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SCLEROBIONTS, SHELL MORPHOLOGY AND BIOSTRATINOMY ON AMMONITES: TWO EARLY CRETACEOUS CASES FROM THE NEUQUÉN BASIN, ARGENTINA

LETICIA LUCI, MARCELA CICHOWOLSKI, AND MARÍA BEATRIZ AGUIRRE-URRETA

Instituto de Estudios Andinos Don Pablo Groeber, Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Ciudad Universitaria, Pabellón II, C1428EGA Buenos Aires, Argentina
e-mail: leticialuci@gl.fcen.uba.ar

ABSTRACT: Shell morphology affects multiple aspects of the biology of ectocochleate cephalopods (e.g., floatability, life habit, *post mortem* behavior of the shell, etc.), so it should impact the establishment and development of sclerobiont faunas as well. In this study, the sclerobiont faunas of *Weavericeras vacaense* (a spherocone) and *Holcoptychites agrioensis* (a discocone), two early Hauterivian ammonites from the Agrio Formation (Neuquén Basin, Argentina) were compared. The coeval nautilid *Cymatoceras perstriatum* (studied previously), was contrasted with both ammonites. Results show that the three sclerobiont faunas had similar abundance, taxonomic composition and distribution of individuals across the shells, but *H. agrioensis* showed a markedly reduced richness, with a fauna almost entirely composed by the oyster *Amphidonte* (*Ceratostreon*) sp. The more evolute and compressed *H. agrioensis* sank more quickly than *W. vacaense* and *C. perstriatum*, which may have undergone longer periods of flotation and exposure on the sea bottom. This agrees with the lower taxonomic richness of the sclerobiont fauna and a better overall preservation of *H. agrioensis* specimens. Differences in the sclerobiont faunas are greater across variations in shell inflation and coiling degree than across nautilids and ammonites; therefore, the latter are important parameters for the sclerobiont fauna as well since they impact how long shells will float and be exposed on the seafloor, and therefore on their time of exposure. The presence of an almost monospecific fauna in *H. agrioensis*, despite its rapid sinking and burial, indicates that *Amphidonte* (*Ceratostreon*) sp. was the earliest settler, and could abundantly colonize hard substrates in a short time.

INTRODUCTION

Sclerobionts (Taylor and Wilson 2002) are organisms of any kind that live attached to any type of hard surface. Paleoecological analysis of sclerobiont faunas on invertebrate shells offers the advantage of working with communities in which species abundances and spatial relationships are preserved (Liddell and Brett 1982; Lescinsky 1996; Taylor and Wilson 2003). Sometimes these communities are also highly sensitive to environmental parameters (see Lescinsky et al. 2002; Schmidt-Röhl and Röhl 2003; Rodland et al. 2004; Brett et al. 2011), allowing paleoenvironmental inferences. But despite these advantages, when studying sclerobiont communities on invertebrate shells it is necessary to determine whether colonization of the shells occurred *in vivo* or *post mortem* (Taylor and Wilson 2002). According to Rodland et al. (2006), the taphonomic history of sclerobionts combines features of hard and soft substrates, since even though sclerobionts are fixed to a common substrate, the latter can be transported and may suffer time averaging as well. The history of *post mortem* sclerobionts is, therefore, linked to the biostratinomy of the basibiont (host organism) shell, and may include several episodes of shell colonization. The colonization history can be especially complex in the case of pseudoplankton (sclerobionts attached to floating hard substrates *sensu* Wignall and Simms 1990) such as the shells of ectocochleate (externally shelled) cephalopods. Necroplanktonic drift may result in significant *post mortem* transport followed by further potential exposure and colonization once the shell has sunk to the sea floor (e.g., Mapes et al. 2010). The complex biostratinomy of ectocochleate cephalopod shells may result in equally complex development of sclerobiont faunas, complicating differentiation of *in vivo* and *post mortem* settlers.

Discussion regarding floatability, life habit, swimming capacity and *post mortem* behavior of the shell of ectocochleate cephalopods remains ongoing, though much recent progress has been made (e.g., Jacobs and Chamberlain 1996; Westermann 1996; Mutvei and Dunca 1999; Westermann and Tsujita 1999; Wani et al. 2005; Ritterbush and Bottjer 2012). Shell morphology has a great impact on all of these parameters (e.g., Reyment 1958; Westermann and Tsujita 1999), and, therefore, it is expected that it should influence the establishment and development of sclerobiont faunas as well.

Ammonites are both abundant and diverse in Lower Cretaceous strata of the Neuquén Basin. Ammonite analyses have provided a detailed biostratigraphic framework for the early Valanginian–earliest Barremian marine Agrio Formation (e.g., Aguirre-Urreta and Rawson 2003, 2010, 2012). Though their taxonomy has been under study for over a century, few studies have focused on their paleoecology, taphonomy, and biostratinomy (but see Riccardi 1980; Cichowolski et al. 2012).

This study focuses on characterizing the sclerobiont faunas of two ammonite species corresponding to two different ammonite zones/subzones. *Weavericeras vacaense* (Weaver 1931) and *Holcoptychites agrioensis* (Weaver 1931), both of early Hauterivian age, are commonly found in the Agrio Formation, and their contrasting morphologies provide a chance to test differences in sclerobiont colonization between distinct shell shapes. *Weavericeras vacaense* has a rather globose and involute morphology closely corresponding to Westermann's (1996) spherocones, while *H. agrioensis* involves morphs with varying degree of involution and compression. However, even its more involute and inflated morphs are much more compressed and evolute than *W. vacaense*, corresponding to a discocone morphology (Westermann 1996). Thus it is expected

that floatability, life habit and swimming capacity, as well as the *post mortem* behavior of the shells, were rather different for both species.

In addition to overall variations in shell morphology, differences between ammonoids and nautiloids (e.g., shell thickness, number, shape and thickness of septa, length and shape of the body chamber, size and position of the siphuncle) could also exert a considerable influence on floatability, life habit and *post mortem* behavior of the shells (Reyment 1958; Westermann 1996; Westermann and Tsujita 1999). Recently, a study was performed on the sclerobiont fauna of the only nautilid from the Agrio Formation, *Cymatoceras perstriatum* (Steuer 1897), which coexisted with the two ammonite species discussed herein (Luci and Cichowolski 2014). *Cymatoceras perstriatum* has an involute, globose morphology much like that of *W. vacaense*, and both greatly differ from *H. agrioensis*. The sclerobiont faunas of these three cephalopod taxa are compared and contrasted in an effort to assess the role that shell morphology plays on sclerobiont faunas.

This contribution describes the sclerobiont fauna of *W. vacaense* and *H. agrioensis* in terms of taxonomic composition, abundance, distribution and diversity; compares the sclerobiont faunas of these ammonites to each other and to the coeval nautilid *C. perstriatum*; and interprets the paleoecology and taphonomy of the ammonite sclerobiont faunas.

GEOLOGICAL SETTING

All ammonite specimens studied here were collected from the Neuquén Basin, located in the west-central part of Argentina (see Fig. 1A), along a convergent margin involving the subduction of the Pacific Plate beneath the south-western margin of Gondwana (Ramos and Folguera 2005). After a Late Triassic to Jurassic rifting phase, the basin experienced thermal subsidence during the Late Jurassic and Early Cretaceous. Consequently, the Pacific Ocean invaded the basin. An active volcanic arc separated the Neuquén Basin from the Pacific Ocean forming a shallow, inland sea (Ramos 1999; Vergani et al. 1995). At this time, the primarily marine Mendoza Group (Tordillo, Vaca Muerta, Mulichinco and Agrio formations) accumulated.

The marine Agrio Formation is divided into three members in the study area, which are, from base to top, the Pilmatué, Avilé, and Agua de la Mula members. The Pilmatue and Agua de la Mula members record marine depositional conditions, whereas the Avilé Member represents a sea level drop, during which 30 to 40 m of fluvial, aeolian and lacustrine sediments accumulated, forming a wedge widely distributed through the central part of the basin (Veiga et al. 2011).

All ammonites were collected from the Pilmatué Member which consists of dark shale with intercalated carbonate and sandstone intervals, and thins towards the north and south of the basin, with carbonate facies gaining dominance over clastics in those directions (Spalletti et al. 2011). The Pilmatué Member has been interpreted as a slowly subsiding marine ramp, developed during a sea level highstand, with deeper marine deposition located towards the west of the basin, shallowing towards the east (Spalletti et al. 2011). Two types of facies predominate; fine-grained clastic sediments, typically shale, which record quiescent deposition, with intercalations of coarser-grained deposits, commonly with abundant fossil content, which correspond to episodes of agitated water caused by storms (Spalletti et al. 2001; Lazo et al. 2005). The base of the Pilmatué Member is diachronous. A late Valanginian age has been provided for most of the Neuquén Province, however an early Valanginian age has been provided for northwestern Neuquén and western Mendoza Province (see Fig. 1B; Aguirre-Urreta and Rawson 1997; Spalletti et al. 2011). Its biota is abundant and diverse, comprising nanno and microfossils, palynomorphs, invertebrates and vertebrates, as well as trace fossils (Aguirre-Urreta and Rawson 1997, 2003, 2010, 2012; Cichowolski 2003; Lazo 2003, 2004, 2006, 2007; Lazo and Cichowolski 2003; Aguirre-Urreta

et al. 2005, 2007, 2011; Concheyro et al. 2009; Ballent et al. 2011; Garberoglio and Lazo 2011; Gasparini and Fernández 2011; Cataldo and Lazo 2012).

Each ammonite species nominates and corresponds to a distinct biostratigraphic subzone/zone (Aguirre-Urreta and Rawson 2003, 2010). *Holcoptychites agrioensis* (early early Hauterivian) is commonly found in shale, limestone, shell beds and sandstone (Aguirre-Urreta and Rawson 2003; Lazo et al. 2005) and the late early Hauterivian *Weavericeras vacaense* occurs in shale intervals and in thin sandstone/coquina interbeds (Lazo et al. 2005).

While the overall environment of the Pilmatué Member has been characterized as a shallow ramp deepening towards the west (e.g., Legarreta and Uliana 1991), a detailed, biostratigraphically accurate, sedimentologic analysis of the development of different ramp sub-environments through the succession remains lacking. Although the overall succession has been analyzed sequence stratigraphically, detailed analyses are limited to the Agua de La Mula Member (e.g., Spalletti et al. 2001; Archuby and Fürsich 2010; Archuby et al. 2011). There is general consensus that the *H. agrioensis* Subzone represents a transitional mid-inner ramp setting (e.g., Lazo et al. 2005; Cirigliano 2009), whereas the *W. vacaense* Zone has been interpreted as a calm, shallow marine environment (e.g., Notta 2008; Cirigliano 2009). In addition, analysis of calcareous nannoplankton in the *W. vacaense* Zone reveals an important decrease in abundance and diversity in comparison to older zones (Lescano 2012), whereas isotopic analyses reveal a peak of reduced salinity within the zone (Lazo et al. 2008), consistent with a shallower depositional setting. Directly above this zone sea level dropped sharply, leading to the deposition of the continental sandstone unit of the Avilé Member.

MATERIALS AND METHODS

Main Features of the Basibiont Ammonites

All materials studied here (Table 1) are deposited in the Área de Paleontología, Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires (UBA), under the acronym CPBA. Decimals in repository numbers indicate multiple specimens collected from a single bed. The ammonites studied here were collected from 12 localities in central and north-central Neuquén (Fig. 1B). More information about access and general features of the localities of collection can be found in Aguirre-Urreta and Rawson (2003). A total of 65 specimens of *Weavericeras vacaense* and 57 specimens of *Holcoptychites agrioensis* are included in this study (see Table 1 for repository numbers).

The Agrio Formation exhibits a considerable diversity of ammonite taxa, with several different morphologies represented. The species chosen for this study belong to two different superfamilies within the Ammonitina. *Weavericeras vacaense* is a desmoceratid with a large, involute shell of depressed to moderately compressed transversal section and deep, steep-walled umbilicus (Aguirre-Urreta 2013). Its body chamber is estimated to have been half a whorl in length. An analysis of its intraspecific variability is required, but currently only *W. vacaense* is recognized as a valid species, since *W. olsacheri* Giovine 1950 is considered to be a junior synonym of the former species (Leanza and Wiedmann 1980). Of all ammonites found in the Agrio Formation, *W. vacaense* is the most similar in morphology to the nautilid *C. perstriatum*, which has a strongly globose and involute shell (see Cichowolski 2003).

Holcoptychites agrioensis (described in detail by Aguirre-Urreta and Rawson 2003) is a large holcodiscid, with a slight to moderately involute shell of subtrapezoidal to suboval transversal section, a narrow venter and shallow umbilicus. The body chamber spans three-quarters of a whorl.

Cymatoceras perstriatum has a large, nautiliconic, involute, globular to subglobular conch, up to 20–30 cm in diameter. The body chamber is half a whorl long. The umbilicus is covered by a callus, and the flanks and venter are rounded, and usually ornamented with low, wide ribs (see Cichowolski 2003, for a more detailed description).
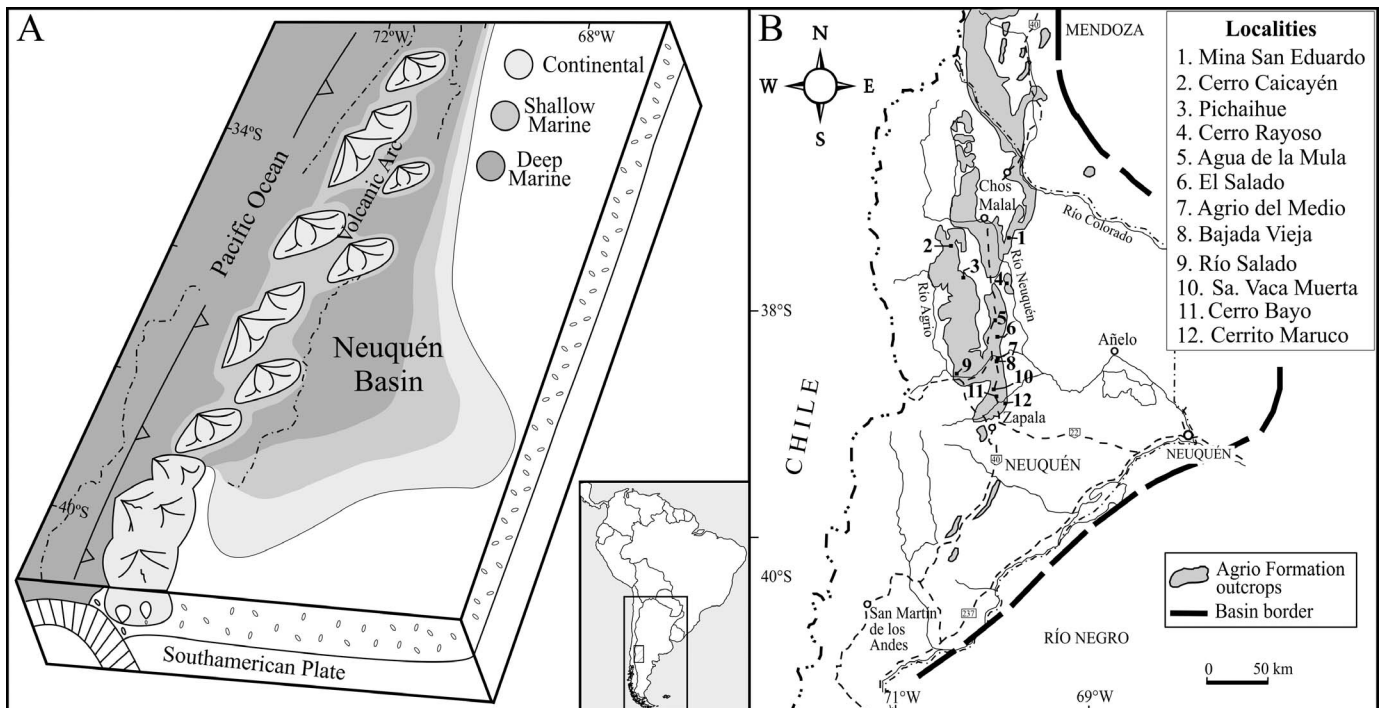
FIG. 1.—Study area. **A)** Configuration of the Neuquén Basin during the deposition of the Pilmatué Member (modified from Howell et al. 2005). **B)** Map of the Neuquén Province displaying the localities of ammonite collection.

Spherocone ammonites such as *W. vacaense* would have been good backward swimmers, with moderate steerage and good vertical motility (Westermann 1996). *Holcoptychites agrioensis*, a discocone, was likely a good backward swimmer, but a poor forwards swimmer, with good vertical motility and moderate maneuverability (Westermann 1996). Its mesodomic (*sensu* Trueman 1941) body chamber likely resulted in a horizontally oriented aperture, whereas the brevidomic body chamber of *W. vacaense* resulted in a vertically oriented aperture (Westermann 1996).

The high inflation and brevidomic body chamber of *C. perstriatum* are not suggestive of a swift swimming style (see Westermann 1996). However, these types of shells were very stable and capable of forward and backward swimming (Westermann 1999) and thus are often interpreted as nectobenthic.

Experiments on shell models carried out by Reyment (1958) showed that the most important factors regulating the shell's *post mortem* floatability are the size of the body chamber, the overall shell shape, the number and thickness of septa and the width of the siphuncle, in that order. More compressed shells

TABLE 1.—*Repository numbers by locality of collection for each studied ammonite, and of the* Cymatoceras perstriatum *specimens from each zone (for more details on the latter see Luci and Cichowolski 2014).*

Ammonite species	Locality	CPBA numbers	CPBA of *C. perstriatum*
Holcoptychites agrioensis	Agua de la Mula	16993, 16995, 17024, 18331, 18357, 18358, 18359, 18361, 18362, 18363, 19983, 20010.1–5, 20011.1–8, 10, 12–17	6896.5,6; 19834.1,2,5,6,9,10,12, 14–18,22,25–27,30,31,35,36
	Bajada Vieja	18029	19848.1,3–4
	Cerro Caicayén	18142.2–4	–
	Cerro Rayoso	19815.1–4, 19816.1–2, 20003	–
	El Salado	19998.1–2	19843.2–8,10–20,22,23,25,27–5,37,39,41–48, 50–55,57–64,66,67; 19859.1; 19874
	Mina San Eduardo	19813.1–8	–
	Pichaihue	19173, 19817	–
	Sa. de la Vaca Muerta	13978	–
Weavericeras vacaense	Agua de la Mula	18392.1–2, 21127.1–7	6899; 19845.1, 3–7, 9–10;
	Agrio del Medio	17003.1–7, 21131	19876.3,7,8
	Bajada Vieja	17004.1–5, 21130.1–5	19840.2,6,7,10,11,14–17
	Cerro Bayo	16307	–
	Cerro Maruco	5154, 5158, 5159, 6157, 17002.1–3	19872.1–3
	El Salado	18391	19852.1–3
	Mina San Eduardo	21129	–
	Pichaihue	21128.1–5	19842.2
	Río Salado	17000.1–19, 17001	–

sink more easily, with variations depending on the length of the body chamber (longer body chambers result in less floatability); its loss facilitates flotation (Reyment 1958). Thus, of the species studied here, *W. vacaense* with a more involute and globose shell likely floated more easily than *H. agrioensis*.

Mapping of Shells and Statistical Design

The methodology employed herein in the analysis of the ammonites' sclerobiont fauna is described in detail in Luci and Cichowolski (2014). All shells were mapped for sclerobionts, with the aid of a binocular microscope (up to 50 ×) when required. The position, relative size and orientation of each sclerobiont individual, along with as precise a taxonomic identification as possible, were noted on equal-sized drawings of each ammonite shell, in order to standardize ammonite shell size.

The shells of both ammonite species were divided into artificial zones, in order to compare colonization of sclerobionts across them (Fig. 2). The shell zonation is based on the work of Landman et al. (1987) on *Nautilus* shells, which were divided into an umbilical zone (one quarter of the shell's diameter centered on the umbilicus) and an extraumbilical zone comprising the remainder of each half of the shell (flanks and right/left part of the venter). A ventral zone was added herein, to assess whether sclerobionts avoided that area as a result of a nectobenthic habit of the host organism (Fig. 2).

All ammonite specimens have some degree of incompleteness of the shell, which results in an underestimation of sclerobiont abundance. The shell wall of the body chambers was commonly absent or incomplete, allowing for examination of sclerobionts that had attached to the inner surface of the body chamber (and thus were preserved encased within the inner moulds). For photography and illustration, all ammonite specimens were coated with ammonium chloride, except for inner moulds with internal sclerobionts.

Count data were preferred over areal coverage for quantifying sclerobionts since most sclerobionts are solitary organisms, which often reach a comparable maximum size within a species. Therefore, total abundances of sclerobionts (as a whole and of each taxon) were calculated in absolute and percentage values. The mean of sclerobionts per ammonite shell was calculated for each ammonite species. The percentage of ammonite shells presenting at least one sclerobiont (calculated for all sclerobionts, and for each sclerobiont taxon separately), or incidence of sclerobiont colonization, was computed. In addition, the incidences of only internal, only external, and simultaneous internal and external colonization of shells were calculated. For those cases in which colonization of internal surfaces took place, the location within the phragmocone or the body chamber was noted. The minimum and maximum number of sclerobionts found in a single shell for each ammonite species was also noted. Variability of sclerobiont abundance across shells was evaluated through histograms plotting the number of shells of each ammonite species versus total number of sclerobionts.

Since most ammonites are mainly preserved as internal molds, features like corrasion and fragmentation could seldom be estimated. As a consequence, five overall categories of shell preservation were defined, as follows: (1) isolated phragmocone chambers (no more than 4 to 5 chambers still in contact); (2) incomplete phragmocones (only 4 to 5 chambers missing); (3) isolated body chambers; (4) incomplete phragmocones with at least part of the body chamber; and (5) complete phragmocones with remains of the body chamber. Percentages of each category were calculated.

Overgrowth among sclerobionts was accounted for by identifying interactions among pairs of different sclerobiont taxa. The outcome of each observed putative interaction (overgrowth of sclerobiont A by sclerobiont B, the opposite, or a ''tie'') was noted.

An analysis of deviance (see Everitt and Hothorn 2006) was carried out in order to compare the mean of sclerobionts per shell between both ammonite species. The incidences of internal and external colonization of shells were compared as well by means of a χ^2 test.

The analysis of the distribution of sclerobionts across shell zones was done through a generalized linear mixed model (GLMM) (see Hedeker 2005; Bolker et al. 2008). For this analysis, only seven shells of *Weavericeras vacaense* (CPBA 5154, 6157, 17000.1, 17000.15, 17004.5, 21127.1, 21127.7) and nine of *Holcoptychites agrioensis* (CPBA 18361, 18362, 19998.1, 20010.5, 20011.2, 20011.3, 20011.8, 20011.16, 20011.17) were included. For the GLMM, specimens were selected among those belonging to the fifth category of shell preservation, which, in addition, lacked internal sclerobionts. This was in order to test those shells that were more likely to have preserved the *in vivo* patterns of sclerobiont colonization (i.e., the most complete shells that exhibit no colonization of internal surfaces).Therefore, the number of specimens that could be included for the GLMM comparison of shell zones was quite reduced, and thus interpretation of the results of this analysis should be made with caution.

Diversity analyses of the sclerobiont fauna of each ammonite basibiont consisted in the calculation of the Simpson's Dominance (see Hammer and Harper 2006) and Pielow's diversity indices (H/Hmax; Hammer and Harper 2006), along with the taxonomic richness.

Statistical results were compared to those previously obtained for *Cymatoceras perstriatum*, as published in Luci and Cichowolski (2014). In addition, the materials of *C. perstriatum* corresponding to each of the zone/subzone of the ammonites analyzed here were separated, and compared with their coeval ammonites. The mean of sclerobionts per shell, total incidence, and diversity indices of each nautilid subset of samples was computed, and compared to the same values for the corresponding ammonite species, using the same statistical methods described above. Samples of *C. perstriatum* from each ammonite zone were also compared to each other.

RESULTS

### Sclerobionts on Weavericeras vacaense

The analyzed shells of *Weavericeras vacaense* consist mainly of phragmocone fragments (66.15%; 43 shells), with the remaining specimens presenting complete or incomplete phragmocones with part of the body chamber preserved (Fig. 3). Of the 65 shells of *W. vacaense* mapped for sclerobionts, 38 presented at least one (58.46%; see Fig. 5A, 5D, 5E). Colonization of the shell took place mainly on its outer surface (86.84%; 33 shells); no sclerobiont settlement took place on the inside of the shell exclusively, and only 13.16% of colonized shells (five shells) presented both internal and external colonization. In all cases where internal colonization of the shell took place, sclerobionts settled within the inside of the body chamber.

A total of 585 sclerobionts were found, with a mean of nine sclerobionts per shell of *W. vacaense*. The maximum number of sclerobionts found in a single shell is 68; the minimum is one. Eight taxa of bivalves (*Amphidonte* (*Ceratostreon*) sp., *Plicatula* sp.), polychaetes (the serpulids *Parsimonia antiquata*, *Mucroserpula mucroserpula* and *Propomatoceros gracilis* and a sabellid, *Glomerula* cf. *serpentina*), bryozoans (a cyclostome corresponding to '*Berenicea*'; see Taylor and Sequeiros 1982) and foraminifers (*Tolypammina vagans*) comprised the sclerobiont fauna (Table 2). Five pairs of interactions between sclerobiont taxa were found (Table 3).

The oyster (*Amphidonte* (*Ceratostreon*) sp.) is the main taxon both in abundance and number of colonized shells, followed distantly by the serpulid *P. antiquata* and the sabellid *G.* cf. *serpentina*. Compared to the oysters, all other sclerobiont taxa have little representation within the fauna, but they gain importance when considering the number of colonized ammonite shells (Table 2). The Pielow index was 0.43, and Simpson's Dominance 0.64.

Results of the GLMM analysis (see Table 4) showed that the venter and the right flank were the most heavily colonized zones, and the umbilici were the least. Variability of sclerobiont distribution across shells was quite high (Fig. 4).
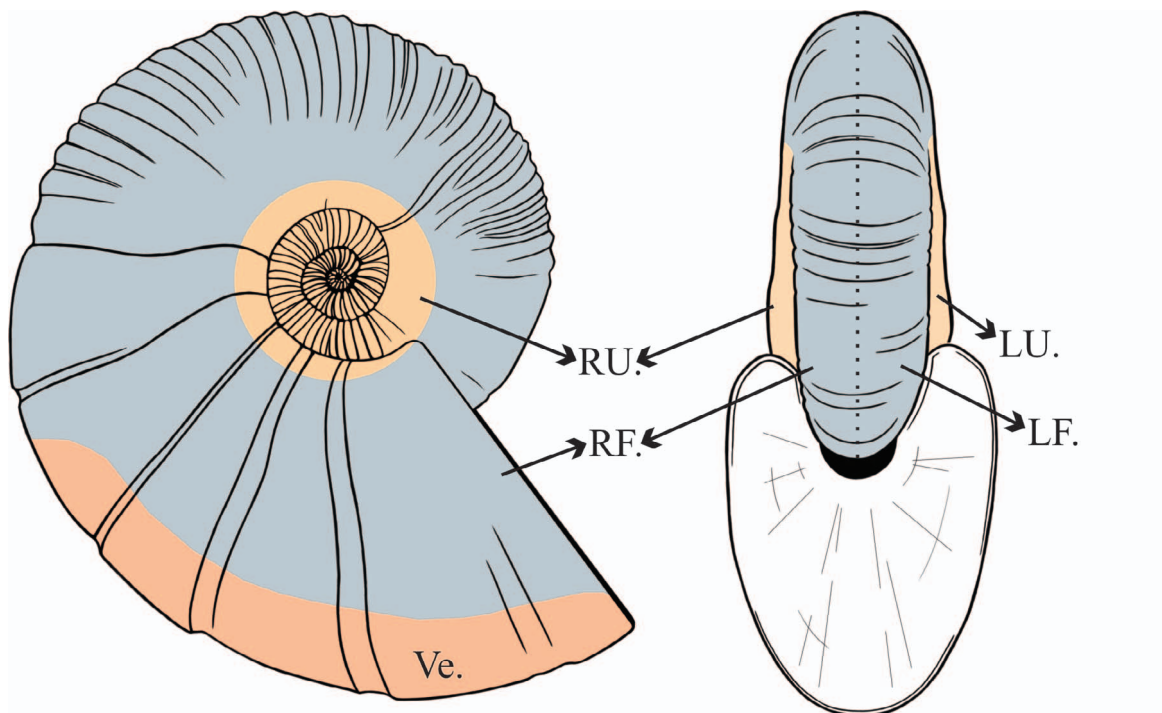
Holcoptychites agrioensis
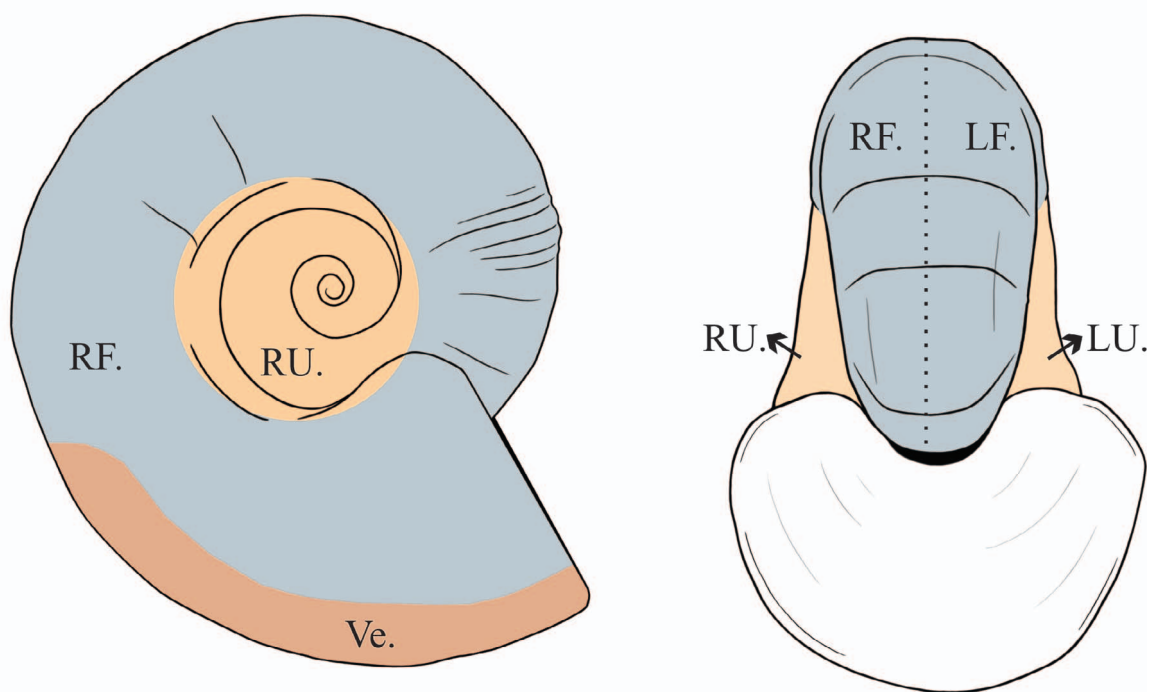
Weavericeras vacaense

FIG. 2.—Shell zonation for the studied ammonite species. Abbreviatios: RF=right flank; LF=left flank; RU=right umbilicus; LU=left umbilicus; Ve=venter.
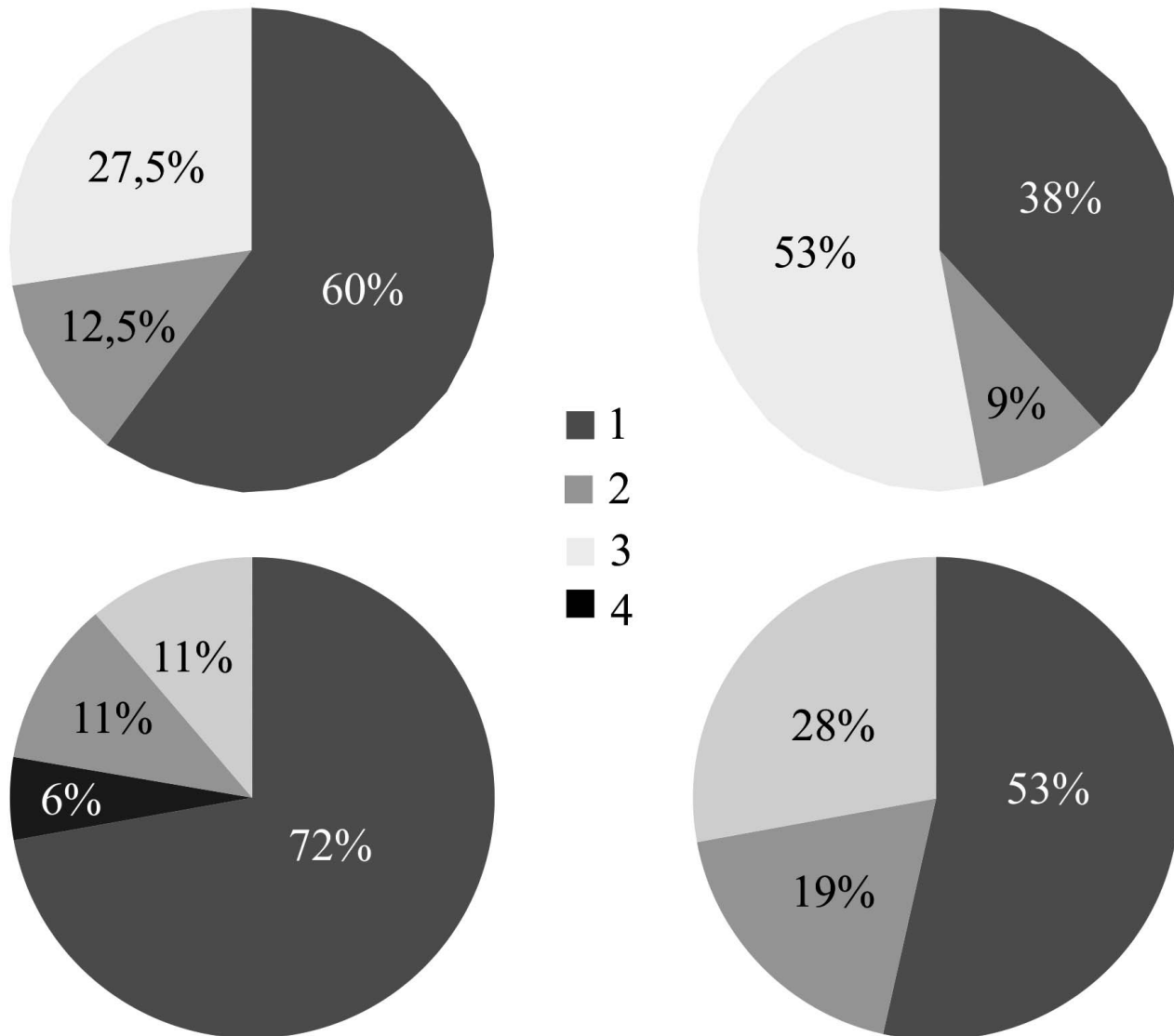
Weavericeras vacaense

Holcoptychites agrioensis

C. perstriatum from the W. vacaense Zone

C. perstriatum from the H. agrioensis Subzone

FIG. 3.—Pie charts showing the state of preservation of the studied cephalopods. Key: 1=Isolated phragmocone chambers; 2=Incomplete phragmocones; 3=Isolated body chambers; 4=Incomplete phragmocones with at least part of the body chamber; 5=Complete phragmocones with remains of the body chamber. No specimen found belonged to category 1.

Finally, no particular alignment of conspecific sclerobionts was observed. Both bivalves and serpulids are randomly oriented on the ammonite's shell, whereas bryozoan colonies have a subcircular outline, favoring no specific growth direction. Oysters were commonly clustered, and so were serpulids, though their clusters were smaller (Fig. 5).

Sclerobionts on Holcoptychites agrioensis

Of the 57 analyzed specimens of *Holcoptychites agrioensis*, many of them are rather complete; 50.87% consist of complete phragmocones with part of

the body chamber (Fig. 3). Sclerobionts were found in 59.65% of the shells (34 shells), mainly on the outer surface (73.53%; 25 shells), but also exclusively on the inside of the shell (8.82%; three shells), and both inside and outside at the same time (17.65%; six shells). All internal sclerobionts were located within the body chamber.

A total of 442 sclerobionts were found, with only three taxa represented. The overwhelming majority consisted of oysters (*Amphidonte* (*Ceratostreon*) sp.), with only a single specimen of the serpulid *P. antiquata*, and a single bryozoan '*Berenicea*' sp. colony. No interactions between sclerobiont taxa

TABLE 2.—*Absolute and relative frequencies of sclerobiont taxa for both ammonites and the nautilids from each ammonite zone. Number of shells presenting each sclerobiont taxon and percentage of shells of each cephalopod bearing a sclerobiont taxon are also given.*

	Weavericeras vacaense				*Holcoptychites agrioensis*				*C. perstriatum* from *W. vacaense* zone				*C. perstriatum* from *H. agrioensis* subzone			
	# Ind.	% fauna	# shells	% shells	# Ind.	% fauna	# shells	% shells	# Ind.	% fauna	# shells	% shells	# Ind.	% fauna	# shells	% shells
Amphidonte (Ceratostreon) sp.	462	78.97	37	97.4	440	99.54	34	100	296	82.68%	17	94.44	296 (82.68%)	556 (77.3%)	37	86.05
'Berenicea' sp.	21	3.59	7	18.4	1	0.22	1	2.94	12	3.35%	6	33.33	12 (3.35%)	6 (0.83%)	2	4.65
Parsimonia antiquata	50	8.55	13	34.2	1	0.22	1	2.94	42	11.73%	7	38.89	42 (11.73%)	120 (16.69%)	19	44.19
Mucroserpula mucroserpula	8	1.37	4	10.5	–	–	–	–	3	0.84%	1	5.56	–	–	–	–
Propomatoceros gracilis	5	0.85	4	10.5	–	–	–	–	–	–	–	–	–	–	–	–
Glomerula cf. *serpentina*	29	4.96	10	26.3	–	–	–	–	1	0.28%	1	5.56	1	0.14	1	2.33
Plicatula sp.	10	1.71	4	10.5	–	–	–	–	3	0.84%	2	11.11	1	0.14	1	2.33
Tolypammina vagans	–	–	4	10.5	–	–	–	–	–	–	1	5.56	–	–	1	2.33
Placostegus cf. *conchophilus*	–	–	–	–	–	–	–	–	–	–	–	–	34	4.73%	4	9.30

were observed. Sclerobionts were randomly oriented with respect to their basibiont's shell. Aggregation of oysters was common (Fig. 5). The mean number of sclerobionts per *H. agrioensis* shell is 7.75. The minimum number of sclerobionts found in a single shell is two, whereas the maximum is 33. Pielow's Index is 0.05, while Simpson's Dominance is 0.99 (see Table 2).

GLMM results showed (Table 4) that the flanks endured the heaviest colonization by sclerobionts whereas the umbilici had the least sclerobionts. Variability of distribution of sclerobionts across shells is less pronounced than in *W. vacaense* (Fig. 4).

The comparison of the mean of sclerobionts per shell of both ammonites (analysis of deviance) yielded no significant differences between them ($z=0.58$; $p=0.56$). Incidence values (χ^2 test) are also comparable between *H. agrioensis* and *W. vacaense*, with no significant differences ($\chi^2=0$; $p=1$).

Sclerobionts on Coeval Specimens of *Cymatoceras perstriatum*

Thirty specimens among the studied materials of *Cymatoceras perstriatum* correspond to the *Weavericeras vacaense* zone, whereas 85 were collected from the *Holcoptychites agrioensis* subzone (for CPBA number see Table 1). This difference in number is due to the presence of an exceptional nautilid accumulation within the latter biozone (see Cichowolski et al. 2012). Results are presented in Tables 2 and 5. Taxonomic composition is almost identical to that of *W. vacaense*, except for the absence of *P. gracilis*, which was replaced by another serpulid, *Placostegus* cf. *conchophilus*.

Mean comparisons between nautilids from both ammonite zones yielded no statistical differences (Tukey comparisons: $z=1.03$; $p=0.30$). The same is true

for the nautilids and the coeval *H. agrioensis* ($z=-0.33$; $p=0.74$), and the nautilids from the *W. vacaense* Zone and the corresponding ammonites ($z=-0.79$; $p=0.43$).

Likewise, no differences in incidence of sclerobiont colonization were found between nautilid samples ($\chi^2=0.12$; $p=0.73$), nor between *H. agrioensis* and coeval nautilds ($\chi^2=0.23$; $p=0.63$). The same was the case of *W. vacaense* and coeval nautilids ($\chi^2=0$; $p=1$).

DISCUSSION

Comparison of Sclerobiont Faunas Between Basibiont Ammonites

The results of the analysis of deviance and the χ^2 test indicate that both ammonites were comparably colonized by sclerobionts, both in frequency and intensity. None of the ammonites presented internal colonization of the phragmocone (which was quite common in nautilids; Luci and Cichowolski 2014), probably due to the smaller siphuncle diameter of ammonites. Thus, internal colonization was limited to the body chamber. It was more common in *Holcoptychites agrioensis* than in *Weavericeras vacaense*, although this is likely a taphonomic bias due to the higher proportion of preserved body chambers in *H. agrioensis* shells.

TABLE 4.—*Results of the Tukey comparisons of the GLMM results for both ammonites. Abbreviations: RU=right umbilicus; LU=left umbilicus; RF=right flank; LF=left flank; Ve=venter.*

	W. vacaense		*H. agrioensis*	
	Z	p-value	Z	p-value
RU-LU	−0.21	0.99	0	1
RU-RF	6.34	<0.001	2.86	0.03
RU-LF	1.09	0.8	3.98	<0.001
RU-Ve	2.89	0.03	0	1
LU-RF	6.38	<0.001	2.86	0.03
LU-LF	1.29	0.68	3.98	<0.001
LU-Ve	3.05	0.01	0	1
RF-LF	−5.99	<0.001	1.62	0.47
RF-Ve	−4.71	<0.001	−2.86	0.03
LF-Ve	1.95	0.28	−3.98	<0.001

TABLE 3.—*Pairs of sclerobiont interactions observed in* Weavericeras vacaense *showing the taxa involved and which one overgrew the other ("won").*

Pairs of interaction (A–B)	Number of cases	A won	B won
Parsimonia–Berenicea	1	0	1
Amphidonte–Berenicea	2	1	1
Mucroserpula–Berenicea	1	1	0
Glomerula–Berenicea	1	1	0
Amphidonte–Parsimonia	1	0	1

Weavericeras vacaense

Holcoptychites agrioensis

Colonized shells: N= 38
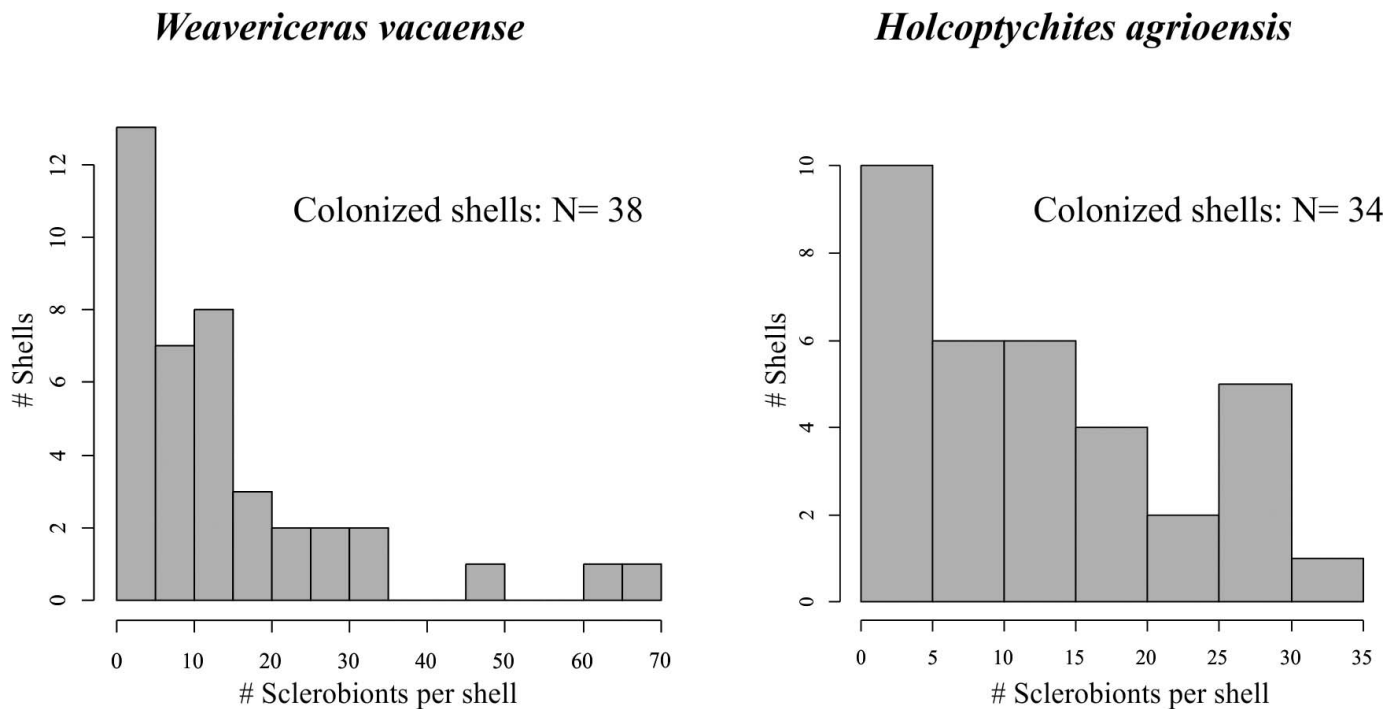
Colonized shells: N= 34

FIG. 4.—Histograms depicting the amount of shells of each ammonite species bearing a given range of sclerobiont individuals per shell. Notice that the maximum of sclerobionts per shell is higher for *W. vacaense*.

In both cases sclerobionts lacked clearly defined growth orientation in relation to the ammonites' shells. Oysters are commonly clustered on both ammonites, which is also typical of oysters on other basibionts (Luci and Cichowolski 2014; Luci and Lazo 2015).

The maximum number of sclerobionts found on a single shell of *H. agrioensis* is half of the maximum number of sclerobionts on *W. vacaense*. This reflects a greater heterogeneity in the number of sclerobionts on the latter, since both minimum numbers are almost the same. In addition, one of the flanks on both ammonites (and the venter in *W. vacaense*) is more heavily colonized than the other. The left and right umbilici, in contrast, are equally encrusted, likely due to their smaller area which could be completely covered by sclerobionts more rapidly. This observation held true for both ammonite species. In this respect it is important to note that the statistical test does not account for the surface area of shell zones.

Sclerobiont richness is quite reduced in *H. agrioensis* in comparison to *W. vacaense*. Almost all sclerobionts found in *H. agrioensis* consist of oysters, resulting in their complete dominance of the fauna. While oysters are by far the main component of the sclerobiont fauna in *W. vacaense* as well, other sclerobiont taxa are also quite common. Likewise, it is not surprising that there were no interactions among sclerobiont taxa in *H. agrioensis*, since almost all individuals belong to the same species. In *W. vacaense*, interactions are rare, not all possible pairs are represented, and many overgrowth cases are likely *post mortem*. For example, interactions with oysters involve the overgrowth of disarticulated left valves, which clearly indicates that the oyster was dead and disarticulated prior to settlement of the succeeding sclerobiont spat.

Comparison of Sclerobiont Faunas of Ammonites and Cymatoceras perstriatum

No significant differences were observed in incidence and mean of sclerobionts per shell between nautilids from the two ammonite zones. The maximum number of sclerobionts found in a single *Cymatoceras perstriatum* shell is greater in the nautilids from the *Weavericeras vacaense* Zone. Diversity indices

have very similar values, richness is the same for both, and taxonomic composition is almost identical, with only a single taxon differing. Oysters dominate both sample sets (both comprise around 80% of the fauna; see Table 5). Likewise, no significant difference was obtained when comparing nautilids to the corresponding ammonites, neither in incidence nor in mean of sclerobionts per shell. Richness and diversity indices are very similar between *W. vacaense* and the coeval specimens of *C. perstriatum*, but strongly differ between *H. agrioensis* and the corresponding nautilids.

Interpretation of Taphonomic Routes

While colonization during the lifetime of the studied ammonites cannot be determined with certainty, known examples of *in vivo* settlement indicate that sclerobiont occupation of cephalopod shells was kept to a minimum, with only a few, small individuals involved, which would not greatly increase the weight or drag of the shell (e.g., Seilacher 1982; Landman et al. 1987; Baird et al. 1989; Checa et al. 2002; Larson 2007; Andrew et al. 2011; Ifrim et al. 2011). After death, once defenses against sclerobionts no longer functioned (for example, a thick periostracum and/or tentacle action; see Landman et al. 1987), the whole shell became available for colonization. The state of colonization shown by the ammonites studied here indicates that the original patterns of *in vivo* colonization, if the latter took place, were obscured by a process of *post mortem* settlement. The lack of orientation of sclerobionts with respect to the ammonite's shells, the occurrence of internal colonization and the great number of individuals attached to some of the shells are all indicative of colonization occurring primarily after the death of the animals.

Consequently, for the greater part, sclerobiont colonization patterns of the studied ammonites respond not to their life habit and live behavior, but mostly to their taphonomic routes. As has been mentioned before, taphonomic routes may be rather complex for externally shelled cephalopods (e.g., Fernández-López 1987; Mapes et al. 2010; Cichowolski et al. 2012). As necroplanktonic drift takes place, the whole shell is exposed for sclerobiont colonization. When
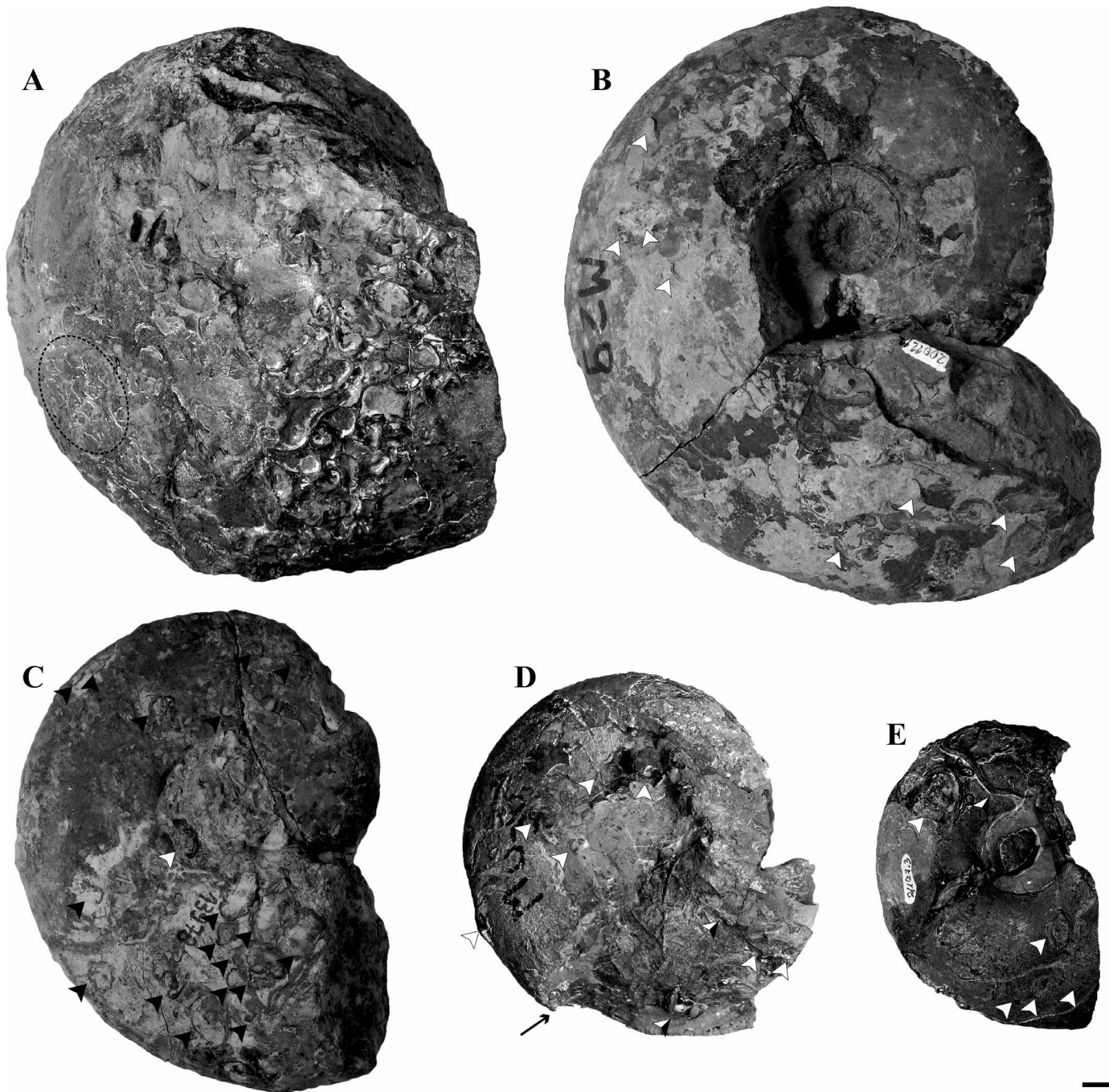
FIG. 5.—**A**) *Weavericeras vacaense*, CPBA 17000.16, with the right flank (within the oval area) and venter partially covered by a great amount of small oysters. **B**) *Holcoptychites agrioensis*, CPBA 20011.12. **C**) *Holcoptychites agrioensis*, CPBA 13978. Both with abundant oysters which had attached themselves to the inside surface of the body chamber. **D**) *Weavericeras vacaense*, CPBA 21127.7, the arrow shows the posterior end of the collapsed body chamber, which externally bears serpulids, bryozoans and oysters. **E**) *Weavericeras vacaense*, CPBA 21127.3, showing considerably large *Glomerula* cf. *serpentina*. All in right lateral view. Scale bar=1 cm. White pointers indicate oysters cemented in the outside of the shell; black pointers indicate oysters cemented on the inside of the shell. Black and white pointers indicate serpulids.

it sinks, the parts of the shell in contact with the sea bottom (typically one of the flanks) are no longer available for settlers. As a consequence, homogeneous colonization of flanks (and venter) would correspond to settlement as the cephalopod retained some floatability (either while alive or after death; see Seilacher 1960, 1982; Rakús and Zítt 1993; Ifrim et al. 2011) or mobility on the sea-floor (i.e., reorientation by waves and currents). In contrast, unequal colonization of the flanks has been regarded as corresponding to a "benthic island"

situation (see Kauffmann 1973), either from the start of sclerobiont settlement, or after some colonization during a necroplanktonic phase.

The common presence of sclerobionts on the venter and flanks of both ammonite species described here indicates that, at least for a time, their whole shells were exposed and available for sclerobiont colonization. This is in agreement with the *post mortem* floating shells scenario (e.g., see criteria used by Ifrim et al. 2011). Since the Pilmatué Member has been interpreted as a rather

shallow marine ramp (Spalletti et al. 2001; Lazo et al. 2005), it is unlikely that these ammonites were below their critical flotation depth (see Maeda and Seilacher 1996; but also Westermann and Tsujita 1999), and, therefore, they probably floated. The involute, globose morphology of *Weavericeras vacaense* makes its shell more prone to floating, and it likely sustained a longer necroplanktonic drift phase than the more evolute, compressed shell of *Holcoptychites agrioensis*. The common preservation of the body chamber of *H. agrioensis* could indicate a more rapid sinking of its shells favored by its morphology and its longer body chamber; flooding of the body chamber increases the weight of the shell and the length of the body chamber is probably the most important factor in shell buoyancy (Reyment 1958).

When loss of shell buoyancy, which was likely caused by shell damage, excess of sclerobionts, or sinking by storm currents (House 1987; Cichowolski et al. 2012), caused the necroplanktonic phase to end, sclerobiont colonization probably continued on the sea bottom. *Weavericeras vacaense* has shown, for the GLMM analysis, unequal colonization of the flanks, suggesting that some shells lay on one flank on the seafloor while exposing the other. This allowed sclerobiont colonization to continue, but in one flank only, causing the number of sclerobionts to differ between the sides. Colonization as shells lay on the sea bottom is likely to have taken place since bivalves and other benthic fauna commonly bear sclerobionts in the Agrio Formation (personal observation; Luci 2010, 2013; Garberoglio and Lazo 2011; Luci and Lazo 2015). The studied ammonites presented ample surfaces for colonization, as well as sheltered habitats within the body chamber. Occupation of inner surfaces of the shell is, however, more common and much more intensely developed in nautilids (Luci and Cichowolski 2014).

Taphonomic routes of both ammonites would then comprise a necroplanktonic phase, likely more prolonged in the case of *W. vacaense*, and a phase of exposure on the sea bottom after sinking. Duration of this phase was likely greater for *W. vacaense* as well, due to the shape of its shell, which produced a greater relief on the seafloor (see Fig. 6) and would have taken longer to be covered by sediment under uniform sedimentation rates, while being more prone to reorientation by waves and currents. This could also result in a more prolonged exposure of *W. vacaense* shells, and thus further colonization and damage of the shells. This agrees with the higher heterogeneity in sclerobiont distribution across *W. vacaense* shells, as well as in the mode of preservation of its shells. In addition, the venter of *W. vacaense* could, therefore, have been colonized both during necroplanktonic drift and while laying on the sea bottom, since most of it would have been exposed as the shell rested on one flank (Fig. 6).

This model could be complicated by two factors: (1) the possibility that some ammonites landed on the seafloor in a vertical position and (2) reorientation of ammonites by waves, currents and benthic fauna. Vertical landing of cephalopod shells is known to take place in extant *Nautilus* and in fossil examples as well (see Fernández-López 1987; Maeda and Seilacher 1996; Olivero

2007), mostly in very shallow settings (but see Olivero 2007, and references therein). While none of the ammonites were found buried in a vertical position (as was the case of the materials studied by Olivero 2007), it is impossible to know if some of them landed and remained in that position for a while. In that case the patterns of sclerobiont colonization would be much like those of floating shells, with the exception of the venter, which would not have been exposed (Mapes et al. 2010). Reorientation of ammonites on the seafloor could also cause successive exposure of different parts of the shell, once again resulting in a pattern similar to necroplanktonic drift. Therefore, the possibility exists that the likely necroplanktonic drift phase could be a misinterpretation due to a vertical landing and/or common reorientation of shells. Since there is no evidence for vertical landing, however, this is only speculation. In contrast, reorientation of shells is quite likely to have occurred, so it cannot be dismissed.

Variations in the ramp sub-environment across zones, if they took place, do not seem to have had a very strong impact on the sclerobiont faunas. This is because when comparing the *C. perstriatum* from the *H. agrioensis* and *W. vacaense* zones, all measured parameters show no significant differences (Table 4). Therefore, differences across the sclerobiont faunas of the studied ammonites (mainly the reduced richness of *H. agrioensis* fauna) should be caused by the features of the ammonites themselves, rather than by environmental parameters.

Interpretation of the Sclerobiont Fauna

The presence of overgrowths on *Weavericeras vacaense* indicates that, though rarely, some of its shells were colonized by more than one generation of sclerobionts, which was not the case of *Holcoptychites agrioensis*. This also agrees with a longer time of exposure of *W. vacaense* shells. Colonization by several generations of sclerobionts does not imply, however, that available space was saturated, since none of the shells were completely covered or close to being covered. Competition among sclerobionts does not appear to have played a major role in the development of the community, not only because space was not saturated, and interactions were uncommon, but also because many of the latter were clearly *post mortem* (as explained above), whereas others resulted in no damage to the overgrown organism regardless of whether the interaction took place during life or after death (for example, serpulid tubes overgrown by bryozoan colonies without affecting the aperture). Uneven presence of sclerobionts across similar available substrates is quite common, as shown by Brett et al. (2011), who observed that within a given environment some shells may be heavily colonized while others remain free from sclerobionts, revealing that settlement of the latter does not follow a linear pattern.

Richness and diversity indices are those parameters that show the greatest difference between the studied ammonites. The richness of the sclerobiont fauna in *W. vacaense* is along the lines of other study cases from the Agrio Formation (Luci 2013; Luci and Cichowolski 2014; Luci and Lazo 2015), which

TABLE 5.—*Summary of the main parameters of the sclerobiont fauna measured in all cephalopods. Notice that percentage values of shells encrusted on the outside, inside, and both surfaces of the shells were calculated from the value of encrusted shells.*

|	*Weavericeras vacaense*	*Holcoptychites agrioensis*	*C. perstriatum* from *W. vacaense* zone	*C. perstriatum* from *H. agrioensis* subzone
% colonized shells	58.46% (38 shells)	59.65% (34 shells)	60.00% (18 shells)	54.12% (46 shells)
Mean scler./shell	9	7.75	11.93	8.46
Minimum number of sclerobionts	1	2	1	1
Maximum number of sclerobionts	68	33	107	64
Pielow's Index	0.43	0.05	0.33	0.36
Simpson's Dominance	0.64	0.99	0.7	0.63
Richness	8	3	8	8
Shells with outer colonization only	86.84% (33 shells)	73.53% (25 shells)	40% (12 shells)	31.76% (27 shells)
Shells with inner colonization only	–	8.82% (3 shells)	10% (3 shells)	7.06% (6 shells)
Shells colonized inside and oustide	13.16% (5 shells)	17.65% (6 shells)	10% (3 shells)	15.29% (13 shells)
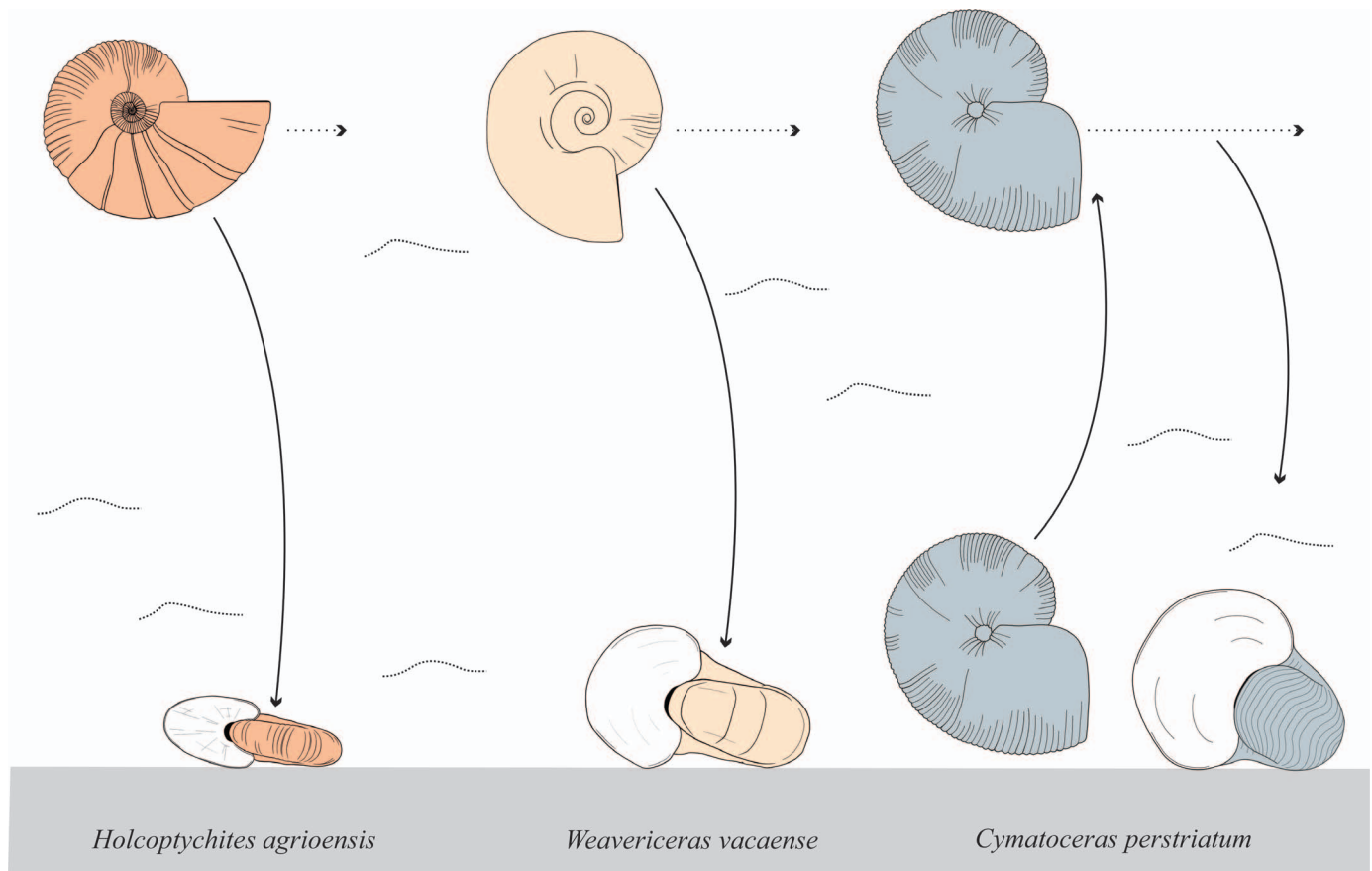
FIG. 6.—Taphonomic routes of the studied cephalopods. The dotted arrow represents the relative duration of the necroplanktonic drift phase; solid arrows represent sinking or flotation. The position of shells as they rest on the sea bottom is shown in order to compare the relief produced by the shell of each species. More involute and inflated shells such as *W. vacaense* and *C. perstriatum* floated for a longer time and produced more relief on the seafloor than the more evolute and compressed *H. agrioensis*. Notice that *C. perstriatum* begins at the sea bottom since it has been inferred to have had a nectobenthic habit (see Lazo et al. 2005; Westermann 1999).

are more or less intensely dominated by *Amphidonte* (*Ceratostreon*) sp., distantly followed by serpulids, sabellids and bryozoans, with a few other rare taxa. Oysters, serpulids, bryozoans and foraminifers are also common components of other known cases of sclerobiont communities on cephalopods (e.g., Hamada 1964; Seilacher 1982; Henderson and McNamara 1985; Lukeneder and Harzhauser 2003; Reyment 2008; Andrew et al. 2011).

When comparing the ammonites to the nautilid *Cymatoceras perstriatum* (see Luci and Cichowolski 2014), the mean number of sclerobionts per shell and incidence of colonization are rather uniform across all basibionts indicating that both ammonites and *C. perstriatum* were equally eligible and suitable for sustaining sclerobiont communities. There is a better overall preservation (higher proportion of specimens with part of the body chamber) of the subset of nautilids from the *H. agrioensis* Subzone, but this is due to the rapid sinking of many specimens trapped within the abundant nautilid concentration (Cichowolski et al. 2012). Despite this, since shells involving a variety of exposure times were buried together (Cichowolski et al. 2012), *C. perstriatum* from the *H. agrioensis* Subzone presents richness and diversity values closer to those of *W. vacaense* and its coeval nautilids, than to its contemporaneous *H. agrioensis*; that is, no decrease in richness of the sclerobiont community is observed in these nautilids. Therefore, the *H. agrioensis* Subzone was not a time of reduced sclerobiont diversity caused by external factors. Reduced richness and diversity are features of the *H. agrioensis* sclerobiont fauna. Since the sclerobiont fauna has been interpreted to have settled mostly *post mortem*, this decrease is probably caused by some feature of the biostratinomic phase of

the ammonite, probably the reduced time of exposure. In this respect, several authors (Rodland et al. 2006; Brett et al. 2011) have observed that there is a non-linear tendency for taxonomic richness to increase with time in sclerobiont communities, which supports the inference of a shorter time of exposure for the shells of *H. agrioensis*.

The better overall preservation of *H. agrioensis*, its morphological features and the reduced richness of its sclerobiont fauna suggest that it sank and was covered by sediment more quickly than *W. vacaense* and *C. perstriatum* (as discussed above). The low richness of the sclerobiont fauna of *H. agrioensis* thus suggests that it remained at the early stages of sclerobiont colonization. *Holcoptychites agrioensis* shells became unavailable before later colonizers could settle upon its shells. Brett et al. (2011) have observed that as a general rule a common set of early established sclerobionts can be found in several different substrates, and for a time no great addition of new taxa takes place. Quick burial facilitates the preservation of these initial stages of colonization. Oysters seem to have been the main, or the only, early settler on basibionts of the Agrio Formation since it is the most common and abundant sclerobiont in these and other cases studied (Luci and Cichowolski 2014; Luci and Lazo 2015). The great amount of *Amphidonte* (*Ceratostreon*) oysters settling on clusters on *H. agrioensis* shells in a reduced time reflects a great abundance of oyster larvae, a capacity for rapid proliferation and settlement, and possibly a gregarious behavior. This oyster was a very prolific, ubiquitous sclerobiont in the Agrio Formation and other marine units of the Mendoza Group (Luci 2010, 2013), to the extent that it could build monospecific barriers of positive relief

upon the seafloor comprising thousands of specimens (see Lazo 2006). These features allowed *Amphidonte* (*Ceratostreon*) sp. not only to settle quickly, but also to rapidly cover a great part of the available shells, since it is likely that once an individual established on a shell, others soon followed, as is the case of many oyster species (e.g., Toonen and Pawlik 1996; Tamburri et al. 2008). The early settlement of *Amphidonte* (*Ceratostreon*) sp. inferred from *H. agrioensis* agrees with the conclusions arrived at by Luci and Lazo (2015) for the sclerobiont fauna on a pectinid bivalve taxon from the Agrio Formation.

CONCLUSIONS

Sclerobiont taxa on two early Hauterivian species of ectocochleate cephalopods (*Weavericeras vacaense* and *Holcoptychites agrioensis*) from the Agrio Formation (Neuquén Basin, Argentina) were compared and contrasted with sclerobionts on the coeval nautilid *Cymatoceras perstriatum*. Morphological differences among the studied cephalopods explain the differential *post mortem* behavior of their shells. The more evolute, compressed shell of *H. agrioensis* sinks more quickly than those of *W. vacaense* and *C. perstriatum*, which may undergo longer periods of flotation and probably also of exposure on the sea bottom. This is corroborated by a lower taxonomic richness of the sclerobiont fauna and a better overall preservation of the *H. agrioensis* materials. Despite this, all other measured parameters of the sclerobiont fauna are rather homogeneous across the studied basibionts. This indicates that shell morphology does not have a great impact in the success rate of colonization of sclerobionts, nor in their abundance, or in how sclerobionts distribute themselves across the shells. Sclerobiont diversity and richness are greater across variations in shell inflation and coiling degree than across nautilids and ammonites. The faunas are more similar, in terms of richness and diversity, for *W. vacaense* and *C. perstriatum* than for both ammonites. Inflation and coiling degree, therefore, seem to have been important parameters in determining how long a planispiral shell will float, and how much relief it will produce on the seafloor, which impacts on its time of exposure, and thus these parameters influence the sclerobiont fauna as well. Analysis of more shell morphologies should shed more light on how important variations in inflation and coiling are in buoyancy, and consequently, time of exposure and availability for colonization.

The rather uniform patterns of colonization rate, abundance and distribution of sclerobionts suggest that these faunas were composed of generalist taxa, capable of adjusting to a variety of conditions; the inside or the outside of a shell, to a pseudoplanktonic or a benthic substrate and to different shell shapes. Of all these taxa, oysters always dominate sclerobiont faunas in the study material. The presence of an abundant, monospecific oyster fauna in *H. agrioensis*, despite its rapid sinking and burial, indicates that *Amphidonte* (*Ceratostreon*) was the earliest settler, and was also able to abundantly colonize available substrates in a short time. Other taxa followed, but the absence of common interactions and of saturated substrates suggests that either competition was not important, exposure of shells did not go on for long enough for competition to become a major control on the development of these communities, or that substrate availability exceeded the sclerobiont requirement for settling space.

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REFERENCES

AGUIRRE-URRETA, M.B., 2013, Amonoideos del Valanginiano-Hauteriviano de la cuenca Neuquina: sistemática, bioestratigrafía y paleobiogeografía: Unpublished PhD thesis, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, 269 p. http://digital.bl.fcen.uba.ar/Download/Tesis/Tesis_5374_AguirreUrreta.pdf

AGUIRRE-URRETA, M.B. AND RAWSON, P.F., 1997, The ammonite sequence in the Agrio Formation (Lower Cretaceous), Neuquén Basin, Argentina: Geological Magazine, v. 134, p. 449–458.

AGUIRRE-URRETA, M.B. AND RAWSON, P.F., 2003, Lower Cretaceous ammonites from the Neuquén Basin, Argentina: the Hauterivian genus *Holcoptychites*: Cretaceous Research, v. 24, p. 589–613.

AGUIRRE-URRETA, M.B. AND RAWSON, P.F., 2010, Lower Cretaceous ammonites from the Neuquén Basin, Argentina: the neocomitids of the *Pseudofavrella angulatiformis* Zone (upper Valanginian): Cretaceous Research, v. 31, p. 321–343.

AGUIRRE-URRETA, M.B. AND RAWSON, P.F., 2012, Lower Cretaceous ammonites from the Neuquén Basin, Argentina: a new heteromorph fauna from the uppermost Agrio Formation: Cretaceous Research, v. 35, p. 208–216.

AGUIRRE-URRETA, M.B., RAWSON, P.F., CONCHEYRO, G.A., BOWN, P.R., Y OTTONE, E.G., 2005, Lower Cretaceous (Berriasian and Aptian) biostratigraphy of the Neuquén Basin, *in* Veiga, G., Spalletti, L.A., Howell, L.A. and Schwarz, E. (eds.), The Neuquén Basin: A Case Study in Sequence Stratigraphy and Basin Dynamics: Geological Society, London, Special Publication, v. 252, p. 57–81.

AGUIRRE-URRETA, B., LAZO, D.G., GRIFFIN, M., VENNARI, V., PARRAS, A .M., CATALDO, C., GARBEROGLIO, R. AND LUCI, L., 2011, Megainvertebrados del Cretácico y su importancia bioestratigráfica, *in* Leanza, H.A., Arregui, C., Carbone, O., Danieli, J.C. and Vallés, J.M. (eds.), Geología y Recursos Naturales de la Provincia del Neuquén. Relatorio del XVIII Congreso Geológico Argentino: Asociación Geológica Argentina, Buenos Aires, p. 465–488.

AGUIRRE-URRETA, M.B., MOURGUES, F.A., RAWSON, P.F., BULOT, L.G. AND JAILLARD, E., 2007, The Lower Cretaceous Chañarcillo and Neuquén Andean basins: ammonoid biostratigraphy and correlations: Geological Journal, v. 42, p. 143–173.

ANDREW, C., HOWE, P., PAUL, C.R.C. AND DONOVAN, S., 2011, Epifaunal worm tubes on Jurassic (lower Lias) ammonites from Dorset: Proceedings of the Geologists Association, v. 122, p. 34–46.

ARCHUBY, F. M. AND FÜRSICH, F. T., 2010, Facies analysis of a highly cyclic sedimentary unit: the late Hauterivian to early Barremian Agua de la Mula Member of the Agrio Formation, Neuquén Basin, Argentina: Beringeria, v. 41, p. 77–127.

ARCHUBY, F.A., WILMSEN, M., AND LEANZA, H.A., 2011, Integrated stratigraphy of the upper Hauterivian to lower Barremian Agua de la Mula Member of the Agrio Formation, Neuquén Basin, Argentina: Acta Geologica Polonica, v. 61, p. 1–26.

BAIRD, G.C., BRETT, C.E., AND FREY, R.C., 1989, "Hitchhiking" epizoans on orthoconic cephalopods: preliminary review of the evidence and its implications: Senckenbergiana lethaea, v. 69, p. 439–465.

BALLENT, S., CONCHEYRO, A., NÁÑEZ, C., PUJANA, I., LESCANO, M., CARIGNANO, A.P., CARAMÉS, A., ANGELOZZI, G., AND RONCHI, D., 2011, Microfósiles mesozoicos y cenozoicos, *in* Leanza, H.A., Arregui, C., Carbone, O., Danieli, J.C. and Vallés, J.M. (eds.), Geología y Recursos Naturales de la Provincia del Neuquén. Relatorio del XVIII Congreso Geológico Argentino: Asociación Geológica Argentina, Buenos Aires, p. 489–528.

BOLKER, B.M., BROOKS, M.E., CLARK, C.J., GEANGE, S.W., POULSEN, J.R., STEVENS, M.H.H., AND WHITE, J.S.S., 2008, Generalized linear mixed models: a practical guide for ecology and evolution: Trends in Ecology and Evolution, v. 24, p. 127–135.

BRETT, C.E., PARSONS-HUBBARD, K.M., WALKER, S.E., FERGUSON, C., POWELL, E.N., STAFF, G., ASHTON-ALCOX, K.A., AND RAYMOND, A., 2011, Gradients and patterns of sclerobionts on experimentally deployed bivalve shells: synopsis of bathymetric and temporal trends on a decadal time scale: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 312, p. 278–304.

CATALDO, C.S. AND LAZO, D.G., 2012, A redescription of *Pleurotomaria gerthi* Weaver, 1931 (Gastropoda, Vetigastropoda) from the Early Cretaceous of Argentina: new data on its age, associated palaeoenvironments and palaeobiogeographical affinities: Ameghiniana, v. 49, p. 75–95.

CHECA, A.G., OKAMOTO, T., AND KEUPP, H., 2002, Abnormalities as natural experiments: a morphogenetic model for coiling regulation in planispiral ammonites: Paleobiology, v. 28, p. 127–138.

CICHOWOLSKI, M., 2003, The nautiloid genus *Cymatoceras* from the Cretaceous of the Neuquén and Austral basins, Argentina: Cretaceous Research, v. 24, p. 375–390.

CICHOWOLSKI, M., PAZOS, P.J., TUNIK, M.A., AND AGUIRRE-URRETA, M.B., 2012, An exceptional storm accumulation of nautilids in the Lower Cretaceous of the Neuquén Basin, Argentina: Lethaia, v. 45, p. 121–138.

CIRIGLIANO, R.L., 2009, Caracterización petrográfica y marco paleoambiental de las concentraciones fósiles de la Formación Agrio: Unpublished MSc thesis, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, 196 p.

CONCHEYRO, A., LESCANO, M., CARAMÉS, A., AND BALLENT, S., 2009, Micropaleontología de la Formación Agrio (Cretácico Inferior) en distintos sectores de la Cuenca Neuquina: Revista de la Asociación Geológica Argentina, v. 65, p. 342–361.

EVERITT, B.S. AND HOTHORN, T., 2006, Chapter 6: Logistic regression and generalised linear models; blood screening, women's role in society and colonic polyps, *in* Everitt, B.S. and Hothorn, T. (eds.), A Handbook of Statistics Analyses Using R: Chapman and Hall, London, p. 3–13.

FERNÁNDEZ-LÓPEZ, S., 1987, Necrocinesis y colonización postmortal en *Bajocisphinctes* (Ammonoidea) de la Cuenca Ibérica. Implicaciones paleoecológicas y paleobatimétricas: Boletín de la Real Sociedad Española de Historia Natural (Geología), v. 82, p. 151–184.

GARBEROGLIO, R.M. AND LAZO, D.G., 2011, *Post-mortem* and symbiotic sabellid and serpulid-coral associations from the Lower Cretaceous of Argentina: Revista Brasileira de Paleontologia, v. 14, p. 215–228.

GASPARINI, Z. AND FERNÁNDEZ, M., 2011, Reptiles marinos mesozoicos, *in* Leanza, H.A., Arregui, C., Carbone, O., Danieli, J.C., and Vallés, J.M. (eds.), Geología y Recursos Naturales de la Provincia del Neuquén. Relatorio del XVIII Congreso Geológico Argentino: Asociación Geológica Argentina, Buenos Aires, p. 529–538.

GIOVINE, A.T., 1950, Algunos cefalópodos del Hauteriviense de Neuquén: Revista de la Asociación Geológica Argentina, v. 2, p. 35–76.

HAMADA, T., 1964, Notes on the drifted *Nautilus* in Thailand: Contributions to the Geology and Palaeontology of Southeast Asia, v. 21, p. 33–61.

HAMMER, Ø. AND HARPER, D.A.T., 2006, Paleobiogeography and paleoecology, *in* Hammer, Ø. and Harper, D.A.T. (eds.), Paleontological Data Analysis: Blackwell Publishing, Melbourne, p. 183–253.

HEDEKER, D., 2005, GLMM, *in* Everitt, B.S. and Howell, D.C. (eds.), Encyclopedia of Statistics in Behavioral Science, http://www.wiley.com//legacy/wileychi/eosbs/pdfs/bsa251.pdf.

HENDERSON, R.A. AND MCNAMARA, K.J., 1985, Taphonomy and ichnology of cephalopod shells in a Maastrichtian chalk from Western Australia: Lethaia, v. 18, p. 305–322.

HOUSE, M., 1987, Geographic distribution of *Nautilus* shells, *in* Saunders, W.B. and Landman, N.H. (eds.), *Nautilus*, the Biology and Paleobiology of a Living Fossil: Plenum Press, New York, p. 53–64.

HOWELL, J.A., SCHWARZ, E., SPALLETTI, L.A., AND VEIGA, G.D., 2005, The Neuquén Basin: an overview, *in* Veiga, G.D., Spalletti, L.A., Howell, J.A., and Schwarz, E. (eds.), The Neuquén Basin, Argentina: A Case Study in Sequence Stratigraphy and Basin Dynamics: Geological Society of London Special Publications 252, p. 1–14.

IFRIM, C., VEGA, F.J., AND STINNESBECK, W., 2011, Epizoic stramentid cirripedes on ammonites from Late Cretaceous platy limestones in Mexico: Journal of Paleontology, v. 85, p. 524–536.

JACOBS, D.K. AND CHAMBERLAIN, J.A., 1996, Ammonoid paleobiology, *in* Landman, N., Tanabe, K., and Davis, R.A. (eds.), Ammonoid Paleobiology: Plenum Press, New York, p. 170–224.

KAUFFMAN, E.G., 1973, Cretaceous Bivalvia, *in* Hallam, A. (ed.), Atlas of Paleobiogeography: Elsevier, Amsterdam, p. 353–383.

LANDMAN, N.H., SAUNDERS, W.B., WINSTON, J.E., AND HARRIES, P.J., 1987, Incidence and kinds of epizoans on the shells of living Nautilus, *in* Saunders, W.B. and Landman, N.H. (eds.), *Nautilus*: the Biology and Paleobiology of a Living Fossil: Plenum Press, New York, p. 163–177.

LARSON, N.L., 2007, Deformities in the late Callovian (late Middle Jurassic) Ammonite Fauna from Saratov, Russia, *in* Landman, N.H. (ed.), Cephalopods Present and Past: New insights and fresh perspectives: Springer-Verlag, Berlín-Heidelberg, p. 344–374.

LAZO, D.G., 2003, The genus *Steinmanella* (Bivalvia, Trigonioida) in the Lower Member of the Agrio Formation (Lower Cretaceous), Neuquén Basin, Argentina: Journal of Paleontology, v. 77, p. 1069–1085.

LAZO, D.G., 2004, Análisis de concentraciones fósiles del Cretácico inferior de Cuenca Neuquina: Unpublished PhD thesis, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, 337 p.

LAZO, D.G., 2006, Análisis tafonómico e inferencia del grado de mezcla temporal y espacial de la macrofauna del Miembro Pilmatué de la Formación Agrio, Cretácico Inferior de cuenca Neuquina, Argentina: Ameghiniana, v. 43, p. 311–326.

LAZO, D.G., 2007, Early Cretaceous bivalves of the Neuquén Basin, west-central Argentina: notes on taxonomy, palaeobiogeography and palaeoecology: Geological Journal, v. 42, p. 127–142.

LAZO, D.G., AGUIRRE-URRETA, M.B., PRICE, G.D., RAWSON, P.F., RUFFEL, A.H., AND OGLE, N., 2008, Palaeosalinity variations in the Early Cretaceous of the Neuquén Basin, Argentina: evidence from oxygen isotopes and palaeoecological analysis: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 260, p. 477–493.

LAZO, D.G. and CICHOWOLSKI, M., 2003, First plesiosaur remains from the Lower Cretaceous of the Neuquén Basin, Argentina: Journal of Paleontology, v. 77, p. 784–789.

LAZO, D.G., CICHOWOLSKI, M., RODRÍGUEZ, D.L., AND AGUIRRE-URRETA, M.B., 2005, Lithofacies, palaeoecology and palaeoenvironments of the Agrio Formation, Lower Cretaceous of the Neuquén Basin, Argentina, *in* Veiga, G., Spalletti, L.A., Howell, J., and Schwarz, E. (eds.), The Neuquén Basin: A Case Study in Sequence Stratigraphy and Basin Dynamics: Geological Society, London, Special Publication, v. 252, p. 295–315.

LEANZA, H.A. AND WIEDMANN, J., 1980. Ammoniten des Valangin und Hauterive (Unterkreide) von Neuquén und Mendoza, Argentinien: Eclogae geologicae Helvetiae, v. 73, p. 941–981.

LEGARRETA, L. AND ULIANA, M.A., 1991, Jurassic–Cretaceous marine oscillations and geometry of back-arc basin fill, central Argentine Andes: Special Publications of the international Association of Sedimentologists, v. 12, p. 429–450.

LESCANO, M.A., 2012, Bioestratigrafía, paleoecología y paleobiogeografía de las asociaciones de nanofósiles calcáreos y nanocónidos del Jurásico tardío y Cretácico temprano de la cuenca neuquina: Unpublished PhD thesis, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, 426 p. http://digital.bl.fcen.uba.ar/Download/Tesis/Tesis_5095_Lescano.pdf

LESCINSKY, H.L., 1996, Don't overlook the epibionts!: PALAIOS, v. 11, p. 495–496.

LESCINSKY, H.L., EDINGER, E., AND RISK, M.J., 2002, Mollusk shell encrustation and bioerosion rates in a modern epeiric sea: taphonomy experiments in the Java Sea, Indonesia: PALAIOS, v. 17, p. 171–191.

LIDDELL, W.D. AND BRETT, C.E., 1982, Skeletal overgrowths among epizoans from the Silurian (Wenlockian) Waldron Shale: Paleobiology, v. 8, p. 67–78.

LUCI, L., 2010, Encrusting patterns and life habits of Mesozoic trigonioids: a case study of *Steinmanella quintucoensis* (Weaver) from the Early Cretaceous of Argentina: Lethaia, v. 43, p. 529–544.

LUCI, L., 2013, La fauna de incrustantes de los invertebrados fósiles del Cretácico Inferior de la cuenca Neuquina: implicancias taxonómicas, paleoecológicas y paleoambientales: Unpublished PhD thesis, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, 353 p.

LUCI, L. AND CICHOWOLSKI, M., 2014, Encrustation in nautilids: a case study in the Cretaceous species *Cymatoceras perstriatum*, Neuquén Basin, Argentina: PALAIOS, v. 29, p. 101–120.

LUCI, L. AND LAZO, D.G., 2015, Living on an island: characterization of the encrusting fauna of large pectinid bivalves from the Lower Cretaceous of the Neuquén Basin, west-central Argentina: Lethaia, v. 48, p. 205–226.

LUKENEDER, A. AND HARZHAUSER, M., 2003, *Olcostephanus guebhardi* as cryptic habitat for an Early Cretaceous coelobite community (Valanginian, Northern Calcareous Alps, Austria): Cretaceous Research, v. 24, p. 477–485.

MAEDA, H. AND SEILACHER, A., 1996, Ammonoid taphonomy, *in* Landman, N., Tanabe, K., and Davis, R.A. (eds.), Ammonoid Paleobiology: Plenum Press, New York, p. 544–578.

MAPES, R.H., HEMBREE, D.I., RASOR, B.A., STIGALL, A., GOIRAND, C., AND RICHER DE FORGES, B., 2010, Modern *Nautilus* (Cephalopoda) taphonomy in a subtidal to backshore environment, Lifou (Loyalty Islands): PALAIOS, v. 25, p. 656–670.

MUTVEI, H. AND DUNCA, E., 1999. Connecting ring ultrastructure in the Jurassic ammonoid *Quenstedtoceras* with discussion on mode of life of ammonoids, *in* Landman, N.H., Davis, R.A., and Mapes, R.H. (eds.), Cephalopods Present and Past: Springer-Verlag, Berlin-Heidelberg, p. 239–256.

NOTTA, R.C., 2008, Estudio sedimentológico y estratigráfico de los Miembros Pilmatué y Avilé de la Formación Agrio en la región de Puerta Curaco, Neuquén: Unpublished MSc thesis, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, 116 p.

OLIVERO, E.B., 2007, Taphonomy of ammonites from the Santonian–lower Campanian Santa Marta Formation, Antarctica: sedimentological controls on vertically embedded ammonites: PALAIOS, v. 22, p. 586–597.

RAKÚS, M. AND ZÍTT, J., 1993, Crinoid encrusters of ammonite shells (Carixian, Tunisia): Geobios, v. 15, p. 317–329.

RAMOS, V.A., 1999, Plate tectonic setting of the Andean Cordillera: Episodes, v. 22, p. 183–190.

RAMOS, V.A. AND FOLGUERA, A., 2005, Tectonic evolution of the Andes of Neuquén: Constraints derived from the magmatic arc and foreland deformation, *in* Veiga, G.D., Spalletti, L.A., Howell, J.A., and Schwarz, E. (eds.), The Neuquén Basin: A Case Study in Sequence Stratigraphy and Basin Dynamics: Geological Society of London, Special Publication v. 252, p. 15–35.

REYMENT, R.A., 1958, Some factors in the distribution of fossil cephalopods: Stockholm Contributions in Geology, v. 1, p. 97–184.

REYMENT, R.A., 2008, A review of the post-mortem dispersal of cephalopod shells: Palaeontologia Electronica, v. 11, p. 1–13. http://palaeo-electronica.org/2008_3/148/148.pdf.

RICCARDI, A.C., 1980, Presencia de epizoos en un amonoideo heteromorfo del Maastrichtiano de Argentina: una inferencia paleoautoecológica: Ameghiniana, v. 17, p. 11–14.

RITTERBUSH, K.A. AND BOTTJER, D.J., 2012, Westermann Morphospaces displays ammonoid shell shape and hypothetical paleoecology: Paleobiology, v. 38, 424–446.

RODLAND, D.L., KOWALEWSKI, M., CARROLL, M., AND SIMÕES, M.G., 2004, Colonization of a 'Lost World': encrustation patterns in modern subtropical brachiopod assemblages: PALAIOS, v. 19, p. 381–395.

RODLAND, D.L., KOWALEWSKI, M., CARROL, M., AND SIMÕES, M.G., 2006, The temporal resolution of epibiont assemblages: are they ecological snapshots or overexposures?: The Journal of Geology, v. 114, p. 313–324.

SCHMID-RÖHL, A. AND RÖHL, H.J., 2003, Overgrowth on ammonite conchs: environmental implications for the lower Toarcian Posidonia shale: Palaeontology, v. 46, p. 339–352.

SEILACHER, A., 1960, Epizoans as a key to ammonoid ecology: Journal of Paleontology, v. 3, p. 189–193.

SEILACHER, A., 1982, Ammonite shells as habitats in the Posidonia Shale of Holzmaden–floats or benthic islands?: Neues Jahrbuch fuer Geologie und Paläontologie Monatshefte, v. 1982, p. 98–114.

SPALLETTI, L., POIRÉ, D., PIRRIE, D., MATHEOS, S., AND DOYLE, P., 2001, Respuesta sedimentológica a cambios en el nivel de base en una secuencia mixta clástica-carbonática del Cretácico de la Cuenca Neuquina, Argentina: Revista de la Sociedad Geológica Española, v. 14, p. 57–74.

SPALLETTI, L.A., VEIGA, G.D., AND SCHWARZ, E., 2011, La Formación Agrio (Cretácico Temprano) en la Cuenca Neuquina, *in* Leanza, H.A., Arregui, C., Carbone, O., Danieli, J.C., and Vallés, J.M. (eds.), Geología y Recursos Naturales de la Provincia del Neuquén. Relatorio del XVIII Congreso Geológico Argentino: Asociación Geológica Argentina, Buenos Aires, p. 145–160.

STEUER, A., 1897, Estratos Jurásicos Argentinos: Actas de la Academia Nacional de Ciencias de Córdoba, v. 7, p. 33–128.

TAMBURRI, M.N., LUCKENBACH, M.W., BREITBURG, D.L., AND BONNIWELL, S.N. 2008, Settlement of *Crassostrea ariakensis* larvae: effects of substrate, biofilms, sediment and adult chemical cues: Journal of Shellfish Research, v. 27, p. 601–608.

TAYLOR, P.D. AND SEQUEIROS, L., 1982, Toarcian bryozoans from Belchite in north-east Spain: Bulletin of the British Museum (Natural History), Geology Series, v. 36, p. 117–129.

TAYLOR, P.D. AND WILSON, M.A., 2002, A new terminology for marine organisms inhabiting hard substrates: PALAIOS, v. 17, p. 522–525.

TAYLOR, P.D. AND WILSON, M.A., 2003, Palaeoecology and evolution of marine hard substrate communities: Earth-Science Reviews, v. 62, p. 1–103.

TOONEN, R.J. AND PAWLICK, J.R., 1996, Settlement of the tube worm *Hydroides dianthus* (Polychaeta: Serpulidae): cues for gregarious settlement: Marine Biology, v. 126, p. 725–733.

TRUEMAN, A.E., 1941, The ammonite body chamber, with special reference to the buoyancy and mode of life of the living ammonite: Quarterly Journal of the Geological Society of London, v. 96, p. 339–383.

VEIGA, G.D., SPALLETTI, L.A., AND SCHWARZ, E., 2011, El Miembro Avilé de la Formación Agrio (Cretácico Temprano), *in* Leanza, H.A., Arregui, C., Carbone, O., Danieli, J.C., and Vallés, J.M. (eds.), Geología y Recursos Naturales de la Provincia del Neuquén. Relatorio

del XVIII Congreso Geológico Argentino: Asociación Geológica Argentina, Buenos Aires, p. 161–173.

VERGANI, G.D., TANKARD, A.J., BELOTTI, H.J., AND WELSINK, H.J., 1995, Tectonic evolution and paleogeography of the Neuquén Basin, Argentina: petroleum basins of South America, Memoir 62: American Association of Petroleum Geologists, Tulsa, p. 383–402.

WANI, R., KASE, T., SHIGETA, Y., AND DE OCAMPO, R., 2005, New look at ammonoid taphonomy, based on field experiments with modern chambered nautilus: Geology, v. 33, p. 849–852.

WEAVER, C.E., 1931, Paleontology of the Jurassic and Cretaceous of West Central Argentina: Memoirs of the University of Washington, v. 1, p. 1–595.

WESTERMANN, G.E.G., 1996, Ammonoid life and habitat, in Landman, N., Tanabe, K., and Davis, R.A. (eds.), Ammonoid Paleobiology: Plenum Press, New York, p. 607–707.

WESTERMANN, G.E.G., 1999, Life habits of nautiloids, in Savazzi, E. (ed.), Functional Morphology of the Invertebrate Skeleton: Wiley, Chichester, p. 263–298.

WESTERMANN, G.E.G. AND TSUJITA, C.J., 1999, Life habits of ammonoids, in Savazzi, E. (ed.), Functional Morphology of the Invertebrate Skeleton: Wiley Chichester, p. 299–325.

WIGNALL, P.B. AND SIMMS, M.J., 1990, Pseudoplankton: Palaeontology, v. 33, p. 359–378.