of smaller patches of the accumulations in plan view or cross-section. In particular, at site 2, the cross-section view of the 1.5-m-thick grainstone bed allowed recognizing clearly at least two

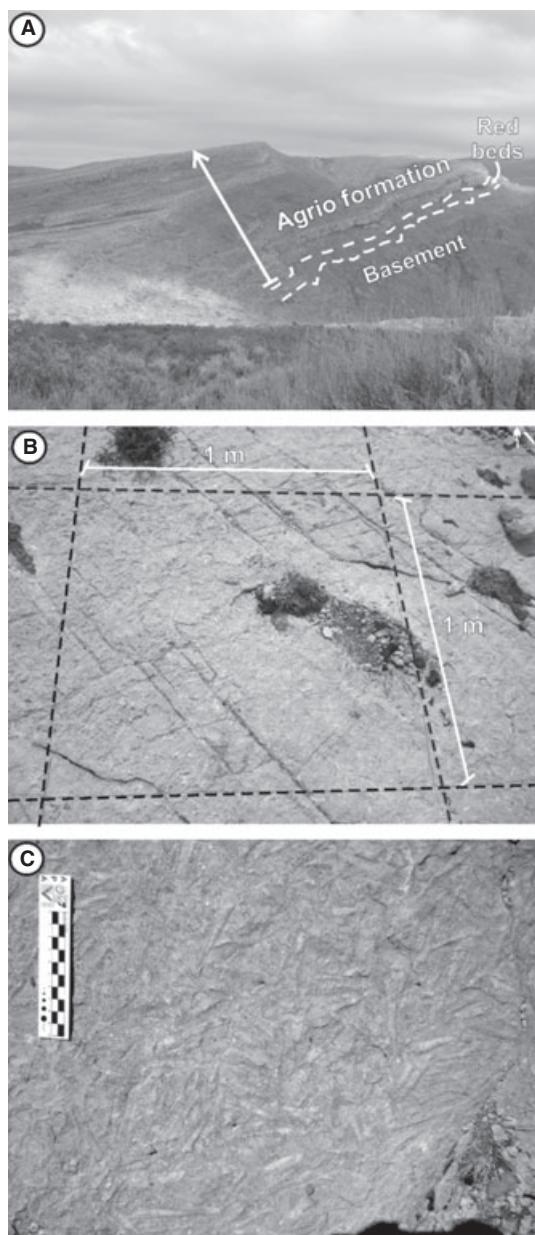


Fig. 3. A, general view of the Agrio Formation at Lomas Bayas from the north bank of the Diamante river. Dotted line indicates the boundaries between units. B, detail of the N–S grid on top of the nerineoid shell beds at site 1. C, top view of the nerineoid shell beds at site 1, depicting high abundance of nerineoid shells.

closely spaced lensoid patches interbedded near the top of the grainstone bed. At this site, the thickness of the shell beds was measured and some three-dimensional specimens were sampled, which were free from the matrix and which preserved part of the shell or were internal moulds.

The available top bedding surface of the nerineoid shell beds at site 1 was divided in a N–S grid of 76 squares of 1 m² of individual surface (Fig. 3B). Only 13 squares were selected from the grid, as they had

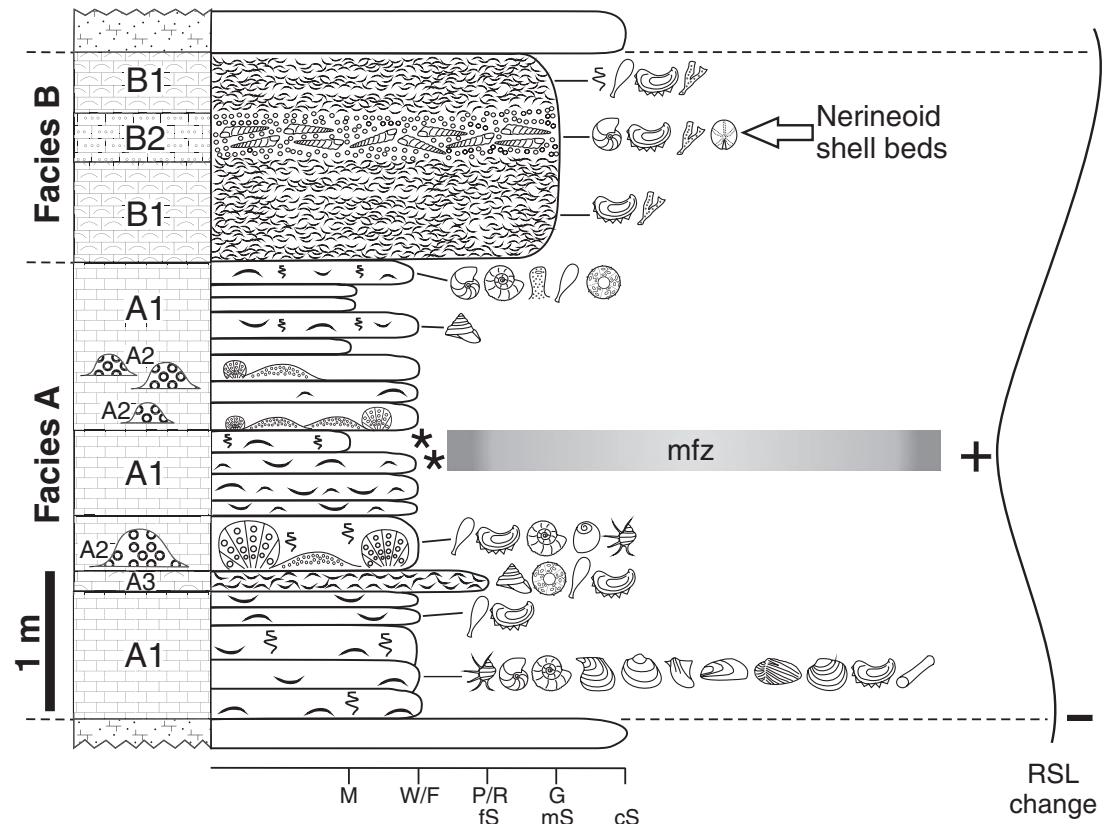
more than approximately 80% of bedding surface clean and available for description and measuring. A thorough taphonomic scoring of all nerineoid gastropods recorded on each of the 13 squares was performed. A mean of 375 specimens were counted in each square, with a total of 4875 specimens (Fig. 3C).

Several taphonomic features were used for the scoring based on the proposals of Kidwell *et al.* (1986), Kidwell (1991) and Kidwell & Holland (1991). Features are as follows: mode of preservation, sedimentary infilling, fragmentation, orientation in plan view and cross-section, encrustation and bioerosion. The mode of preservation includes calcite recrystallized shells and internal moulds with recrystallized internal shell features such as the columella or folds, named here ‘ghost preservation’. The sedimentary infilling includes empty shells and shells with sediment infill. Geopetal structures were identified among those shells showing sediment infill. Fragmentation was classified as whole shells, major fragments, i.e., with more than two whorls and minor fragments, i.e., with two or less whorls. Orientation in plan view was measured in azimuths of the apex of shells. After correction for structural deformation, azimuths were plotted in a rose diagram and the mean resulting vector was calculated. Orientation in cross-section was determined as concordant, oblique or perpendicular. Encrustation and bioerosion were determined as present or absent. Besides the taphonomic scoring, other important features were also recorded, including thickness, lateral extent, geometry, internal complexity, contacts, position in sequence, close packing of shells, relative abundance, size sorting, type of matrix, associated macrofauna and ecological spectrum.

Sedimentary facies and palaeoenvironment

The detailed section, 4.8-m thick, of the carbonates that include the nerineoid shell beds is interpreted as deposited in a homoclinal ramp system, based on previous studies on the sedimentology of the Agrio Formation in Mendoza (see Sagasti 2005). A synthesis of the studied sedimentary facies is presented in Table 1. The carbonate succession was divided in two parts.

The lower part of the succession, belonging to facies A, was deposited in a mid-ramp setting, and is characterized by the presence of low-energy, mud-supported beds with diverse faunal content (subfacies A1) interbedded with oyster shell beds, indicative of sporadic storm reworking of seafloor and bioclasts (subfacies A3). Coral build-ups (subfacies A2) are also interbedded with subfacies A1, and correspond to low coral meadows of the distal mid ramp. In particular, the



References

Facies	Bivalvia	Cephalopoda	Polychaeta
Allochemic sandstones	<i>Cucullaea gabrielis</i> Deshayes	Ammonoid bearing-levels	Serpulid tubes
Bioclastic wackestones, floatstones and mudstones	<i>Gervillaria alatior</i> (Imay)	Nautilid bearing-levels	
Shell beds	<i>Isognomon</i> sp.		
Bioclastic and oolitic grainstones	<i>Amphidonte (Ceratostreon)</i> sp.		
Coral buildups	<i>Ptychomyia koeneni</i> Behrendsen		
	<i>Myoconcha transatlantica</i> Burckhardt		
	<i>Eriphylla argentina</i> Burckhardt		
Bioclasts			
Oolites			
Abundant calcispheres			
Bioturbation			
mfz			
Grain size			
M			Mudstones
W/F			Wackestones/Floatstones
P/R			Packstones/Rudstones
fS			Fine sandstones
mS			Medium sandstones
cS			Coarse sandstones

Fig. 4. Detailed section near the top of the Agrio Formation including the nerineoid shell beds and associated sedimentary facies and subfacies, with the interpreted relative sea level (RSL) change.

presence of calcispheres in subfacies A1 indicates that the deposition took place during a transgressive phase and beds with a high concentration of them are interpreted as the maximum flooding zone (see Flügel 2004) of the analysed succession.

The upper part of the succession, belonging to facies B, including the nerineoid shell beds, is

characterized by the presence of grainstones and rudstones with abundant ooids, coated grains and micriticized bioclastic fragments, suggesting its deposition in agitated, warm and shallow waters. The low amount of micritic matrix and the facies association suggest that these beds were deposited in a shoreface area with shoals affected by fair-weather waves developed in an

Table 1. Synthesis of the sedimentary facies and subfacies of the studied carbonate succession including the nerineoid shell beds at the top of the Agrio Formation in Lomas Bayas locality, Mendoza Province. Biv, bivalves; bry, bryozoans; ech, echinoids; cri, crinoids; cor, corals; spo, sponges; FWWB, fair-weather wave base.

Description	Interpretation	Notes
Facies A: mid-ramp deposits		
A1 Wackestones to floatstones, tabular beds, <20-cm thick; concordant, poorly size sorted angular/subangular bioclasts (biv, bry, ech, cri) <5-cm long to shell debris. Variable proportion of bioclasts versus calcispheres	Open marine conditions indicated by calcispheres and echinoderms. Deposition on a mid-ramp setting below FWWB under overall low energy. Eventual bottom current action indicated by convex-up bioclasts. Abundant calcispheres indicate mfz (Flügel 2004)	RMF7 of Flügel (2004). Figs 5A,C; 6A
A2 Coral build-ups. Several stacked beds of colonial scleractinian corals mostly in growth position and very closely spaced. Globose and flat colonies with large cementing area, <40 cm in height and 50 cm in length. Moderate to high levels of encrustation and macrobioerosion	Low coral meadows (not a coral barrier) that started growing during a transgressive interval in a distal mid-ramp setting. Taphonomic alterations point to significant residence time on seafloor	Fig. 5B
A3 Discontinuous, lensoid oyster-dominated shell beds <20-cm thick interbedded with facies A1. Sharp basal contact. Loosely to densely packed. Homogenous. Shell debris to 5-cm-long bioclasts. Dispersed cidaroid tests and spines and pleurotomariid gastropods	Eventual mid-ramp storm deposits affecting seafloor and reworking bioclasts	Proximal tempestites of Aigner (1982)
Facies B: inner ramp shoals		
B1 Bioclastic grainstones to rudstones, tabular beds, <30-cm thick, sharp basal contact, diverse faunal elements (biv, cor, spo, ech, cri, bry), abundant sparry calcite. Most bioclasts micritized	High-energy open marine inner-ramp setting, near to FWWB. Abundant micritization reflects shoal stabilization (Bádenas & Aurell 2010)	RMF26 of Flügel (2004). Figs 5A; 6B
B2 Nerineoid-bearing oolitic grainstones. Tangential ooids, abundant coated grains, shell debris and nerineoid gastropods. Well-sorted simple ooids, 0.2–0.7 mm in diameter, nuclei micritized, replaced by calcite or a bioclast. Minor proportion of compound ooids. Gastropod shells infilling discordant with host matrix	Sand shoal environment in moderate to high-energy (Strasser 1986) shallow inner-ramp setting above FWWB	RMF29 of Flügel (2004). Figs 5D; 6C–D

inner-ramp setting. However, this setting can be influenced by storm waves and coast-parallel bottom currents (Flügel 2004). The present-day inner ramps range from sea level to the fair-weather wave base, which in most cases is between 5 and 15-m water depth (Somerville & Strogen 1992; Bassi & Nebelsick 2010). This setting, although turbulent, is characterized by a high diversity of shelly faunas that produce large volumes of carbonate sediments. The upper part shows a regressive, shallowing-upward trend that corresponds to inner-ramp deposits overlying the mid-ramp deposits of the lower part.

Nerineoid shell beds

Morphological features of the studied nerineoids

The taxonomic study of the nerineoids was somewhat difficult as the specimens could hardly be removed from the rock matrix and were visible mostly in longitudinal and oblique sections. Only a few three-

dimensional specimens, which preserve the shell only in part, were available. Nonetheless, we could determine that the nerineoid shell beds recorded near the top of the Agrio Formation in Lomas Bayas are formed by only one nerineoid species, belonging to the genus *Eunerinea* Cox, 1949, Family Nerineidae. Several authors have pointed out the rarity of monospecific nerineoid associations (e.g. Wieczorek 1979; Waite & Strasser 2011), and Dauwalder & Remane (1979) stated that they indicate extreme ecological conditions.

The studied shells, analysed mostly in longitudinal section, showed the diagnostic features of *Eunerinea*, namely a moderately acute shell, concave to flat whorls, convex sutural region, rhomboidal or sub-quadrangular aperture with oblique anterior canal and three columellar folds: one well-developed, triangular labial fold, one less-developed, slightly curved towards the apex columellar fold and one short, spiniform parietal fold (fold formula: 1.1.1.0) (Fig. 7A). Other features showed by the studied specimens are a thin, slightly cyrtoconoid shell and a

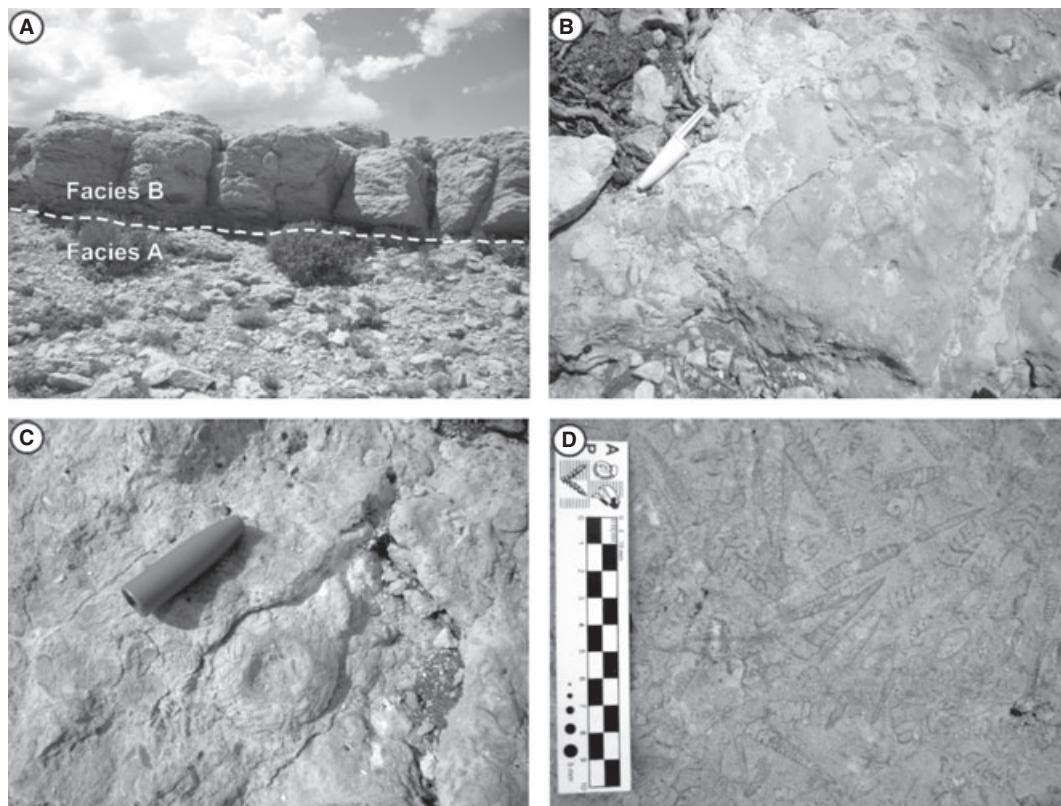


Fig. 5. A, field picture of the contact between wackestones to floatstones of subfacies A1 and bioclastic and oolitic grainstones of subfacies B1. B, plan view of scleractinian coral head from subfacies A2. C, plan view of regular echinoid test from subfacies A1. D, close plan view of nerineoid-bearing oolitic grainstones of subfacies B2.

massive columella. Shell thickness does not seem to exceed 0.6 mm measured in the penultimate preserved whorl of several specimens. Diameter of columella ranges between 1.6 and 2.8 mm, measured in the last preserved whorl of several specimens. The outer surface of shells, observed in a few three-dimensional specimens recovered from the matrix, is smooth except for a thin spiral thread adjacent to the adapical suture in early whorls. Total height of shells was hard to measure, even for those preserved parallel to the bedding plane, as most specimens missed part of the last whorl and/or the apical whorls, or cuts through the shell were imperfect. Waite & Strasser (2011) report similar difficulties. Nevertheless, we estimate, through proportions of specimens available, that the maximum shell height and maximum diameter could have reached 120 mm and 15 mm respectively. Shell acuteness in species of *Eunerinea* is moderate in comparison with other nerineoid genera, for instance, *Nerinella* Sharpe. Mean spire angle of the study specimens ranges from 6° to 11°, and was measured in several specimens whenever possible, i.e., in those in which the section plane is close to the spire axis, which is not always the case.

Stratigraphical and sedimentological features

The nerineoid shell beds are thin lensoid patches of less than 100 m² of maximum surface in plan view. The maximum thickness of each shell bed is approximately 14 cm, but their thickness decreases laterally as they grade into pavements of 1–2 shells thick. At each site, more than one lensoid patch was identified, but it was difficult to ascertain with certainty how many of them were present at each site, let alone the total number of patches embedded within the top of facies B. The shell beds are internally homogenous and massive and have a simple microstratigraphy in cross-section: the base of the shell beds is transitional from pure oolitic carbonates to dispersed shells between densely packed oolites and an interval of loosely packed shells towards the top. The shell beds are recorded near the top of a 1.5-m-thick bioclastic and oolitic grainstone bed, which in turn is located at the top of the 4.8-m-thick, logged-in-detail carbonate succession.

The shell packing is loose and matrix supported with an estimated 15% of abundance of bioclasts. The shells are embedded in an oolitic matrix that also fills their internal cavities.

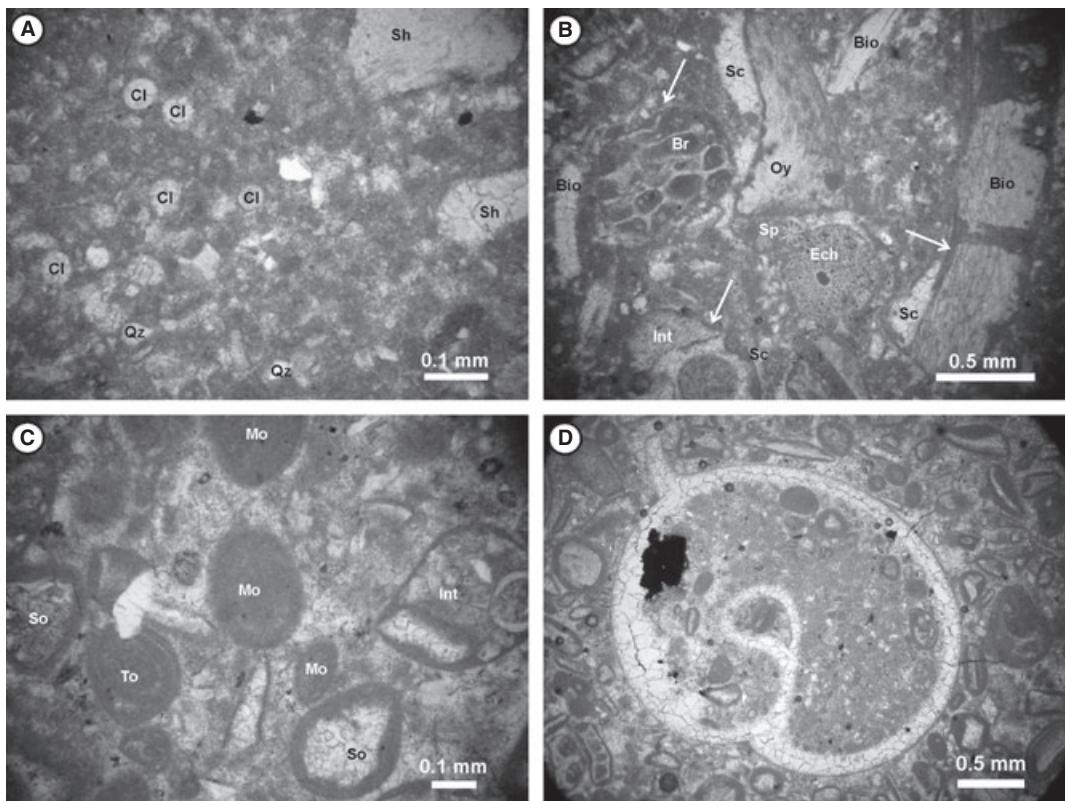


Fig. 6. A, subfacies A1, wackestones to floatstones. Calcispheres (Cl) and shell debris (Sh) immersed in a micritic matrix with quartz fragments (Qz). B, subfacies B1, bioclastic grainstones to rudstones. Various benthic skeletal grains: echinoderm spine (Sp), bryozoan (Br), oyster (Oy), echinoderm plates (Ech) and other bioclastic fragments (Bio) are cemented by sparry calcite (Sc); note that most of the bioclastic fragments and the intraclast (Int) have a micritic coating (arrows). C, subfacies B2, nerineoid-bearing oolitic grainstones; detail of the different types of coated grains: tangential ooids (To), micritized ooids (Mo), intraclasts (Int) and superficial ooids (So) cemented by sparry calcite. D, subfacies B2, nerineoid-bearing oolitic grainstones; transversal section of a nerineoid specimen immerse in an oolitic grainstone; note that the infilling of the nerineoid is similar to the host matrix; most of the bioclastic fragments, oolites and intraclasts have a micritic coating or are micritized. All samples were stained with Alizarine Red and potassium ferricyanide.

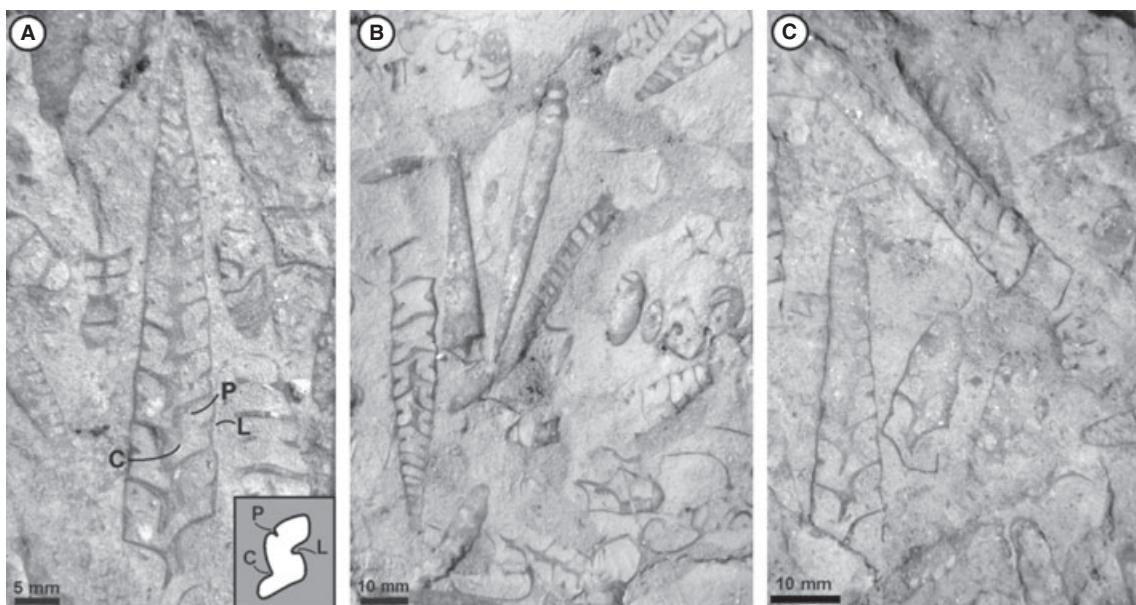


Fig. 7. A, plan view of longitudinal sections of *Eunerinea* shells showing general morphology and internal folds (P, parietal fold; L, labral fold; C, columellar fold). B, C, examples of taphonomic features in plan-view longitudinal sections. B, concordant, oblique and perpendicular orientations of *Eunerinea* shells. C, geopetal structure in concordant *Eunerinea* shells.

Taphonomic and palaeontological features

Mode of preservation. – Most specimens are preserved as calcite recrystallized shells (96.4%) and a minor portion as internal moulds with recrystallized internal shell features, such as the columella or folds, i.e. ‘ghost preservation’ (3.6%). Shell replacement has left no trace of the original structure of the nerineoid shell.

Orientation in plan view and cross section (Figs 7B, 8). – The rose diagram resulting from the azimuth measurements of 4187 shells in plan view is bimodal with a mean NE-SW vector (Fig. 8A). A great majority of shells are concordant in cross-section (76.7%), but some are oblique (15.1%) or perpendicular (8.2%, Fig. 8B).

Fragmentation (Fig. 9A). – Most shells are quite well preserved, including pristine shells and fragments with several whorls preserved (85.8%), whereas only a small portion is recorded as minor fragments

containing up to two whorls (14.2%). The aperture is the most fragile portion, as it is almost always missing in major fragments (74.7%). This is consistent with the fact that the weakest part of the nerineoid shell are the lips of the aperture, composed of lesser shell layers than the older parts of the last whorl (Wieczorek 1979; Waite *et al.* 2008). The apex is lost less frequently (25.3%).

Size sorting (Fig. 9B). – Nerineoid shell beds are interpreted as well-sorted, given that the central 80% of gastropod shells lie within two adjacent size classes: 16–32 mm and 32–64 mm. It is noteworthy that fragments of less than 8 mm in size are absent.

Sedimentary infilling (Figs 7C, 9C). – Most shells show sediment infill concordant with the surrounding oolitic matrix (95.28%), whereas a low number of shells are empty (4.72%). Among those showing sediment infill, there is a significant portion (39.14%) showing geopetal structure.

Associated fauna (Fig. 9D). – Shell beds are dominated by a single nerineoid gastropod species. Oyster fragments and occasional irregular echinoids, corals and nautilids are also recorded.

Interpretation of the shell beds

The nerineoid shell beds are interpreted as primary sedimentological concentrations as different taphonomic features such as fragmentation, orientation and size sorting point to a physical accumulation of locally produced gastropod shells (see Kidwell *et al.* 1986). They represent event concentrations *sensu* Kidwell (1991), as they are thin and internally homogeneous, which evidences a single mechanism of deposition by fair-weather waves. In particular, the bimodal orientation pattern seen in plan view indicates that waves reoriented long axes of shells parallel to wave crests (Nagle 1967). Thus, fair-weather waves seem to be the main genetic mechanism of the studied shell beds.

However, these nerineoid shell beds cannot be regarded only as the result of relative enrichment in shells by wave action. Local production of nerineoid shells was high, evidencing a secondary biogenic imprint on the concentrations. Shells may be considered, at the most, paraautochthonous, with occurrence of autochthonous shells, as a small portion is recorded as minor fragments and most shells include several whorls and sediment infill is similar to surrounding matrix, all of which suggests that they did not undergo significant lateral transport, but were subject to reorientation by wave action. Several gastropod cohorts were probably preserved amalgamated and embedded

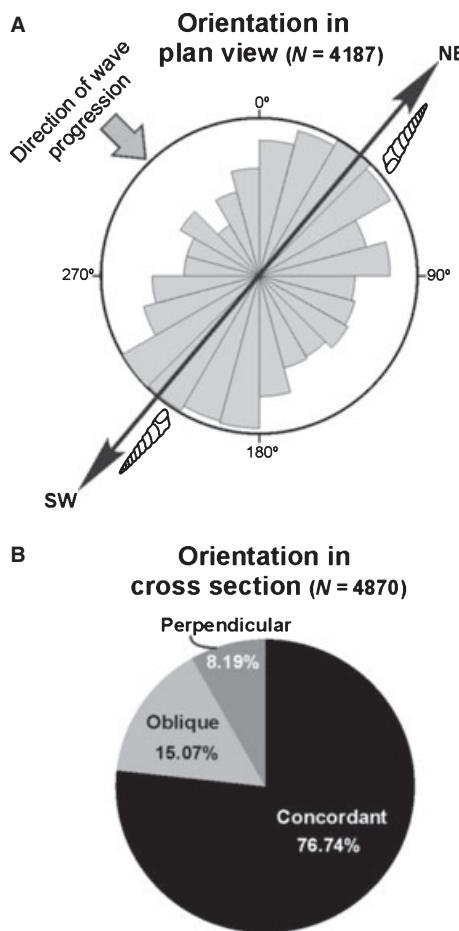


Fig. 8. Orientations of *Eunerinea* shells at site 1. A, in plan view on a rose diagram showing a bimodal distribution pattern. B, in cross-section.

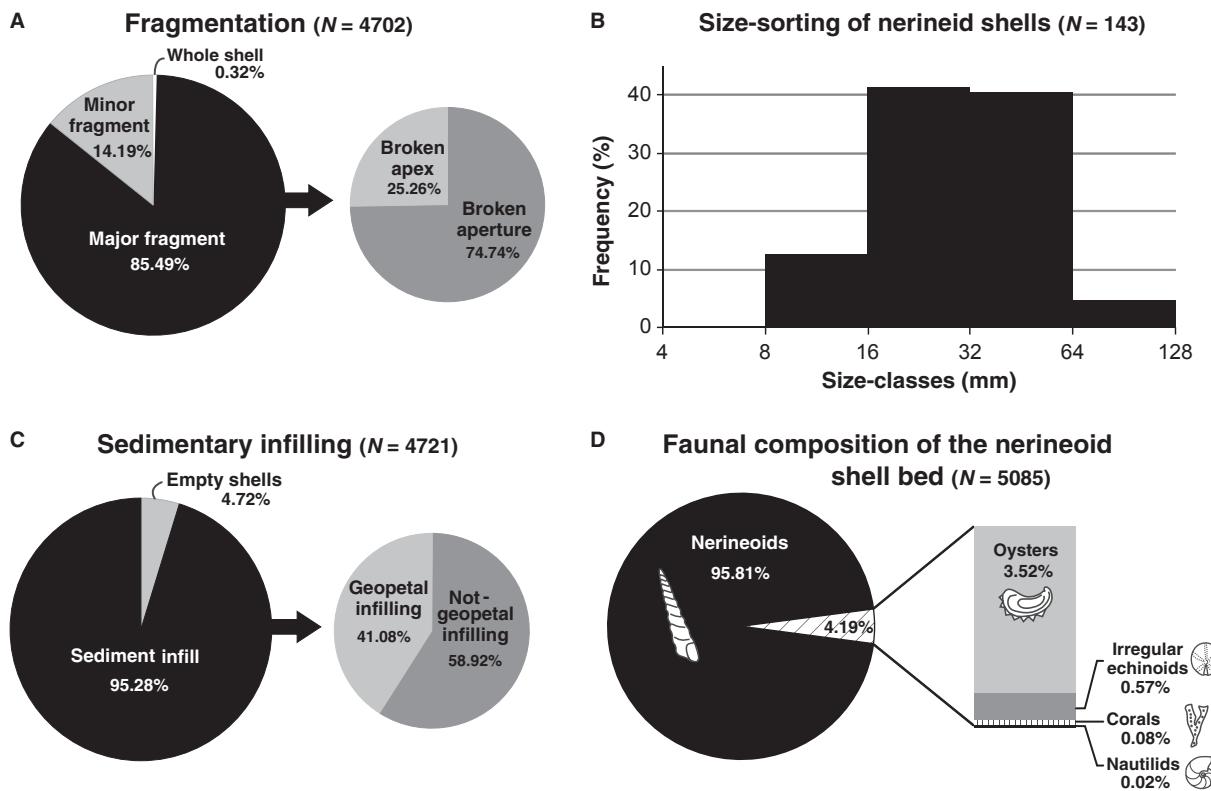


Fig. 9. A–C, distribution of the states of the different taphonomic features scored on the nerineoids at site 1. D, faunal composition of the nerineoid shell beds at site 1 showing that gastropods are clearly dominant.

in an oolitic substrate and subject to the same repetitive physical reworking by fair-weather waves.

The studied shell beds may be classified as within-habitat time-averaged assemblages *sensu* Kidwell (1997). These are shell accumulations, time-averaged over a period of environmental stability so individuals derived from different cohorts of the same palaeocommunity are mixed and preserved together. Estimations of absolute durations for this type of assemblage range from the scale of years to 10 My, but our case study is considerably less time-averaged. The maximum degree of time-averaging is limited by the standard duration of one ammonoid biozone of the zonation proposed by Aguirre-Urrreta *et al.* (2007) for the Hauterivian of the Neuquén Basin, which is 0.5 My. The overall absence of external encrustation and bioerosion, plus the presence of empty and non-fragmented shells are suggestive of relatively short residence time of shells at the sediment–water interface, therefore indicating minor time-averaging, probably below 1 ky, falling within the range of coastal-settings assemblages of Kidwell (1997, Fig. 1). Empty and non-fragmented shells, although a minority, reflect zero time-averaging and probably mean that they were not subject to wave reworking, reorientation and/or minor lateral transport, but remained buried. These shells got mixed

with older, wave-reworked and reoriented shells that were partially filled with sediment concordant with the surrounding matrix. Moreover, the shell beds are not associated with local or regional unconformities and thus they were not connected with significant interruptions or hiatuses that would have increased the degree of time-averaging.

Palaeoecological remarks

Much has been discussed about nerineoid life and feeding habits, though conclusive evidence is scarce. Many authors agree that an epifaunal mode of life is most likely for most nerineoid genera (Vogel 1968; Wieczorek 1979; Buitrón-Sánchez & Pantoja-Alor 1994; Sirna 1995, 1999). This assumption is made on the basis of rather frequent occurrence of pre-mortem encrustation (Vogel 1968; Wieczorek 1979), the co-occurrence of nerineoids with *in situ* corals and rudists (Wieczorek 1979) and functional morphology of large and thick-shelled taxa. A sedentary epifaunal mode of life on firm substrates has been specifically suggested for those nerineoids with large, heavy, thick-walled shells (Buitrón-Sánchez & Pantoja-Alor 1994; Waite *et al.* 2008; Waite & Strasser 2011) living in high-energy environments as this type of shell does not

allow for much mobility (Vogel 1968; Waite *et al.* 2008).

Other authors have proposed that nerineoids were most probably infaunal or semi-infaunal (Taylor *et al.* 1980; Barker 1990), especially those with very long, thin, acicular shells, like the Nerinellidae (Buitrón-Sánchez & Pantoja-Alor 1994). Barker (1990) suggested that early nerineoids were infaunal on account of the lack of epibionts and the presence of those shell features that Signor (1982) regarded as characteristic of modern high-spined infaunal gastropods, i.e., absence of prominent sculpture, presence of columellar folds, flat whorls and opisthocline aperture.

Recently, Waite *et al.* (2008) attributed a sedentary or semi-sessile epifaunal mode of life to large (shell height up to 20 cm), heavy, thick-shelled (2–2.5 mm) specimens of *Eunerinea* with markedly concave whorls from mass accumulations of the Kimmeridgian of the Swiss Jura Mountains. They proposed that these nerineoids lived in large numbers in stable substrates in high-energy environments with a high amount of food available in the water column provided by an external source. Through the floral and faunal composition of the nerineoid-bearing beds, the functional morphology of the individuals and the very large number of those in these communities, feeding mode was interpreted as sedentary suspension feeding.

The specimens of *Eunerinea* studied herein are medium-sized in comparison with other *Eunerinea* specimens in the literature, possibly up to 120 mm in height and 15 mm in width. Shells do not seem to be heavy, as they show a rather thin shell wall (≤ 0.6 mm) although with a relatively thick, massive columella (1.6–2.8 mm). Whorls are flat to very slightly concave and smooth, sometimes with a fine spiral thread near apical suture. Therefore, from a functional morphology point of view, it seems that an epifaunal mode of life is not justified for the nerineoids from the top of the Agrio Formation. Moreover, neither macrobioerosion nor external encrustation was detected on the studied shells and thus an epifaunal mode of life seems unlikely.

Besides functional morphology, the analysis of the nerineoid-bearing facies can contribute substantially to the inference of the mode of life and feeding habit of the group, especially the nature of the substrate, water energy, nutrient level, turbidity, oxygenation, depth, rate of sedimentation, temperature and associated fauna. As several authors have pointed out, nerineoids have been recorded in a variety of carbonate facies, suggestive of a broad spectrum of environments within the euhaline carbonate platform/ramp, from low- to high-energy settings (e.g. Buitrón-Sánchez & Pantoja-Alor 1994; Sirna 1995; Waite & Strasser 2011).

In our case study, nerineoid gastropods are restricted to oolitic grainstones that correspond to shoals within the inner ramp, which indicates that they thrived and accumulated under a shallow, well-lit, high-energy setting above fair-weather wave base. The substrate was probably oxygenated and loose due to the influence of waves, whereas fine-grained sediments were constantly winnowed towards deeper and quieter settings. The presence of irregular echinoids in association with nerineoids also point to soft substrates of a very shallow marine setting. Fragments of coral colonies and small oysters are interpreted as reworked elements, out-of-life position, and true hardgrounds were not recorded in the studied succession.

Therefore, on the basis of functional morphology, associated sedimentary facies and palaeoenvironment, an infaunal or semi-infaunal life habit may be envisaged for the studied nerineoids.

Regarding feeding mode, a clear choice does not seem readily possible. The sedimentary succession studied here shows variable siliciclastic input from the continent to the ramp, which was detected through microfacies analysis. However, this fact does not help interpreting the availability of nutrients in the water column and substrate. It was argued that a high supply of nutrients is necessary to sustain high-density populations of nerineoids (Barker 1990; Buitrón-Sánchez & Pantoja-Alor 1994; Waite *et al.* 2008). In this sense, Saul & Squires (2002) suggested that given the abundance of nerineoid individuals in the Ladd Formation, Upper Cretaceous of California, they may have had a suspension feeding habit. We agree with the view that suspension feeding seems more likely for high-density populations of nerineoids, which do not allow for deposit feeding or predatory habits (Saul & Squires 2002; Waite *et al.* 2008; Waite & Strasser 2011).

Nerineoid shell beds have never been characterized in the Cretaceous of South America prior to this article. However, the nerineoid assemblages of the latest Hauterivian–early Barremian of the Neuquén Basin are not comparable to those from the Jurassic and Cretaceous of the Tethyan Realm in terms of nerineoid species diversity, thickness, lateral extension and association with rudists and coral reefs. The mono-specific nerineoid shell beds described herein indicate that the palaeoenvironmental conditions may have been favourable for the colonization and development of abundant populations of nerineoids in the northern part of the Neuquén Basin during a brief time interval. In spite of its smaller extent, they are significant for the Cretaceous of this basin as this is the first and yet only record of nerineoid-dominated facies, even when other extensive carbonate units are present, e.g. the

Valanginian Chachao Formation (see Legarreta & Kozlowski 1981; Palma *et al.* 2008). Moreover, there is an overall absence of extended coral reef systems and rudist aggregations in the Lower Cretaceous of the Neuquén Basin.

The occurrence of this nerineoid shell beds may reflect what Sohl (1987) describes as brief incursions of Tethyan faunal elements into temperate regions, which he indicates to represent warming episodes. Although a number of palaeoenvironmental factors may have been involved, at present we hypothesize that a change in water temperature towards warmer conditions may have allowed the emergence and growth of these nerineoid populations. At this point, it is worth to note that we essayed oxygen-stable isotopes on calcitic oyster shells from the analysed succession to determine palaeotemperature, but shells were highly recrystallized and thus useless. Future isotopic studies on more and better-preserved calcitic shells from the same locality might prove useful to test our hypothesis.

Conclusions

The sedimentary, palaeontological and taphonomic data gathered near the top of the Agrio Formation at Lomas Bayas locality, and the palaeoenvironmental and palaeoecological analysis of the section and, particularly, of the nerineoid shell beds allowed the following conclusions:

1. The 4.8-m-thick carbonate section including the nerineoid shell beds was deposited in a homoclinal ramp system and depicts a shallowing upward trend from mid to inner ramp. The nerineoid shell beds are interpreted as having been formed in oolitic shoals within the inner ramp.
2. The studied nerineoid shell beds are monospecific assemblages of the genus *Eunerinea*. The individuals thrived and accumulated in a shallow-water, well-lit, high-energy setting affected by fair-weather waves. The substrate was oxygenated and loose due to wave influence.
3. The nerineoid shell beds represent primary sedimentological concentrations as taphonomic features point to a physical accumulation of autochthonous to paraautochthonous gastropod shells. Fair-weather waves were the main physical mechanism generating these beds, reorienting long axes of shells perpendicular to the direction of propagation. A secondary biogenic imprint on the assemblage is evident, as a result of a high local production of shells. We believe that several generations of the same population, subject to the same

constant physical reworking by fair-weather waves, were probably preserved amalgamated and embedded in an oolitic matrix. Time-averaging is low and these beds are classified as within-habitat time-averaged associations.

4. Functional morphology of the shells points to an infaunal or semi-infaunal life habit for these nerineoids. They probably had a suspension-feeding mode.
5. Palaeoenvironmental conditions in the northern part of the Neuquén Basin around the Hauterivian–Barremian boundary must have been favourable for the colonization and development of these nerineoid populations at least for a short term. Although several palaeoenvironmental factors may have been involved, we hypothesize that a change in water temperature towards warmer conditions may have allowed the establishment of the nerineoid communities.

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