ENCRUSTATION IN NAUTILIDS: A CASE STUDY IN THE CRETACEOUS SPECIES *CYMATOCERAS PERSTRIATUM*, NEUQUÉN BASIN, ARGENTINA

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ABSTRACT: Despite many advances in the study of the paleoecology of nautiloids and amonoids, there is still much ground to cover. Study of their encrusters provides information on their paleoecology and taphonomy. In this work the encrusting fauna of abundant material of the nautilid *Cymatoceras perstriatum* (Steuer) is statistically and taxonomically analyzed in order to infer paleoecological and taphonomic features of the fossil organism. The available material of *C. perstriatum* consists mainly of phragmocone fragments, with rare cases in which the body chamber was preserved. Nine encrusting taxa, evenly distributed across the nautilid shell (cementing bivalves, serpulids, sabellids, cyclostome bryozoans, and agglutinated foraminifers), were observed in and on *C. perstriatum*. Of these taxa, oysters are dominant. Encrusters are abundant, with a mean of 12 encrusters per shell. Internal encrustation is common, especially inside the body chamber. The orientation of encrusters is variable. Intensity of encrustation varies, with some shells heavily colonized while others remained clean. The encrusting fauna is interpreted as mainly postmortem. Encrusters are distributed across the shell in a uniform way, lack particular orientation, and are common on the inside of the body chamber, suggesting that encrustation occurred both during necroplanktonic drift and as the shell rested on the sea bottom. A few encrusters were trapped between shell whorls, indicating that less extensive in vivo encrustation took place. Some differences in encrustation parameters were found among localities, corresponding to minor paleoenvironmental differences. Variable encrustation intensity suggests moderate to prolonged duration of exposure of the shells. However, those collected from an exceptional concentration at the El Salado locality were probably buried shortly after death.

INTRODUCTION

Ancient nautiloid and ammonoid shells in the geologic record exhibit a great variety of morphologies that are in many cases difficult to interpret in paleoecological terms (e.g., Jacobs and Chamberlain 1996; Westermann 1996, 1999). The shells of these organisms were commonly encrusted by a variety of epibionts that are useful in evaluating the paleoecological traits of extinct ectocochleate cephalopods. True epibionts (sensu Taylor and Wilson 2002) are those organisms attached to shells that settle on it during the life of their basibiont (the host organism; Taylor and Wilson 2002). In contrast, settlers for which the time of establishment on the host shell cannot be determined (that is, whether they settled while the basibiont was alive or after its death) are herein regarded as "encrusters." Analyses of encrusters and epibionts provide information on both the basibiont cephalopods and the encrusters themselves, allowing paleoecological inferences to be made with regard to both (i.e., Seilacher 1960, 1982; Baird et al. 1989; Schmid-Röhl and Röhl 2003; Andrew et al. 2011; Ifrim et al. 2011). Many cases of encrustation on Jurassic and Cretaceous ammonoids have been described. Criteria for differentiating in vivo and postmortem encrustation have been proposed by a number of authors (Seilacher 1982; Rakús and Žítt 1993; Lukeneder and Harzhauser 2003; Lukeneder 2008; Ifrim et al. 2011). Cases in which deformation of the shell and deviation from the normal planispiral coil were caused by encrusters provide incontrovertible evidence that encrusters on ammonoids occasionally colonized the shell while the basibiont remained alive (Checa et al. 2002; Larson 2007).

Some nautiloids and ammonoids were nektonic (though many nautilids were nektobenthic; Westermann 1999). Individual organisms could therefore have died at a variety of depths and in various parts of a basin. It is thus important to determine when encrustation took place. Settling of encrusters after the death of the ammonoid or nautiloid could have happened under environmental conditions that differed significantly from those within the normal habitat of the cephalopod. Examples of encrusted shells of extinct cephalopods are quite common in the scientific literature and include nautiloids (e.g., Henderson and McNamara 1985; Baird et al. 1989; Cichowolski et al. 2012) and, more commonly, ammonoids (e.g., Lange 1932; Seilacher 1960, 1968, 1982; Cope 1968; Riccardi 1980; Tanabe 1983; Nicosia 1986; Rakús and Žítt 1993; Checa et al. 2002; Lukeneder and Harzhauser 2003; Schmid-Röhl and Röhl 2003; Larson 2007; Lukeneder 2008; Ifrim et al. 2011). In many cases the timing of encrustation cannot be established, but in others evidence may suggest, with more or less certainty, that encrustation took place while the basibiont remained alive. Rakús and Žítt (1993) summarized the main criteria used by researchers to identify likely cases of in vivo colonization of the cephalopod shell: (1) both flanks are encrusted but the apertural area remains free of encrusters; (2) encrusters are trapped between successive whorls of the shell; (3) changes in the growth direction of encrusters are observed that may relate to the changes in shape and position of the cephalopod shell as the latter is secreted; and (4) the cephalopod "reacts" to its encrusters by developing some kind of behavior that is reflected in its shell (usually nonplanispiral coiling and other deformations; Checa et al. 2002; Larson 2007). Criteria 2 and 4 are undisputable examples of in vivo colonization of the shell, while criteria 1 and 3 need to be evaluated more carefully, since postmortem attachment during necroplanktonic drift may result in similar patterns.
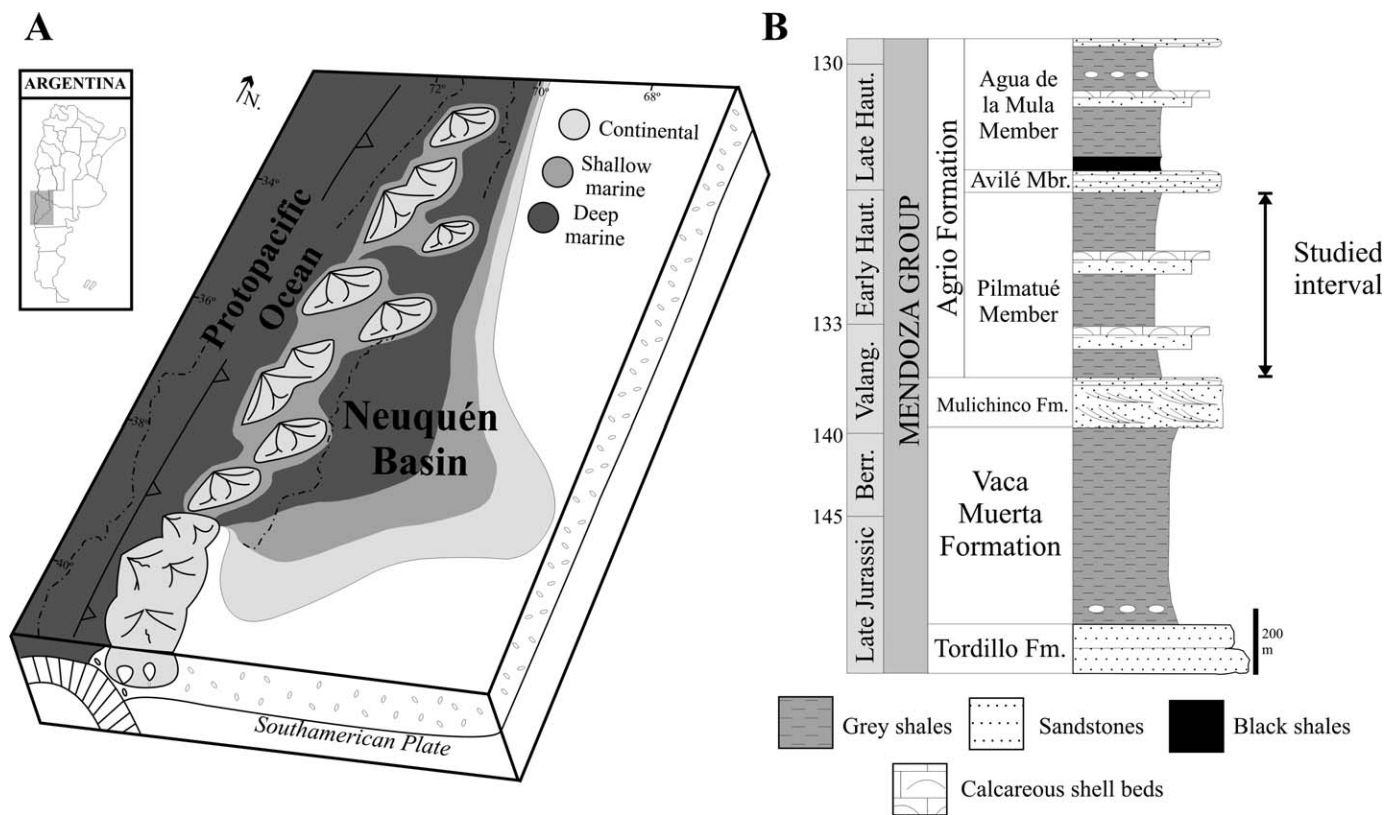
FIG. 1.—Geological setting of the study area. **A)** The Neuquén Basin during the deposition of the Pilmatué Member of the Agrio Formation (redrawn from Spalletti et al. [2008]). **B)** Generalized section of the Mendoza Group. The Pilmatué Member is indicated. Modified from Aguirre-Urreta et al. (2007). Ages, in millions of years, are indicated on the left side of the diagram.

When true *in vivo* patterns are recognized, useful paleoecologic information can be extracted from the analysis of encrusters. When postmortem encrustation predominates or obscures the original in vivo pattern, these inferences will likely be biased. However, analysis of the latter cases of mainly postmortem encrustation may yield valuable taphonomic information.

Even though extant *Nautilus* has been challenged as a reliable comparison for ammonoids (Jacobs and Landman 1993; Engeser 1996),
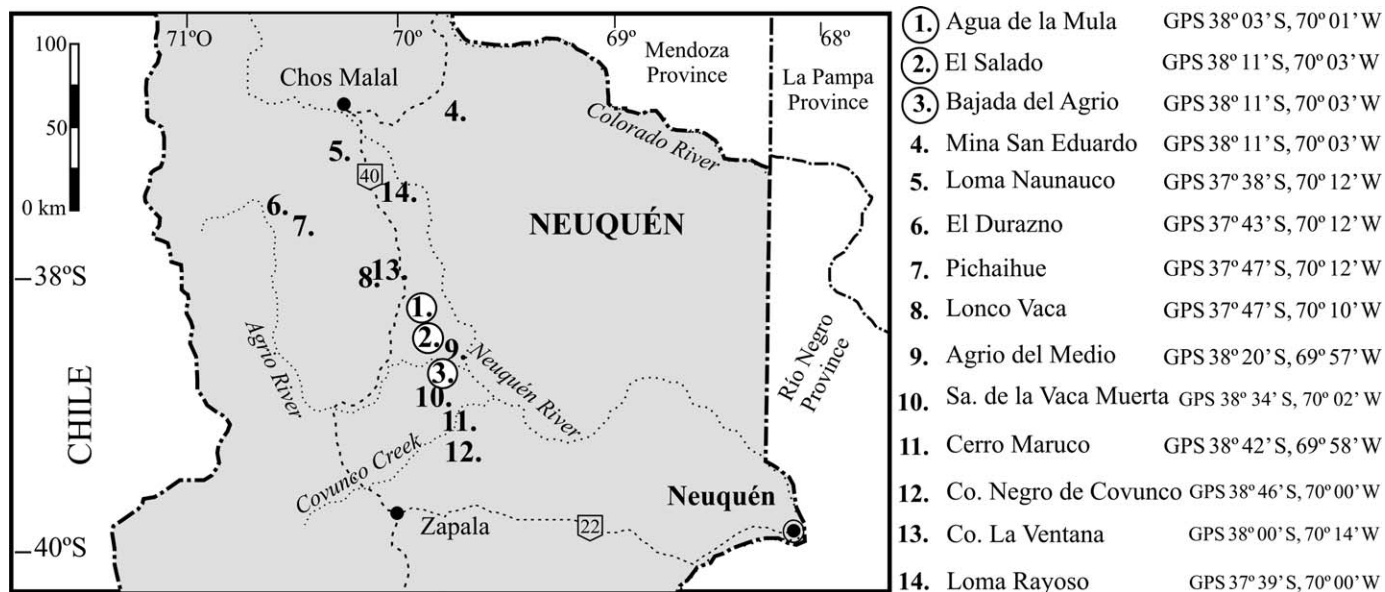

FIG. 2.—Map of Neuquén Province (*pars.*) showing localities of collection of *Cymatoceras perstriatum* shells. Main localities circled.

Age	Ammonite Zone	Subzone	Bajada del Agrio	Agua de la Mula	El Salado
Early Hauterivian	*Weavericeras vacaense*		9 (19840)	10 (19845) 1 (6899)	3 (19852)
	Hoplitocrioceras gentili	*H. gentili*	3 (19849)	6 (19836) 1 (6900)	1 (19858)
		H. giovinei			
	Holcoptychites neuquensis	*Olcostephanus (O.) laticosta*		1 (19838)	
		H. agrioensis	3 (19848)	22 (19834) 2 (6896)	4 (6895) 58 (19843) 5 (19850) 1 (19859) 1 (19874)
		H. neuquensis	1 (19855)	7 (19835) 1 (6901)	
Late late Valanginian	*Pseudofavrella angulatiformis*	*Decliveites crassicostatus*	4 (19860)	10 (19837) 3 (6897)	
		Chacantuceras ornatum			
		P. angulatiformis			

FIG. 3.—Distribution of *C. perstriatum* specimens across ammonite biozones for the late Late Valanginian–Early Hauterivian interval in the main localities. Numbers in brackets correspond to the repository numbers; the specimen numbers for each repository number can be consulted in Table 1.

it is very similar to post-Triassic coiled Nautilidae and is considered to be closely related to them (Engeser 1999). Cases of encrusted *Nautilus* shells are widely known, both in vivo and postmortem (Seilacher 1982; Landman 1983; Landman et al. 1987; Suzuki and Hayasaka 1988; Mapes et al. 2010a, 2010b). One of the most thorough studies was that by Landman et al. (1987), which revealed marked differences, both in abundance and taxonomic composition of the encrusting fauna, between animals captured alive and drifted shells. The latter were extensively encrusted by serpulids, bryozoans, oysters, algae, spirorbids, and balanids (Hamada 1964; Landman et al. 1987; Suzuki and Hayasaka 1988; Reyment 2008; Mapes et al. 2010b), while live specimens were minimally encrusted (mainly by serpulids, balanids, bryozoans, foraminifers, and scyphozoans). Both Landman et al. (1987) and Suzuki and Hayasaka (1988) noticed that most epibionts on live *Nautilus* seemed to prefer the

umbilicus. Landman et al. (1987) attributed this preference to increased currents formed near the umbilicus, while Suzuki and Hayasaka (1988) considered it to be due to the more rugose texture of the umbilicus shell surface. Drifted shells of *Nautilus* were also studied by Mapes et al. (2010a, 2010b), who found a great variety of organisms extensively encrusting both the outer and inner surfaces (within the phragmocone as well as in the body chamber) of shells lying on the sea bottom in various positions. Compared with modern nautilids, few studies have focused on encrustation of coiled fossil nautilid shells. A rare example is the work of Henderson and McNamara (1985), who found oysters, serpulids, pectinids, foraminifers, and bryozoans encrusting inner phosphatic moulds of the nautilid genus *Cimomia* Conrad and several ammonoids of Maastrichtian age. These encrusters were interpreted to have settled postmortem (Henderson and McNamara 1985).

One of the most conspicuous genera of Cretaceous nautilids is *Cymatoceras* Hyatt, which presents a worldwide distribution and a similar overall morphology to that of *Nautilus*. One of the species of this genus, *Cymatoceras perstriatum* (Steuer), is commonly and abundantly recorded in the Lower Cretaceous Agrio Formation of the Neuquén Basin (Cichowolski 2003). Since encrustation of its shells is quite common, it provides an opportunity to evaluate encrustation patterns and to compare them to those observed in *Nautilus* in order to infer paleoecologic and taphonomic features of the extinct species. In this study, abundant material of *C. perstriatum* from the Agrio Formation is examined and its encrusting fauna is described and analyzed in detail by qualitative description as well as statistical analysis.

GEOLOGICAL SETTING

The Neuquén Basin was a backarc basin located in west–central Argentina, bounded to the west by the Andean chain (Fig. 1A). The Agrio Formation is included within the Mendoza Group (Fig. 1B), a primarily marine succession of Late Jurassic to Early Cretaceous age. The base of the Agrio Formation represents a flooding event within the Mendoza Group and is divided into three members: the Lower or Pilmatué Member, the Middle or Avilé Member, and the Upper or Agua de la Mula Member (Leanza et al. 2001). The first and last are of marine origin, while the Avilé Member is composed by eolian and fluvial sandstones accumulated during a regional fall in sea level (Veiga et al. 2011). Both marine members are highly fossiliferous with abundant invertebrate faunas, composed mainly by cephalopods, bivalves, gastropods, corals, crustaceans, sponges, serpulids, and echinoids (Cichowolski 2003; Lazo et al. 2005; Lazo 2006, 2007; Aguirre-Urreta et al. 2011; Garberoglio and Lazo 2011; Cataldo and Lazo 2012). The Pilmatué and the Agua de la Mula members have both been interpreted as shallow ramps gradually deepening to the west, with sediment accumulation occurring during an interval of slow subsidence (Spalletti et al. 2011). Both units are dominated by shale in which storm-deposited sandstone and shell beds are intercalated. Transition from the inner to the outer ramp is gradual. Stratigraphic analysis of the Agrio Formation has revealed smaller flood cycles within the unit (Spalletti et al. 2011).

Figure 2 presents a list of the 14 localities in which specimens of *C. perstriatum* were collected from the Pilmatué Member, of early Valanginian to earliest Barremian age; however, in most localities, only a few specimens were recovered, rarely exceeding five shells (Fig. 3). Three localities account for the largest collection of the studied shells (at least 10 specimens collected): Agua de la Mula (69 specimens), Bajada del Agrio (20 specimens), and El Salado (78 specimens; see Fig. 3). These three localities are referred to herein as the main localities. Nautilids from these localities were collected exclusively from shell beds and sandstone beds interpreted as proximal to distal tempestites (Cichowolski and Aguirre-Urreta 2005), which are intercalated within gray shale beds. Although *C. perstriatum* occurs throughout the Agrio Formation, it is most abundant in the

TABLE 1.— *Repository numbers of* Cymatoceras perstriatum.

Repository no.	Specimen nos.	Locality
MOZ 6895	1,5,12,13	El Salado
MOZ 6896	5,6	Agua de la Mula
MOZ 6897	1–3	Agua de la Mula
MOZ 6899-6901	——	Agua de la Mula
CPBA 18028	——	Bajada del Agrio
CPBA 18293	1,2	Cerro La Ventana
CPBA 18377.6	——	Agua de la Mula
CPBA 19834	1,2a,2b,4,5,6,9,10,12,14–18, 22,25–27,30,31,35,36	Agua de la Mula
CPBA 19835	1–3,5–8	Agua de la Mula
CPBA 19836	1,4–8	Agua de la Mula
CPBA 19837	1,3–8,10–12	Agua de la Mula
CPBA 19838	——	Agua de la Mula
CPBA 19839	1–4	Lonco Vaca
CPBA 19840	2,6,7,10,11,14–17	Bajada del Agrio
CPBA 19842	2	Pichaihue
CPBA 19843	2–8,10–20,22,23,25,27– 35,37,39,41–48,50–55,57– 64,66,67	El Salado
CPBA 19844		Bajada del Agrio
CPBA 19845	1a,1b,3–7a,7b,9,10	Agua de la Mula
CPBA 19846	——	El Salado
CPBA 19847	——	El Durazno
CPBA 19848	1,3,4	Bajada del Agrio
CPBA 19849	1–3	Bajada del Agrio
CPBA 19850	4–6,8,9	El Salado
CPBA 19852	1–3	El Salado
CPBA 19854	1–4	Agua de la Mula
CPBA 19855	——	Bajada del Agrio
CPBA 19857	1,2,5	Mina San Eduardo
CPBA 19858	——	El Salado
CPBA 19859	1	El Salado
CPBA 19860	1–4	Bajada del Agrio
CPBA 19867	1,2	Cerro Negro
CPBA 19868	1,2	Mina San Eduardo
CPBA 19871	——	Pichaihue
CPBA 19872	1–3	Cerro Maruco
CPBA 19874	——	El Salado
CPBA 19875	——	Naunauco
CPBA 19876	3,5,7,8	Agrio del Medio
CPBA 19878	1,2	El Salado
CPBA 20177	——	Pichaihue
CPBA 20178	1	Loma Rayoso
CPBA 20180	——	Agua de la Mula
CPBA 19853	1	Sierra de la Vaca Muerta
CPBA 19870	1–4	Pichaihue

Pilmatué Member, especially within early Hauterivian–aged sediments (*Holchoptychites agrioensis* Subzone, see Fig. 3).

The Agua de la Mula locality is situated in the central zone of Neuquén Province (GPS 38°03′S, 70°01′W). It is accessed via National Road 40 by taking a lateral road 80 km south of Chos Malal city, in the northern sector of the El Salado Cordillera. A section was illustrated by Lazo et al. (2005), who interpreted the Pilmatué Member at this locality as outer and middle ramp, with little representation of the inner ramp.

The El Salado locality (GPS 38°11′S, 70°03′W) is also in Central Neuquén, east of National Road 40 in the Agua Amarga region, 15 km south of Agua de la Mula (Fig. 2). Lazo (2006, 2007) interpreted the depositional environment to be similar to that at Agua de la Mula. Most nautilids from El Salado were found within a single layer, an exceptional accumulation within the early Hauterivian *H. agrioensis* Subzone (see Cichowolski et al. 2012).

Bajada del Agrio (central Neuquén) is located south–southwest from Bajada del Agrio town, along the southern margin of the Agrio River. It can be accessed by Provincial Road 10, 6 km south–southwest from the town (GPS 38°27′4.78″S, 70°4′41.26″W). The Pilmatué Member is thinner

Step 1: Mapping   Step 2: Shell zonation

Specimen CPBA 19840.16   Scheme of CPBA 19840.16   Previously defined shell zones are
Right lateral view   superposed to the scheme of CPBA
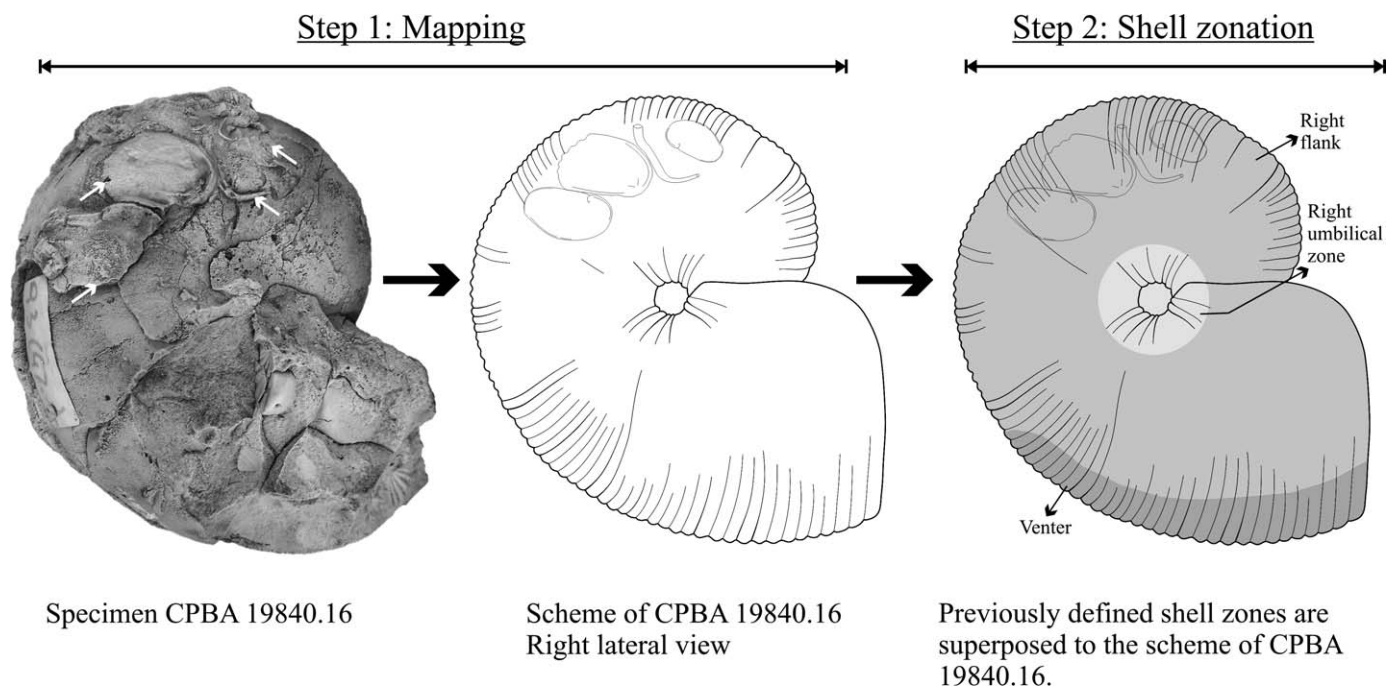19840.16.

FIG. 4.—Methodology for mapping encrusters on *C. perstriatum* shells. In Step 1, position, orientation, and relative size of encrusters are registered on each examined shell of *C. perstriatum*. Since CPBA 19840.6 presents no further encrusters, the schemes of the other views are left blank. Step 2 was done by superimposing an acetate sheet with the shell zones drawn on it onto the drawings of the nautilid shell: the zone of fixation of each encruster was recorded and the information was statistically processed.

here than at other localities and is the most proximal of the three main localities, with evidence of salinity fluctuations and the greatest benthic faunal complexity and diversity (Lazo 2006, 2007). The depositional environment is interpreted as moderate- to high-energy sandy shoreface (Lazo 2006).

Analysis of ammonite faunas has resulted in a solid biostratigraphic framework for the whole Agrio Formation (e.g., Aguirre-Urreta and Rawson 2003, 2010, 2012), which facilitated assignment of the study material to the late Valanginian to early Hauterivian.

MATERIALS AND METHODS

A detailed revision of the taxonomy of *C. perstriatum* as well as a full description can be found in Cichowolski (2003). The overall morphology of *C. perstriatum* is close to that of *Nautilus*, although it is commonly larger, with a much more inflated shell. Materials discussed herein (Table 1) are deposited either in the Museum of Olsacher in Zapala (MOZ) or in the Área de Paleontología, Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas y Naturales (CPBA). Decimals in repository numbers indicate multiple specimens collected from a single bed.

Figure 3 presents a list of materials from the main localities only, showing their distribution across ammonite biozones (see Aguirre-Urreta and Rawson 2010). Sampled biozones provide a rather uniform number of shells, with the exception of higher numbers collected from the early Hauterivian *H. agrioensis* Subzone. Material for which biozone assignment was not possible is not listed in this figure.

The high inflation and brevidomic body chamber of *C. perstriatum* are not indicative of a swift swimming style (see Westermann 1996). However, according to Westermann (1999), these types of shells are highly stable and capable of forward and backward swimming and are often interpreted to reflect a nektobenthic habit in which defense was

favored over speed. Thus, Lazo et al. (2005) have interpreted *C. perstriatum* as a nektobenthic scavenger.

Although extant *Nautilus* is most commonly found inhabiting depths of 50 to 500 m in the Indo-Pacific region (Saunders and Ward 1987), many Cretaceous nautilids may have inhabited shallower waters, as suggested by their shell and siphuncle structure, shell thickness, and ornamentation (up to 100 m deep; Westermann 1999; Mutvei et al. 2011). This was likely the case for *C. perstriatum* as well, since the Pilmatué Member of the Agrio Formation has been interpreted to occur in a shallow ramp setting. Supporting a shallow marine habitat, Cichowolski et al. (2012) calculated the Septal Strength Index (see Westermann 1973) on two specimens, obtaining an implosion depth of approximately 350 m. Correcting this value by the safety factor between maximum habit and implosion depth of Westermann (1999) results in a maximum habitat depth of 175 m. Both values exceed by far the likely depth of the Pilmatué Member.

Juvenile *Nautilus* are known to hatch in shallower, warmer water than is associated with the adult habitat and later migrate to deeper, colder environments (Landman et al. 1994; Chirat and Rioult 1998). This migration is not reflected in the isotopic composition of Cretaceous nautilid shells (Landman et al. 1994), in agreement with a life-long shallow habitat preference.

Mapping of Encrusters and Statistical Analysis

A total of 200 shells in different states of preservation were observed under a binocular microscope and with the naked eye. Each nautilid shell was drawn in as many views as required, and the location, relative size, relative position, orientation, and completeness of each encruster were recorded (Fig. 4). In this way all shells were mapped for encrusters. The drawings of the nautilid shells were of equal size in order to standardize these observations. Since the *C. perstriatum* shell is markedly inflated, some minor errors resulted from the transfer to a two-dimensional
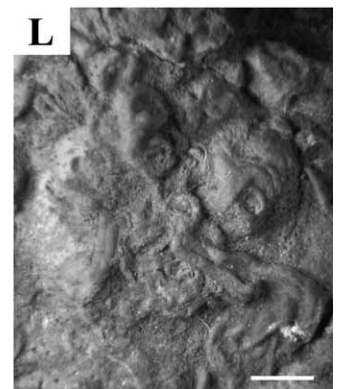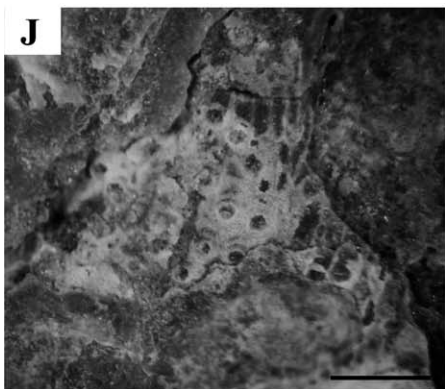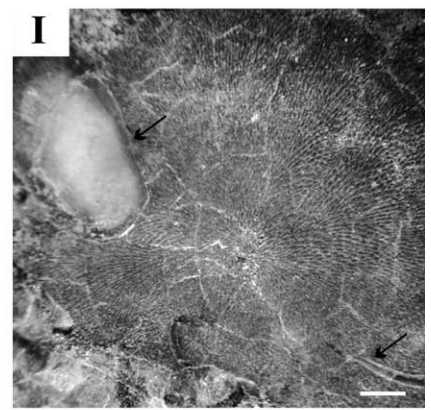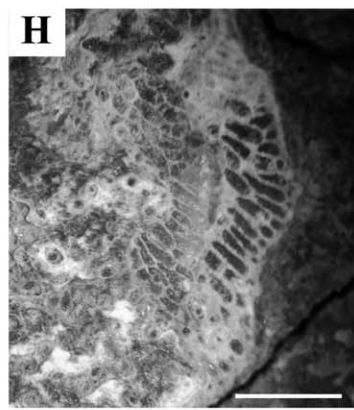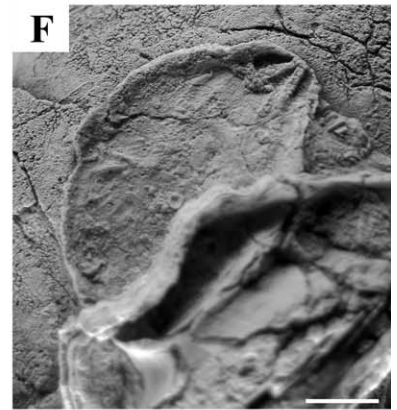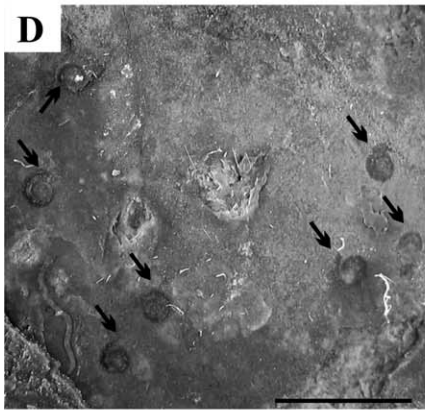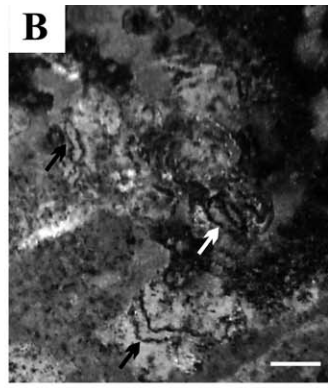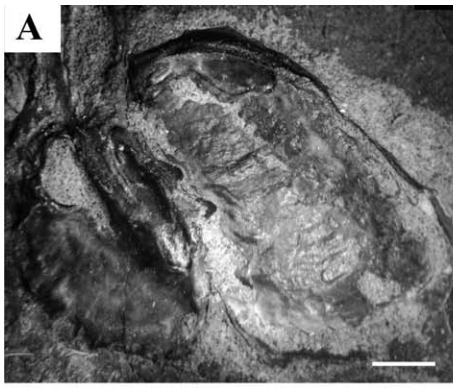
drawing; however, the use of photographs for mapping would have led to the same errors.

The shell of *C. perstriatum* was artificially divided into zones (Fig. 4), with the purpose of comparing the state of encrustation among them. This shell zonation is based on the work of Landman et al. (1987), in which *Nautilus* shells were differentiated into an umbilical zone, comprising approximately 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). While Landman et al. (1987) did not specify why they divided the shell in this manner, it is likely that they considered the umbilicus (a depressed area of the shell) to represent a different pattern of water circulation that could have a different effect on encrusters, in comparison to the flatter shell of the flanks. Indeed, they concluded that the umbilicus was preferred by some encrusters (Landman et al. 1987), and, thus, this separation of the shell was used in the present study. A ventral zone was also differentiated herein in order to evaluate whether there was a significant decrease in encrustation on the venter. This additional zone was deemed necessary to assess if encrusters avoided that area as a result of a nektobenthic habit of the host organism (i.e., due to its frequent adjacency to the substrate surface). In cases in which an encruster was found crossing the boundary between shell zones, it was counted as belonging to the zone in which the attachment took place. If this could not be determined, these encrusters were excluded from the mapping analysis. The orientation of encrusters was qualitatively evaluated and described.

Incomplete shell preservation likely resulted in underestimation of encrustation, since it is impossible to know whether the missing parts of the nautilid shells were encrusted or not. Most of the studied nautilids lack about 50% or more of the shell, mainly as a result of dissolution but also because of breakage. In some specimens the outer layer of the shell was lacking, and thus all external encrusters were lost. Some specimens from El Salado also presented wear facets, as described by Fernández-López (1997). Body chambers were most commonly absent or partially broken, and while encrusters, which are mainly calcitic, often ''protect'' the aragonitic cephalopod shell from dissolution, it is impossible to be certain that all encrusters were preserved and that only uncovered parts of the shell were dissolved. While the lack of part of these shells is problematic, it allowed for examination of encrusters attached to the inside of the shell within the inner moulds, which would otherwise have been unnoticed. While it is impossible to know if specimens in which the shell was preserved are also encrusted on the inside, at the same time it is impossible to know if internal moulds were also encrusted on the outside of the shell.

Identification of internal encrusters could only be made to higher taxonomic levels since only their undersurface was visible. Observation of encrusters trapped between whorls of the nautilid shell was made by means of polished sections and thin sections of a few nautilid shells. This includes two polished sections each from Agua de la Mula (CPBA 19834.35, 19836.9) and El Salado (CPBA 19834.42, 19843.67) and thin petrographic slides from eight different specimens (slide numbers

37482–37487, five specimens from Agua de la Mula, one from Bajada del Agrio, one from El Salado, and one from Pichaihue).

All figured specimens of *C. perstriatum* were coated with ammonium chloride, except for those inner moulds in which encrusters had attached to the inside of the phragmocone and the body chamber.

Count data (number of epibionts in one shell or shell area) was preferred over areal coverage since the great majority of the encrusting fauna studied here are composed of solitary organisms, which often reach a similar maximum size within a species. While areal coverage focuses on the intensity of utilization of available space, the objective herein is to analyze the distribution of encrusters across the shell. Areal coverage does not directly reflect abundance of each taxon and may underestimate the occurrence of small and solitary organisms (Lescinsky 1997), which predominate in the study material. Count data have, however, some drawbacks as well, such as the necessity to individualize colonies or the impossibility of counting all foraminifers (because of aggregation of individuals and very poor preservation). Foraminifers were accounted for as present or absent from shells. Foraminifers are not a main component of the encrusting fauna, though, so this likely caused minimal bias.

The total abundances of encrusters and of each encrusting taxon were calculated in both absolute and percentage values. The mean of encrusters per nautilid shell was calculated for all the shells and for each subgroup of shells from the main localities. The incidence of encrustation, considered to be the proportion of shells encrusted (by any and by each encruster taxon individually), was also calculated for all 200 *C. perstriatum* shells and then separately for those from the main localities. Likewise, incidences of internal, external, and both internal and external encrustation simultaneously occurring on shells were calculated. For those cases in which internal encrustation was present, location within the phragmocone or the body chamber was noted.

The general state of preservation of encrusted *C. perstriatum* shells was observed. Since most are mainly internal moulds, features like corrasion and fragmentation could seldom be estimated. Hence, five overall preservational categories were defined, as follows: (1) isolated phragmocone chambers; (2) incomplete phragmocones (two or [usually] more phragmocone chambers still in contact with each other but clearly lacking more chambers); (3) isolated body chambers (body chambers to which no phragmocone chambers have remained attached); (4) incomplete phragmocones with remains of the body chamber (body chambers attached to part of the phragmocone, some chambers of which are missing); and (5) complete phragmocones with remains of the body chamber. Percentages of each category were calculated.

Overgrowth among encrusters was accounted for by identifying pairs of interactions and the outcome of the putative interaction (overgrowth of encruster A by encruster B, the opposite, or a ''tie'').

An analysis of deviance (see a similar application of this method in Everitt and Hothorn [2006]) was carried out in order to compare the mean of encrusters per shell among the main localities. The incidence of internal and external encrustation was compared among the main localities as well by means of a χ^2 test.

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FIG. 5.—Encrusters on *C. perstriatum*. **A, C)** *Amphidonte* (*Ceratostreon*) sp. encrusting specimens CPBA 19836.4 and 19849.1, respectively. **A)** Articulated specimen (right) and a left valve (left). In **C,** chomatas along the margin of a left valve. Notice the smooth tubes of *Parsimonia antiquata* below. **B)** *Tolypammina vagans* in specimen MOZ 6896.1 (internal mould). The outline of the foraminifer shells can be observed. **D)** Spirorbids in specimen CPBA 19837.8. The underside of the small, planispiral tubes is visible within an internal mould of the nautilid. Notice the variable coiling direction. **E, G)** *Placostegus* cf. *conchophilus* encrusting CPBA 19843.10 and 19834.15, respectively. Worn tubes with initial planispiral coiling. Notice larger size in comparison with spirorbids. **F)** *Plicatula* sp. on CPBA 19867.1, cemented right valve and typical plicatulid hinge. **H–J)** '*Berenicea*' sp. In **H,** colony in CPBA 19840.17, partially covered by an oyster to the left. In **I,** the underside of a colony in an internal mould of *C. perstriatum* is observed; an oyster to the left and a small serpulid to the right, which were overgrown by the bryozoan, are arrowed (CPBA 6896.3). In **J,** zooecia and zoecial openings in the same specimen as in **H. K, L)** *Glomerula* cf. *serpentina*. **K)** On specimen CPBA 19835.7. Typically thin and very convoluted tube. **L)** On specimen 19849.1, tube showing typical coils and spirals. Scale bars: **A, C–G:** 5 mm; **B, H–J, K, L:** 2 mm.
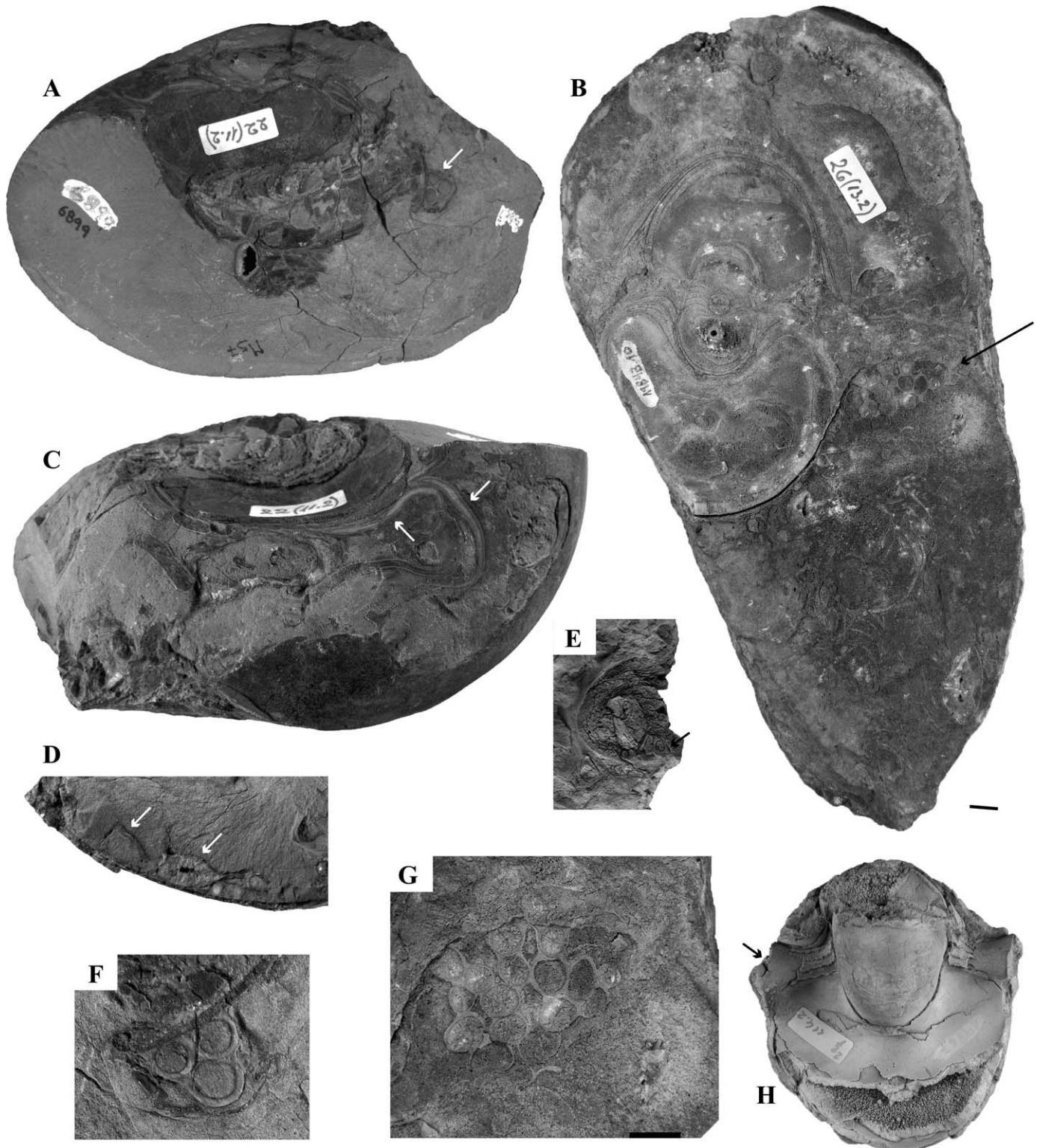
Fɪɢ. 6.—Internal moulds of *C. perstriatum* containing encrusting serpulids and oysters. A, C, D, F) MOZ 6899 (from Agua de la Mula), fragment of the internal mould of a body chamber. **A)** Frontal view. A cluster of three serpulids is arrowed. **C)** Upper view, showing serpulid tubes formerly attached to the roof of the body chamber. Darkest gray areas are remains of the nautilid's shell. **D)** Oysters in left section of the specimen (arrowed) were empty at the moment of burial. **F)** Detail of cluster in A. B, H) CPBA 19843.10 (El Salado), fragment of phragmocone with remains of the body chamber. **B)** Frontal view with right truncation facet. A cluster of over 15 serpulids is arrowed. **G)** Detail of serpulid cluster. **H)** CPBA 19867.2 (Cerro Negro de Covunco), fragment of an inner whorl of the phragmocone (see umbilicus). **E)** Right view, showing a serpulid attached to its anterior side. **G)** General view. Scale bar: 1 cm (A–F, G); 5 mm (H).

TABLE 2.—*Incidence of absolute and internal, external, or internal and external encrustation on* Cymatoceras perstriatum *shells.*

Encrustation	No. of shells	Percentage
Absent	79	39.5
Present	121	60.5
External	78	64.46
Internal	13	10.74
Both	30	24.80
Total	200	100

TABLE 3.—*Distribution of encrusters situated on the inside of shells, including both cases of only internal encrustation and simultaneous internal and external encrustation.*

Encrustation	Location	No. of shells	Percentage
Internal	Body chamber	32	72.73
	Phragmocone	10	22.73
	Both	2	4.54

The analysis of the distribution of encrusters across shell zones defined for *C. perstriatum* was done with a generalized linear mixed model (GLMM) (for a general review of GLMMs and their use in ecology, see Hedeker 2005; Bolker et al. 2008). For this analysis, only six shells (CPBA 6896.5, 19834.5, 19834.7, 19834.10, 19834.16, and 19859.14) could be included, since it was necessary that specimens be both in the best condition possible and lack internal encrusters, which are undoubtedly postmortem. None of the specimens, however, presents the whole outer shell. Specimens for this analysis were chosen among those of the fifth preservation category. Finally, the Shannon–Wiener (H; including H_{max} as the natural logarithm of the richness; see Hammer and Harper 2006), Simpson's Dominance (see Hammer and Harper 2006), and Pielow's (H/H_{max}; Hammer and Harper 2006) diversity indices were calculated for the total of shells as well as for the main localities, along with taxonomic richness.

RESULTS

Composition of the Encrusting Fauna

Nine taxa of invertebrate encrusters (Fig. 5) were found in the study material of *C. perstriatum*. All encruster taxa share a cementing habit and are suspension feeders.

Bivalves.—Two genera were identified: the oyster *Amphidonte* (*Ceratostreon*) Bayle and the plicatulid *Plicatula* Lamarck. The first is a small (rarely longer than 3 cm) exogyrid gryphaeid, with well-developed chomatas along all margins (except for the dorsal one) and a crenulated commissure. Specimens are rarely articulated, so left valves were most commonly observed. *Amphidonte* commonly occurred in aggregates, but orientation is variable, even within clusters. This genus was globally common during the Early Cretaceous (Stenzel 1971; Cooper 1997). As adults, oysters may acquire a reclining habit, and gryphaeids were very common in fine-grained sediments of low-energy marine settings during the Mesozoic (Lewy 1976).

The genus *Plicatula* is easy to recognize as a result of its characteristic hinge. This bivalve is cemented by the right valve. In the study material the left one is commonly missing, but when present it is ornamented with thin radial ribs and subtle growth lines. Most inner details are lost as a result of corrasion. According to Kauffmann (1973), during the Cretaceous plicatulids were widespread. Extant species inhabit shallow depths, from the intertidal region to up to 140 m deep (Bernard 1983). Adults can also become free recliners (El-Hedeny et al. 2001).

Serpulids and Sabellids.—Four serpulid taxa and the sabellid taxon *Glomerula* cf. *serpentina* were found encrusting *C. perstriatum*. Serpulid taxa include a spirorbid (*Neomicrorbis?* Rovereto) and the serpulids *Mucroserpula mucroserpula* Regenhardt, *Parsimonia antiquata* (J. de C. Sowerby), and *Placostegus* cf. *conchophilus* Radwańska. All have been described in more detail in Luci et al. (2013). They are all found attached throughout their whole length, but many could have included an erect portion, since all tubes are broken at one or both ends. Aggregation is quite common, especially within nautilid body chambers where, in some cases, clusters of more than 15 tubes cemented upon each other were observed (Fig. 6B, F, G). Tubes exhibit moderate corrasion and variable breakage. Most serpulid tubes reach a length of a few centimeters. The distribution of extinct serpulid species is poorly known as a result of uneven knowledge of serpulid faunas across the world. Extant serpulids occur in all marine and marginal marine environments (ten Hove and van den Hurk 1993).

Bryozoans.—Only the widespread '*Berenicea*' Lamouroux, a cyclostome bryozoan, was found encrusting *C. perstriatum*. Colonies are usually subcircular and rather easy to individualize, with autozooecia radiating from the center. This genus is here notated in quotes since it has been deemed invalid by Taylor and Sequeiros (1982), given that the type material was lost during a fire, and there are several issues regarding its definition and subsequent taxonomic treatment. As a consequence, the name is retained for bereniciform colonies in which the gonozooids, of great taxonomic value, are not present, as is the case for the bryozoans encrusting *C. perstriatum*. Colonies are commonly corraded, with frontal walls missing.

Foraminifers.—A single species of agglutinated foraminifer, *Tolypammina vagans* (Brady), was found in the encrusting fauna. The agglutinated material was very fine grained so the shells present a smooth aspect, and even though there are more or less regular constrictions along the shell there are no true septa. These foraminifers are often aggregated and heavily corraded. Some agglutinated foraminifera taxa can tolerate salinity variations, and they can be found at a great range of depths, although they are usually more common at shallow depths (see White 2002).

Statistical Analysis

For the total of 200 shells available for study, it was found that the encrusting fauna of *C. perstriatum* was composed of the nine genera and species described above. A total of 2386 individuals (mean, 11.96 encrusters per nautilid shell) were identified on these shells. The general incidence of encrustation is moderate to high (60.5%), and while external encrustation predominates (63.64%), internal encrustation is also common. Cases of external and internal encrustation in the same basibiont shell are also quite common (Table 2). Internal encrusters are mainly concentrated in the body chamber (Table 3; Fig. 6). The highest number of encrusters found on one shell was 107. The lowest number of encrusters observed on a single shell was one.

Some polished sections of *C. perstriatum* shells revealed encrusters (oysters, serpulids, and bryozoans) trapped between successive whorls of the nautilid (Fig. 7). Of a total of 12 polished specimens and polished thin sections, only three presented encrusters (25%). Serpulids, some of which were covered by bryozoans, were most common, with only one small oyster found trapped within the nautilid shell (Fig. 7E, F). The specimen bearing the oyster is so strongly altered that it is uncertain whether the
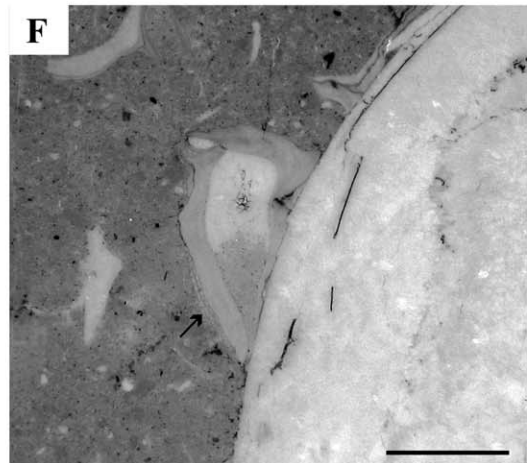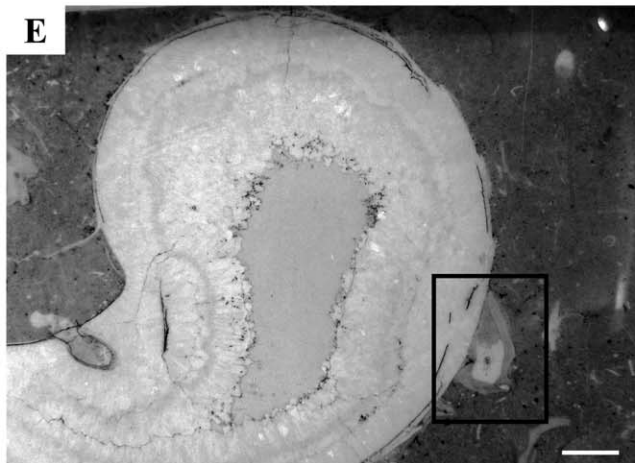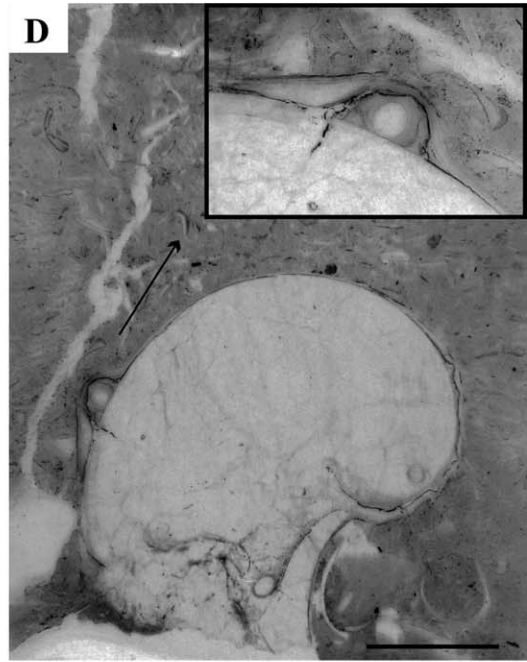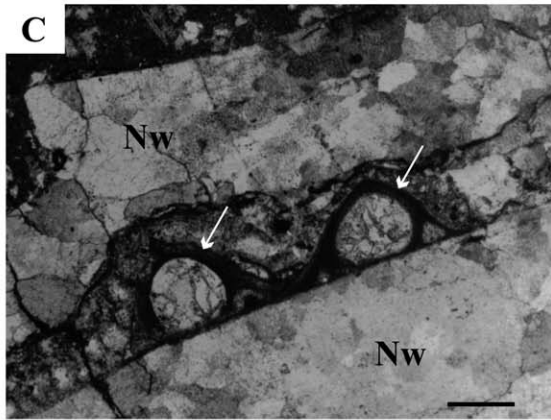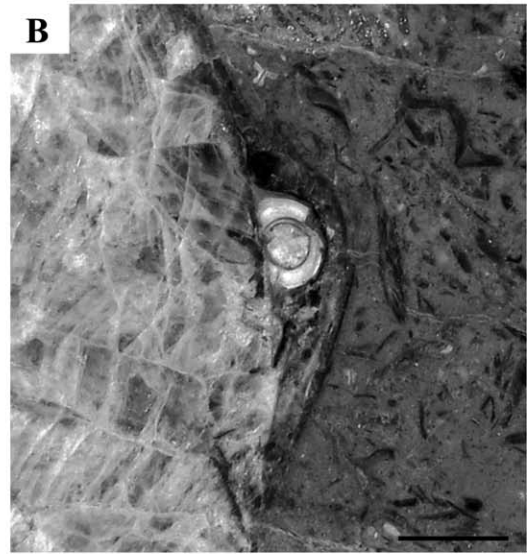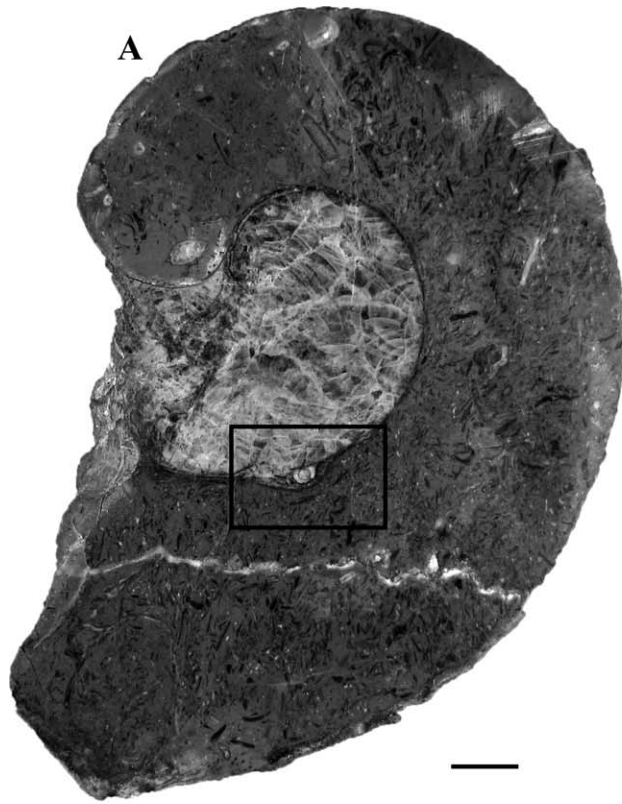
TABLE 4.—*Absolute abundance of encrusting taxa (No. of ind.), relative abundance of each (% Fauna), and number of* Cymatoceras perstriatum *shells in which a taxon was found (No. of shells). Percentage of the latter for the total shells studied is given, but total percentage and number of shells is not computed, given that some shells present more than one taxon and, thus, the sum exceeds the total of 200 shells studied.*

	Beren.	Parsim.	Mucro.	Placost.	Spiror.	Glom.	Amphi.	Plic.	Tolyp.	Total
No. of ind.	64	307	4	45	10	10	1940	6	—	2386
% Fauna	2.68	12.87	0.17	1.89	0.42	0.42	81.31	0.25	—	100
No. of shells	23	51	2	11	1	8	113	5	4	—
% Shells	19.01	42.15	1.65	9.09	0.83	6.61	93.39	4.13	3.31	—

Beren. = 'Berenicea' sp.; Parsim. = Parsimonia antiquata; Mucro. = Mucroserpula mucroserpula; Placost. = Placostegus cf. conchophilus; Spiror. = Spirorbinae; Glom. = Glomerula serpentina; Amphi. = Amphidonte (Ceratostreon) sp.; Plic. = Plicatula sp.

oyster is trapped between whorls; ignoring this uncertain encruster, the incidence is 16.67%.

Of the nine taxa represented in the encrusting fauna, the oysters are markedly dominant (81.31% of the total of encrusters), followed by the serpulid *P. antiquata* (12.87%) and the bryozoan '*Berenicea*' (2.68%). The remaining components of the fauna rarely represent more than 1% each of the total number of encrusters (Table 4). The number of nautilid shells colonized by at least one individual of a given encrusting taxon shows that some of them are rather common among shells, despite their low relative abundance, but oysters are still the most common (Table 4).

Of the encrusted shells, most are fragments of the phragmocone, followed (distantly) by complete phragmocones with part of the body chamber (Fig. 8). Intensity of encrustation on individual shells is highly variable (Fig. 9).

Six pairs of putative interactions between encrusters were observed. Table 5 shows the number of each type of interaction observed and indicates which taxon overgrew the other.

Results of the GLMM are shown in Table 6. Significant differences were not found among any of the shell zones defined for *C. perstriatum*, meaning that encrusters are evenly distributed across the shell. No zone was preferred for attachment over the others.

The taxonomic richness of the encrusting fauna is nine taxa (genera and/or species, as identified to the lowest possible rank); the Shannon–Wiener index is 0.7 (H_{max} = 2.2), while the Simpson's Dominance is 0.6. Pielow's Equitability is 0.3. Hence, the fauna is strongly dominated by a single taxon (oysters), and while several other taxa are present, they are very unequally distributed, most of them being very uncommon.

Encrusters exhibited no preferential orientation on the nautilid shells. Both bivalves and serpulids occur in multiple orientations and growth vectors, even within the same basibiont specimen. Only the body chamber serpulids were observed to be aligned relative to the major axis of the basibiont (and parallel to the sagittal plane of the shell).

Comparison Between Main Localities

The number of nautilid specimens differs among Bajada del Agrio (N = 20), El Salado (N = 78), and Agua de la Mula (N = 69). Encrusters occur mainly on the outside of the shell in the three sample subsets. Agua de la Mula has the highest values of internal encrustation (44.2%), while specimens from Bajada del Agrio have the lowest (23.1%) (Table 7). The incidence of total encrustation is lowest in El Salado (46.1%) and highest in Agua de la Mula (75.4%), although Bajada del Agrio also has high total encrustation (65%). The abundance of encrusters varies (as does the heterogeneity of encrustation; Figs. 9B–D, 10), with a mean value of encrusters per shell of 17.8 in Agua de la Mula, 10.8 in Bajada del Agrio, and 6.4 in El Salado. The maximum numbers of encrusters in one shell are 107 at Agua de la Mula, 43 at Bajada del Agrio, and 64 at El Salado. The minimum number of encrusters is one in all three localities. Overall preservation of nautilid shells varies as well (Fig. 8), with the main difference being that only fragments of phragmocones are preserved at Bajada del Agrio (hence, not figured). Taxonomic composition and richness of the encrusting fauna varies from eight taxa at Agua de la Mula to six taxa at Bajada del Agrio and to seven taxa at El Salado (Table 8; Fig. 11).

Through the analysis of deviance, significant differences were observed between the mean number of encrusters per shell on the El Salado vs. Agua de la Mula (p < 0.001); Bajada del Agrio has values intermediate to both the former and is not significantly different from either of them. χ^2 tests were also significant for the incidence of encrustation between El Salado and Agua de la Mula (p = 0.00009), being lowest in the first location. Diversity measures for the three localities are shown in Table 8; Agua de la Mula presents the greatest richness but also the most pronounced dominance. Bajada del Agrio displays the highest equitability among the main localities.

DISCUSSION

The first and most important issue that needs to be determined before any inferences can be made on the studied material is whether encrustation took place before or after death of the nautilid. In ectocochleate cephalopods, three distinct moments during which encrustation may take place can be recognized: (1) in vivo encrustation, which occurred while the basibiont was alive; (2) postmortem encrustation, which occurred after the cephalopod died and while it floated in the water column; and (3) postmortem encrustation, which occurred after the shell lost buoyancy and settled on the sea bottom. Observations made on the studied shells as well as the results of statistical analysis strongly suggest that for the most part, encrustation took place after the death of the nautilids. This is based on the following points: (1) similar observations made by other authors on live and drifted specimens of *Nautilus* and other externally shelled cephalopods, (2) absence of clearly defined encrustation patterns on the nautilid shells and of coordinated or determined orientation within conspecific encrusters with respect to the basibiont shell, (3) the elevated incidence of internal encrustation on the

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FIG. 7.—In vivo encrustation of *C. perstriatum*. **A, B)** CPBA 19834.15 (from Agua de la Mula). **A)** Polished sagittal section of the nautilid shell; a serpulid is trapped between whorls. **B)** Detail of **A. C)** Detail of a petrographic section of two serpulids covered by bryozoans, all trapped between successive whorls of the shell. **D)** CPBA 19836.10 (Agua de la Mula), serpulid between whorls in a polished section. **E, F)** CPBA 19834.37 (Agua de la Mula), oyster encrusting the external shell wall of an internal whorl. **F)** Detail showing that no shell was secreted over it, so this can't be considered to represent in vivo encrustation with certainty. A thin layer of bryozoans growing on the bivalve is arrowed. Nw = nautilid whorl wall. Scale bars: **A:** 1 cm; **B–F:** 5 mm.

Preservation of encrusted shells

All shells (N=200)   Agua de la Mula (N=69)   El Salado (N=78)
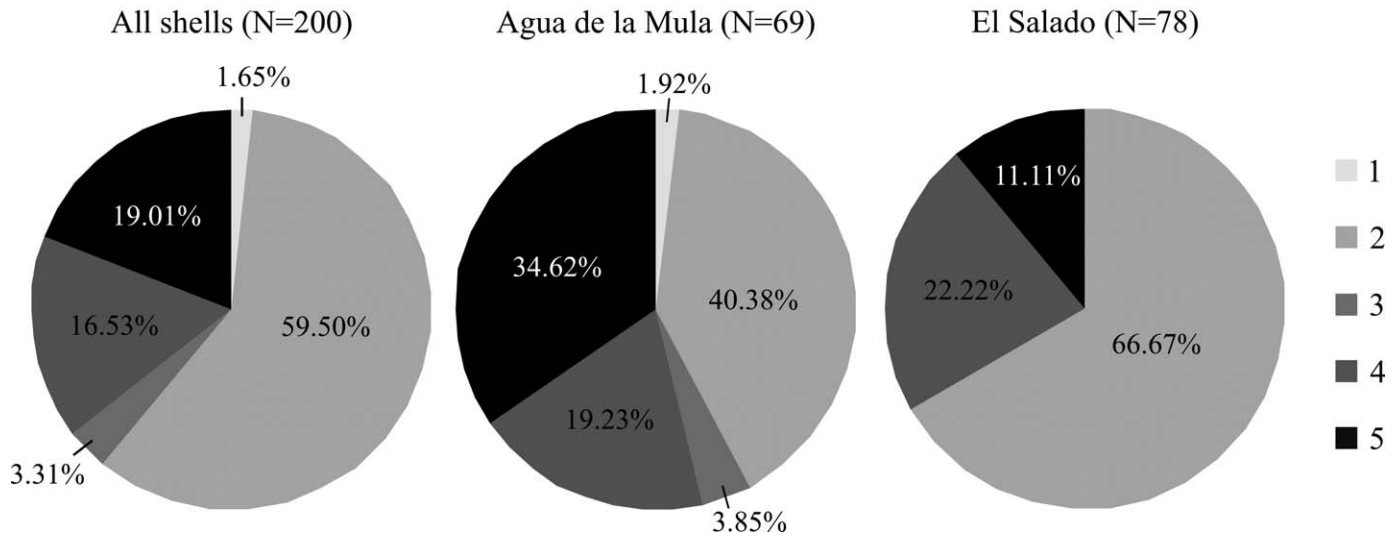

Fig. 8.—Preservation of *C. perstriatum*–encrusted shells, separated by locality. 1. Body chambers. 2. Fragments of phragmocones. 3. Isolated chambers. 4. Fragments of phragmocones with remains of the body chamber. 5. Whole phragmocones with remains of the body chamber.

studied material, and (4) the poor preservation of the great majority of the studied basibiont shells. These points are discussed individually below.

1. The exhaustive study on shell encrusters on *Nautilus* performed by Landman et al. (1987; see "Introduction") revealed marked differences, both in abundance of encrusters and in taxonomic composition of encrusting faunas, between animals captured alive and drifted shells. Taking into account that an overabundance of encrusters would likely affect the nautilid's flotability and balance, it is reasonable to assume that in vivo encrustation should ideally be kept to a minimum in ectocochleate cephalopods. This was possibly achieved by some protective strategy employed by the cephalopod to keep the shell clean, or possibly by other types of defense, such as the thick periostracum observed in *Allonautilus scrobiculatus* (Lightfoot) studied by Landman et al. (1987). This is in agreement with the contrasting encrusting features among drifted and captured specimens observed by Landman et al. (1987). In many of the specimens observed in this study, *C. perstriatum* shells present numerous encrusters. Encrustation of the internal surface is also common. Both of these observations support the interpretation that, similar to modern *Nautilus* shells, most encrustation occurs postmortem.

2. The small number of shells that could be included in the analysis of comparison of encrustation among shell zones and the overall poor state of preservation of even these specimens for this purpose (no specimens with over 50% of shell surface preserved, resulting in likely underestimation of encrustation intensity) are clearly not ideal, and, hence, results must be examined with caution. No consistent pattern of either preferred or avoided shell zones is apparent. This indicates that the whole shell was at one time or another available for encrustation and that apparently specific shell zones awarded no particular benefits or disadvantages to encrusters. In addition, no preferred orientation was observed, even within oyster clusters. If encrustation had taken place in vivo, most likely some preferential orientation, possibly related to swimming direction (rheotropic orientation; see Seilacher 1968; Landman

et al. 1987; Baird et al. 1989; Andrew et al. 2011) or to the living position of the basibiont (if encrusters settled on a fully grown animal, as described in Seilacher [1960]) or to the effort of keeping up with the growth of a juvenile basibiont (Andrew et al. 2011), would occur.

3. Although Suzuki and Hayasaka (1988) observed colonies of "*Berenicea*" attached to the inside of the body chamber in living specimens of *Nautilus* (as did Dunbar [1901]), the extensive encrustation of the body chamber in a considerable proportion of the shells of *C. perstriatum* in the study area indicates that encrusters settled after the body of *C. perstriatum* had been removed from the shell or had rotted away (e.g., Figs. 6A–C, G, 12). In some cases encrustation was observed on the outer surface of the last septum (Figs. 6A, C, 13). Colonization of phragmocone camerae probably reflects damage of the outer wall of the shell or breakage of septa while the shell was empty. The body chambers of *C. perstriatum* likely functioned as a cryptic habitat, sheltering encrusters from predators and other threats, and were widely occupied by serpulids, bryozoans, foraminifers, and, to a lesser degree, by oysters. Body chambers and phragmocones could have acted as a refuge for these encrusters, particularly if soft-bodied, rapid-growing organisms (i.e., algae, tunicates, sponges) colonized the outer part of the shell.

4. Most *C. perstriatum* shells examined are rather poorly preserved, which is consistent with some degree of exposure on the surface prior to burial. The exception is given by some well-preserved shells from El Salado that were likely buried soon after death (Cichowolski et al. 2012). According to Fernández-López (1997), abundance, size, and diversity of encrusting faunas could be directly proportional to the time of exposure of a shell. If the shell was carried across different environments, more species would have had access to it. This hypothesis is valid so long as this increase in time of exposure does not result in increased alteration and destruction of the basibiont shell, which is also likely. Both increased encrustation and increased shell degradation would greatly depend on various environmental parameters. Rodland et al. (2006) estimated the resolution of an encrusting community on extant
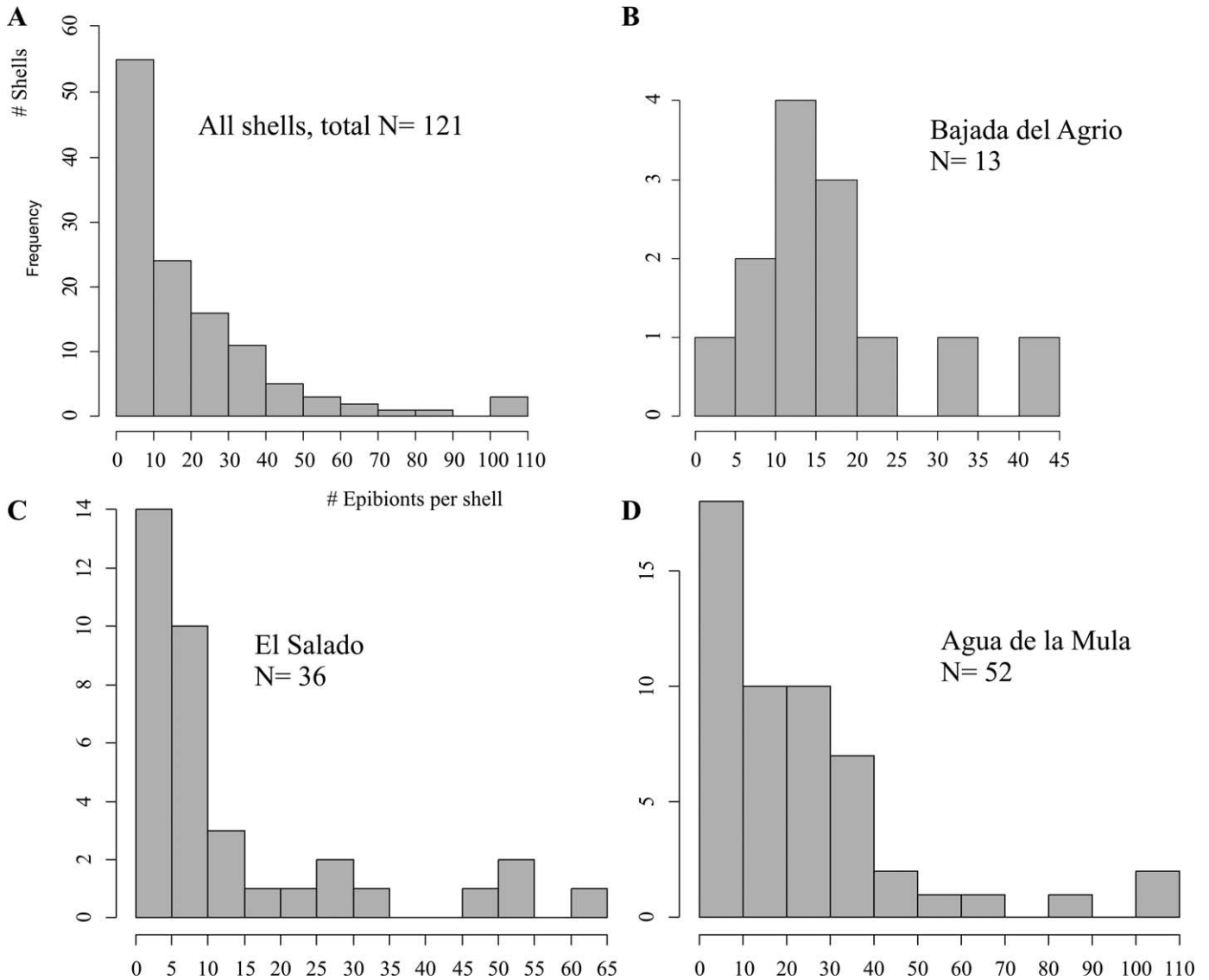
FIG. 9.—Histograms showing the number of encrusters per *C. perstriatum* shell. **A)** Total encrusted shells. **B–D)** Main localities. **B)** Bajada del Agrio. **C)** El Salado. **D)** Agua de la Mula.

brachiopods at weeks to decades. Mapes et al. (2010a) dated recent shells of *Nautilus* (using $^{210}Pb/^{226}Ra$ radionuclide analyses) recovered from various depths within the photic zone, obtaining ages from 12 to 40 years. Assuming equal sedimentation rates, a larger shell such as *C. perstriatum* would take longer to bury than would either *Nautilus* or brachiopods. The *C. perstriatum* shells could have remained available for encrustation for a considerable period of time. In addition, considering that large portions of the shell are commonly missing, the values obtained for incidence and intensity of encrustation in the studied material are minimum estimates.

All of these factors indicate that most of the encrusters observed on *C. perstriatum* fossils settled after the organism's death. However, a few shells in the study material preserve clear evidence of some in vivo colonization (i.e., encrusters trapped between whorls of *C. perstriatum,* as observed in polished sections). The frequency of this in vivo colonization is hard to estimate, since it would require sectioning the whole shell of several complete specimens in order to cover as much as the shell's surface as possible. The limited data available at present reveal a rather low incidence and small number of encrusters (serpulids, bryozoans, and small oysters) involved in in vivo encrustation. Successful overgrowth of encrusters in the instances recorded herein indicates that *C. perstriatum* could easily have covered small encrusters without suffering major shell deformation. This could be due to the large size attained by most *C. perstriatum* with respect to their epibionts, in comparison to the strongly deformed small ammonites studied by Checa et al. (2002) and Larson (2007).

TABLE 5.— *Pairs of putative interactions observed among encrusting taxa.*

Pairs of interaction (A–B)	No. of occurrences	"Won" by "A" (No.)	"Won" by "B" (No.)
Amphidonte–Parsimonia	3	2	1
Amphidonte–Berenicea	3	0	3
Amphidonte–Glomerula	3	0	3
Amphidonte–Mucroserpula	1	0	1
Parsimonia–Berenicea	1	1	0
Placostegus–Berenicea	1	1	0

TABLE 6.—*Results of the mapping of the six specimens included in the GLMM analysis.*

CPBA	Area	*P. antiquata*	*Amphidonte* (*C.*)	'*Berenicea*' sp.
6896.5	RU	0	0	0
	RF	0	0	0
	LU	0	1	0
	LF	0	2	0
	Ve	0	0	0
19834.5	RU	0	0	0
	RF	0	6	0
	LU	0	0	0
	LF	0	2	0
	Ve	0	0	0
19834.7	RU	0	12	0
	RF	0	1	0
	LU	0	0	0
	LF	0	2	0
	Ve	0	9	0
19834.10	RU	0	3	0
	RF	0	7	2
	LU	0	3	1
	LF	0	2	0
	Ve	0	0	0
19834.16	RU	0	0	0
	RF	0	1	0
	LU	0	0	0
	LF	0	0	0
	Ve	2	8	0
19859.14	RU	0	0	0
	RF	0	4	0
	LU	0	3	0
	LF	0	3	0
	Ve	0	0	0

The Issue of Necroplanktonic Drifting

While it is clear that most of the encrusters observed on *C. perstriatum* are of postmortem origin, the questions of the timing of the encrustation remain, specifically if it happened during shell drift or after sinking to the seafloor. The shells of *C. perstriatum* studied probably did float after death, similar to modern nautilids, instead of immediately sinking in the place where death occurred, considering both their morphological characteristics and the likely depth of the habitat of *C. perstriatum* (see "Materials and Methods"; Chamberlain et al. 1981; Cichowolski and Aguirre-Urreta 2005). The positive buoyancy of cephalopod shells after death was likely common, with a high likelihood of postmortem drift (Wani et al. 2005; Reyment 2008). This would have been particularly true for larger shells (Wani et al. 2005) and even more so for shallow-water inhabitants than for deep-water ones (Chamberlain et al. 1981), as is the case of the nautilid studied here.

House (1987) reported *Nautilus* shells that drifted 1000 km, presumably over several years. Donovan (1989) and Reyment (2008) also inferred that shells could drift considerable distances over months to years. Hence, the issue arises of whether *C. perstriatum* was preserved within the limits of its true habitat. While all cephalopods undergo some degree of transport, the association of *C. perstriatum* and tempestites is strong (Lazo et al. 2005). Since the Pilmatué Member was deposited in the Neuquén Basin, which was an embayment during the Cretaceous, open to the ocean only on the west, where it was partially constrained by an active volcanic arc, it is likely that the organisms lived, died, and were deposited/redeposited during storms within the basin.

It is likely, then, that those *C. perstriatum* shells that were undamaged at the time of death floated for some time. Under these circumstances the whole surface of the shell, both outer and, after removal of the soft parts, inner, would have been available for colonization. This is

TABLE 7.—*Distribution of encrusters situated on the inside of shells, including cases of only internal encrustation and simultaneous internal and external encrustation, for the three main localities of collection of* Cymatoceras perstriatum.

	Agua de la Mula		El Salado		Bajada del Agrio	
Encrustation	No. of shells	%	No. of shells	%	No. of shells	%
Internal						
B. cha.	17	73.91	12	92.31	0	
Phrag.	5	21.71	1	7.69	3	100
Both	1	4.35	0		0	

consistent with the homogeneous distribution of encrusters across the shell's outer zones.

The nautilid shells eventually sank, either as a result of shell damage or through the weight of an abundance of encrusters. *C. perstriatum* shells were found solely in recumbent positions; however, no preferred orientation was observed (Cichowolski et al. 2012). As they rested on the seafloor, these globose shells provided large and prominent benthic islands, with the side facing the water column elevated above the adjacent sediment surface, providing hard substrates upon which encrusters settled. However, given their morphology, these shells were probably quite unstable, rocking with water movement (since the Pilmatué Member was a shallow ramp with wave action), and were easily reoriented on the seafloor. This resulted in the occasional death of some encrusters as they were suddenly pressed against the seafloor.

Although *C. perstriatum* was likely encrusted both during a phase of nekroplanktic drift and later, after it sank to the bottom, it is not clear how much encrustation occurred in each phase. As the shell floated in the water column, both flanks and the venter were all available for encrustation. In general, after the shell sank only the upper flank was available for encrustation. In Cretaceous material from the Italian dolomites, two pulses of colonization involving different kinds of encrusters are apparent on flat ammonoids that settled in calm depositional settings with minimal chance of overturning (Lukeneder 2008). In contrast, the dynamic shallow setting in which *C. perstriatum* shells were deposited likely saw frequent shallow overturning, and, thus, both sides of the shell could be encrusted, albeit not simultaneously. Encrusters that colonized floating shells were overprinted and obscured by colonizers that settled after the shell had sunk. Thus, phases of colonization on *C. perstriatum* shells are undistinguishable.

Dynamics of the Encrusting Fauna

The encrusting fauna of *C. perstriatum* is strongly dominated by a single oyster taxon. None of the other components of the fauna are comparable in absolute numbers to *Amphidonte* (*Ceratostreon*). Serpulids are more diverse, but with the exception of *Parsimonia antiquata*, which follows the oyster in abundance (though in a distant second place), all serpulid taxa are quite rare, sometimes occurring on a single shell, as is the case of the spirorbids. The cyclostome '*Berenicea*,' third in

TABLE 8.—*Diversity indices calculated for the subsets samples of* Cymatoceras perstriatum *from the main localities.*

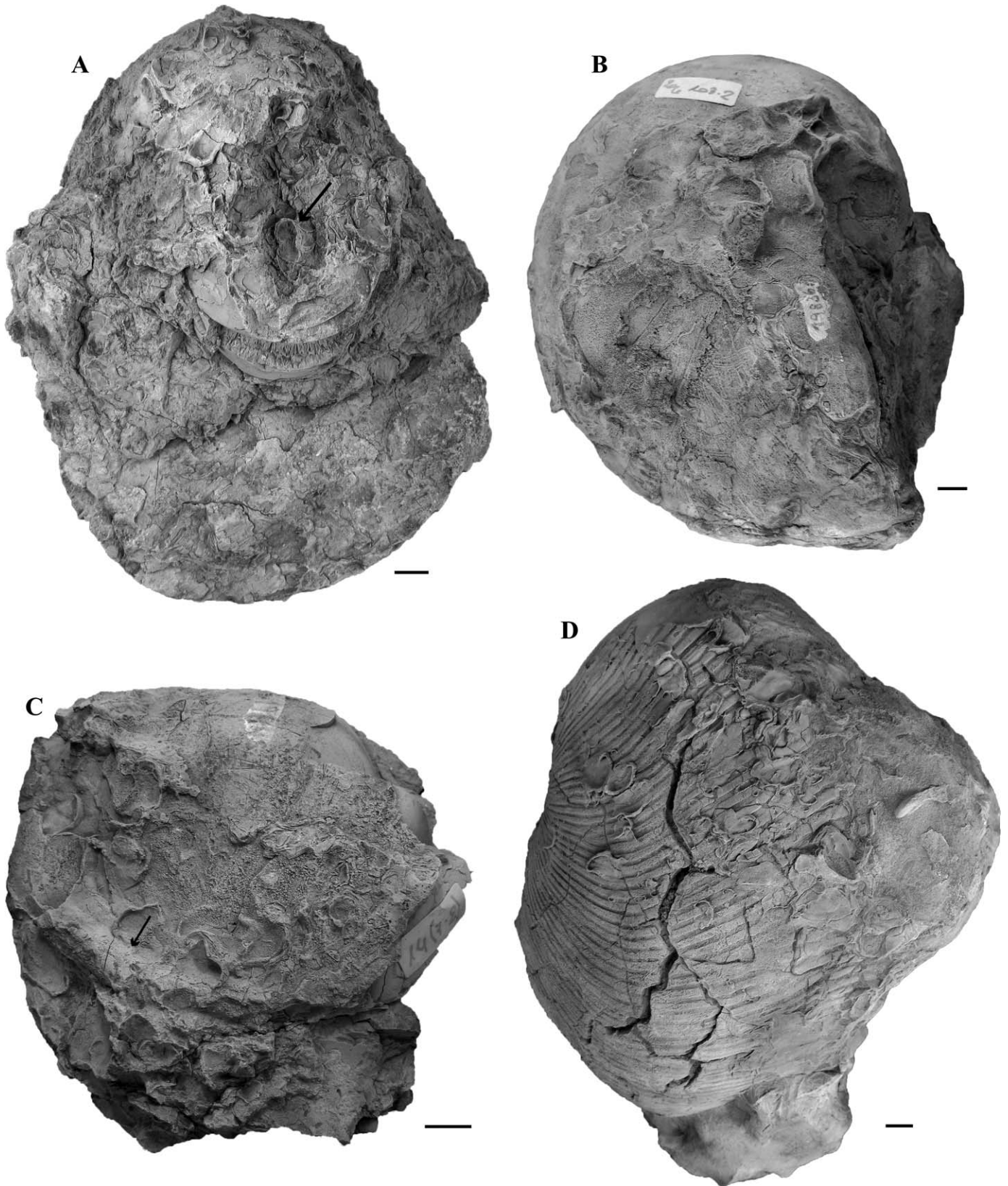|	Shannon's H	H_{max}	Simpson (Dm)	Pielow's Equit.	Richness
Agua de la Mula	0.69	2.08	0.67	0.33	8
El Salado	0.74	1.95	0.59	0.38	7
Bajada del Agrio	0.87	1.79	0.58	0.48	6

FIG. 10.—External encrustation on *C. perstriatum*. **A)** CPBA 19837.10, phragmocone with part of the body chamber; the frontal part of the phragmocone is partially collapsed. Numerous oysters and bryozoans cover the shell. **B)** CPBA 19836.4 in right lateral view, showing encruster oysters on the umbilicus. **C)** CPBA 19845.4, ventral view of a specimen heavily covered by oysters; the arrow points to a serpulid partially overgrown by these bivalves. The outline of the serpulid tube is visible below the oysters. **D)** CPBA 20180, body chamber preserving the original ribs on the shell. To the right of the picture some concretions formed attached to the specimen. Numerous small oysters encrust the outside of the body chamber. All from Agua de la Mula. Scale bars: 1 cm.
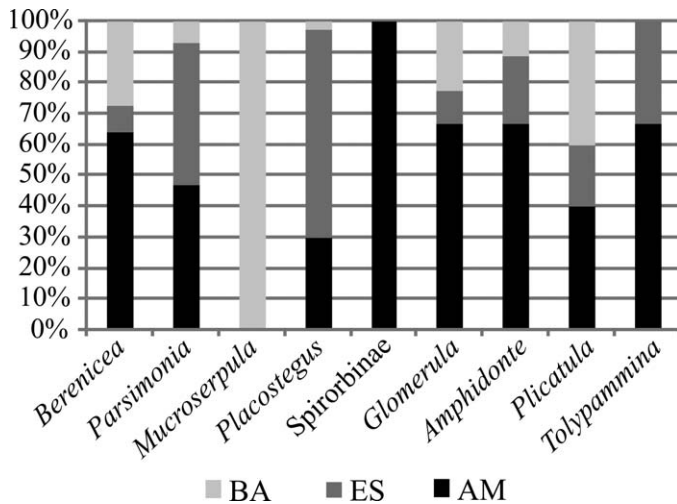
FIG. 11.—Distribution and relative abundances of encrusting taxa for the three main localities. Notice that some taxa are present in only one locality.

abundance, is quite common. The plicatulid and the foraminifer are, like most serpulids, found only occasionally on shells.

Very few interactions between encrusters were observed on the fossil material, indicating either that encrusting communities did not prosper long enough for competitive interactions to develop or that evolution of the community was not controlled in a major way by competitive interactions. Given that the great majority of encrusters belong to a single taxon, which presents a strong tendency to aggregation, and given that many of the nautilid shells were large enough to accommodate a considerable number of encrusters (including the inner space within the body chamber and phragmocone), the latter option seems more likely. Encrustation of other mollusks is quite common in the Pilmatué Member of the Agrio Formation, and, hence, nautilids were not the only available substrate. In addition, most of the interactions found on *C. perstriatum* were likely postmortem (i.e., the interaction was not between two living organisms but rather resulted from colonization of the empty shell of a previous encruster). This is exemplified by bryozoans and oysters that settled on the inner side of disarticulated, cemented left valves of other oysters (Table 5). This suggests at least two pulses of encrustation, consistent with a moderate to prolonged time of exposure of the shells. The size of the encrusters suggests as well that nautilid shells were exposed, either partially or completely, for weeks to months (i.e., most oysters need 2 to 3 months to achieve a length of about 3 cm; Stenzel 1971). Likewise, serpulids grow from 1 to 40 mm per month (most commonly 10–20 mm/mo) depending on biotic and environmental parameters (ten Hove and van den Hurk 1993). Serpulids the size of those found on *C. perstriatum* would have grown at least for a few weeks to a few months.

In many cases overgrowth was likely harmless to the overgrown encruster. For example, serpulid tubes overgrown by bryozoans would
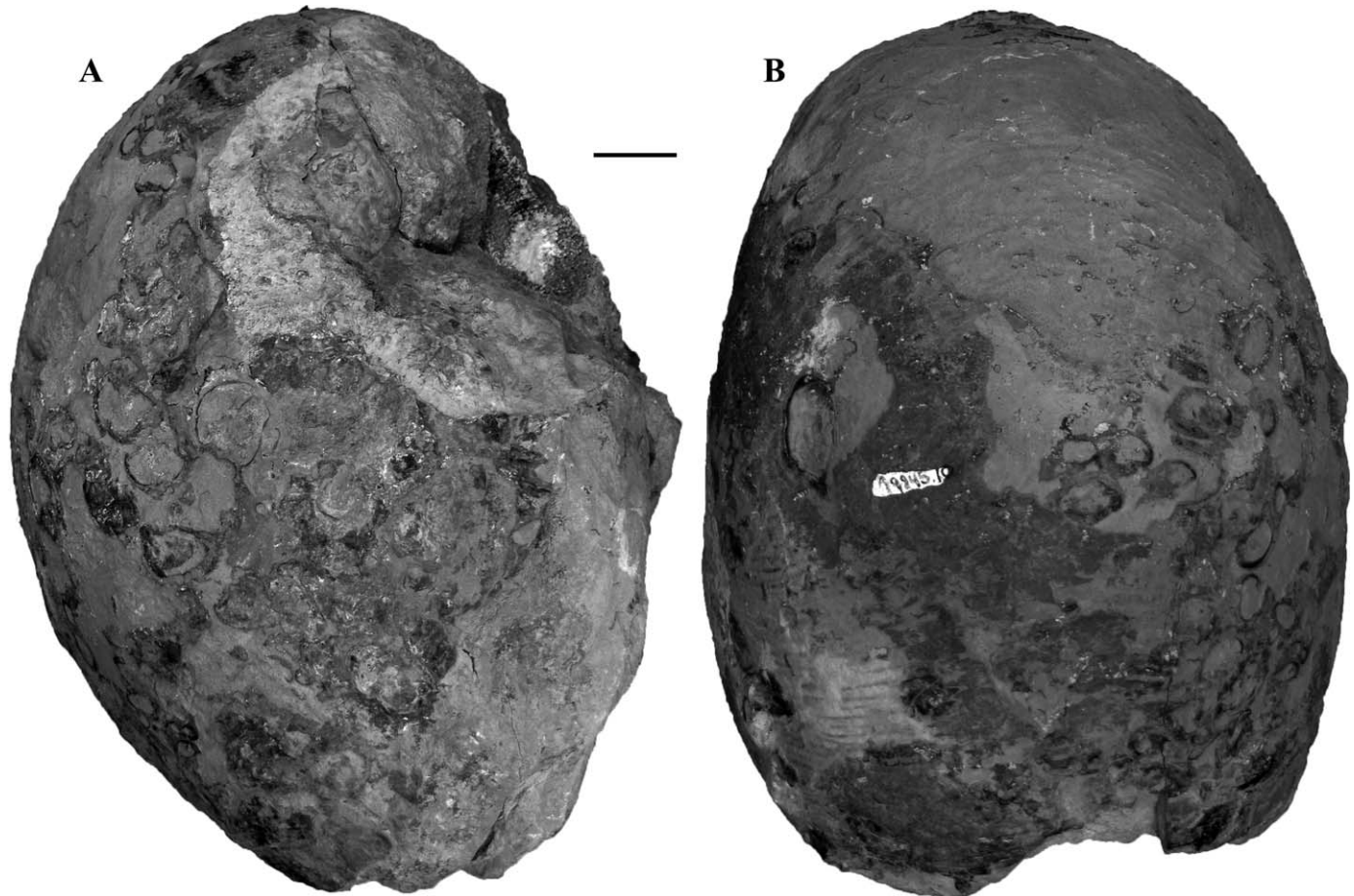

FIG. 12.—Large specimen of *C. perstriatum* (CPBA 19845.10 from Agua de la Mula) missing a portion of the anterior part of the phragmocone. **A)** Right lateral view with sparse remains of the shell (darkest gray) and internal mould showing remains of oysters attached to the inside of the body chamber and phragmocone. **B)** Posterior view in which more oysters are visible and remains of the ribs ornamenting the nautilid are still appreciated. Scale bar: 3 cm.
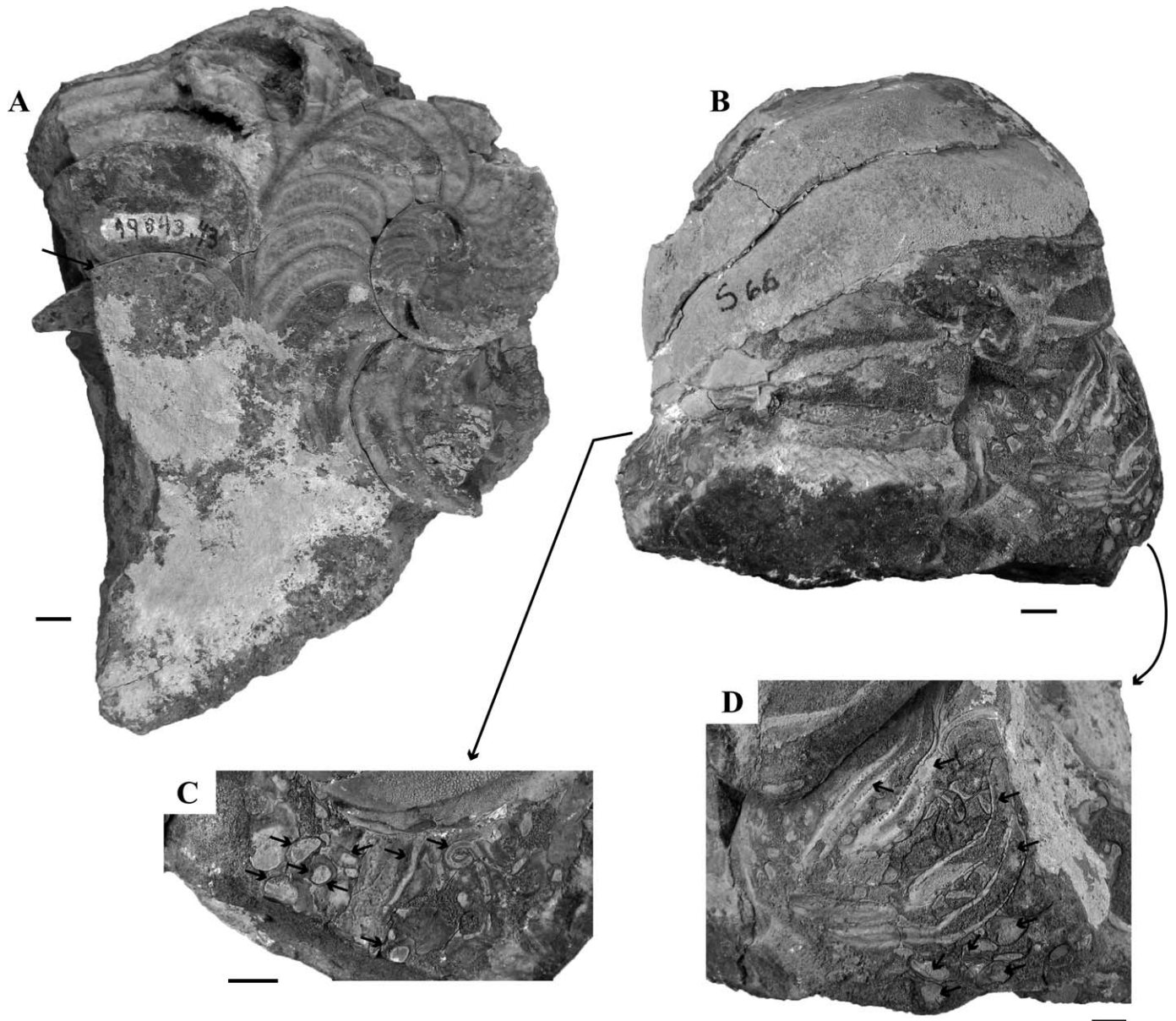
FIG. 13.—Internal encrustation on *C. perstriatum*. **A–D)** CPBA 19843.43. Fragment of phragmocone (naturally worn with the wear facet subparallel to the sagittal plane of the shell) with remains of the body chamber. **A)** Right view showing chambers of the phragmocone and the last septum (arrowed). **B)** Posterior view, showing exposed upper part of the internal mould of the body chamber. **C, D)** Details of the latter showing encrustation by serpulids, sabellids (smaller diameter, coiling tubes), and small oysters. Scale bars: 1 cm.

have been minimally affected as long as the overgrowth stayed away from the tube opening. It was also observed that there was no consistent pattern by which taxa overgrew others, thus indicating a lack of a clearly established superior competitor.

While no remains of algae were observed on *C. perstriatum*, their former presence on these shells cannot be ruled out since they were deposited within the photic zone and, thus, growth of algae was not impeded. Apart from algae and balanids, all other encrusting groups observed in Recent drifted *Nautilus* (see "Introduction") were also observed on *C. perstriatum*. However, the composition of encrusting faunas on living *Nautilus* differs from that of drifted specimens (Landman et al. 1987), whereas the composition on *C. perstriatum* appears uniform between encrustation on living vs. drifted specimens. It is likely that the

proportion of these groups varied between in vivo and postmortem scenarios and that smaller, less voluminous encrusters, such as small serpulids and bryozoans, were more important as in vivo encrusters, in comparison to larger organisms such as oysters.

Overall, the encrusting fauna of *C. perstriatum* comprises a typical Cretaceous shell-encrusting fauna (e.g., Bromley and Nordmann 1971; Dhondt and Dieni 1996; Wilson and Taylor 2001; Lukeneder and Harzhauser 2003; Taylor and Wilson 2003; Žítt et al. 2003; Lukeneder 2008; Zamora et al. 2008; Taylor et al. 2009; Ifrim et al. 2011). Most of the known examples occur in the Tethys region and are of Late Cretaceous age. Information on Early Cretaceous shell-encrusting faunas from the Southern Hemisphere remain sparse (exceptions include Villamil et al. [1998], Luci [2010], and Luci et al. [2013]). The marked dominance

of oysters is characteristic not only of the encrusting fauna of *C. perstriatum* but also of most encrusting faunas from the Early Cretaceous of the Neuquén Basin. The faunal composition is suggestive of shallow, well-oxygenated, agitated warm to temperate waters, as is generally interpreted for the Pilmatué Member of the Agrio Formation (discussed above).

Comparison of the Subsets of C. perstriatum *from the Main Localities*

The comparison of the encrusting faunas from Agua de la Mula, Bajada del Agrio, and El Salado revealed some differences in the nature of the encrusting faunas. Agua de la Mula presents the highest species richness, but differences among localities are small, due primarily to the absence of some of the rare species found in Agua de la Mula and Bajada del Agrio (i.e., spirorbids were only found in one specimen from Agua de la Mula and *M. mucroserpula* was found only in two specimens in Bajada del Agrio). The dominance of oysters is highest in Agua de la Mula as well, as indicated by the lowest Shannon–Wiener and Pielow's index values and the highest Simpson's Dominance value among these three localities. The highest Shannon–Wiener and Pielow index values are those of Bajada del Agrio, possibly as a result of the presence of fewer rare taxa in the encrusting fauna.

Agua de la Mula and Bajada del Agrio present a similar incidence of encrustation, indicating that availability of shells for encrustation was similar in both localities. However, only fragments of phragmocones were preserved in Bajada del Agrio, which accounts for the low internal encrustation values at this locality. In addition, the sample number of host shells from Bajada del Agrio is rather low when compared to those of the other two localities, which is reflected in a lower total abundance of encrusters, as compared to that of Agua de la Mula. However, the difference between the mean numbers of encrusters per shell values is not statistically significant. Interestingly, at Agua de la Mula all the preservational categories defined are represented, while at Bajada del Agrio only one category is found, and three categories occur at El Salado. On the other hand, El Salado presents intermediate richness and diversity values and the lowest total abundance, total incidence of encrustation, incidence of internal encrustation, and mean of encrusters per shell (despite which the latter does not significantly differ from that of Bajada del Agrio).

Variations among the encrusting fauna and preservation of *C. perstriatum* are probably related to slight environmental differences among the main localities. According to Lazo (2007), Bajada del Agrio is the most proximal of the three and the only one in which shoreface facies associations are represented. Normal marine conditions were maintained, as salinity was found to be within normal marine values through the study interval (Lazo et al. 2008). Once shells sank to the bottom, the higher water energy and the presence of a diverse benthic fauna in this locality exposed nautilid shells to increased physical breakage and bioerosion, facilitating the rapid infilling of the phragmocones. Body chambers most likely were destroyed, since they are the weakest part of the shell (Wani 2004). While Mapes et al. (2010a) reported stranded *Nautilus* in which the body chamber was preserved, it must be taken into account that those shells were found in a coastal lagoon protected by a reef barrier.

The Agua de la Mula section was deposited primarily in a mid- to proximal outer ramp setting (Lazo et al. 2005), with *C. perstriatum* shells occurring in both proximal and distal tempestites. Shells deposited below fair weather and/or storm wave base would have been exposed for longer intervals on the seafloor. Fossils at this locality include specimens with complex infills, as well as isolated chambers and body chambers that were probably destroyed in a more agitated environment like that of Bajada del Agrio and transported basinward during storms.

Most of the specimens at El Salado were collected from an exceptional concentration preserved in a storm bed, the matrix of which is identical to the infill of the shells. Many specimens observed in the field, but which could not be extracted, preserved complete body chambers (Cichowolski et al. 2012). The common presence of empty phragmocones and good preservation of body chambers are strongly suggestive of rapid burial of many of these specimens. Cichowolski et al. (2012) proposed that a number of empty floating shells were sunk and buried during a storm event. However, since some specimens were rather heavily encrusted, the storm bed likely includes a mix of shells, some of which had been floating for a considerable amount of time and others of which had been floating for a lesser period of time. The low incidence of encrustation at this locality is in agreement with the generalized observation of little in vivo encrustation of ectocochleates. The common occurrence of encrusters in the body chambers of rapidly buried specimens could be due to early colonization of the inside of the shell during necroplanktonic drift or to their favored preservation within inner moulds in which most of the shell was lost (Cichowolski et al. 2012). Since body chambers are the widest part of the shell, they may have remained only partially buried, allowing colonization by encrusters (some of them have strong wear facets, indicating that they did in fact protrude from the deposit and were exposed to erosion by sediment-laden currents or waves; Fig. 6B).

The *Nautilus* shells studied by Mapes et al. (2010a) present a similar case as the one described here for *C. perstriatum*. Shells were found stranded on the beach and on the subtidal sediment surface, encrusted by macroalgae, cyanobacteria, and invertebrates. Shells were oriented both vertically and horizontally. Specimens with both equal and unequal encrustation on the two flanks were observed, and thus the authors inferred periodic reorientation of shells due to waves and currents. Mapes et al. (2010a) also observed that originally vertically oriented shells could be toppled to lie on their sides. A great variability in intensity of encrustation across shells was also observed, and part of it is considered to have originated during necroplanktonic drift (Mapes et al. 2010a). In general, shells lying on their flanks were more encrusted than were vertically oriented shells, but no significant difference was found between both groups. This reflects the difficulty in differentiating encrustation that took place during drift from encrustation that took place on the seafloor. Reorientation of shells lying on the seafloor resulted in death of encrusters when the shell was flipped on top of them. Upon finding that intensity of encrustation varied greatly with no relation to type of substrate, geographic location, size, and degree of damage of basibiont shells, Mapes et al. (2010a) concluded that time of exposure is the main control on encrustation intensity.

CONCLUSIONS

C. perstriatum experienced minor levels of encrustation in vivo; however, extensive encrustation occurred postmortem. Abundant encrusters settled on the shell, both during necroplanktonic drift as well as after the shell sank. These latter two phases are impossible to differentiate in *C. perstriatum* since its globose shell resulted in common reorientation on the seafloor with concomitant encrustation on both flanks. As a result of extensive two-stage postmortem encrustation (i.e., during necroplanktonic drift and on the seafloor), the original in vivo patterns of encrustation are completely obscured, and hence it cannot be established if the umbilical zone was preferred by encrusters, as in extant *Nautilus*. As the time of exposure increased, so did colonization of shells, with more than one generation of encrusters present in some specimens and resulting in a heterogeneous distribution of encrusters across shells (even within the same locality).

Many of the features observed on *C. perstriatum* are coincident with observations made by previous authors with regard to *Nautilus* and *Allonautilus* (e.g., Landman et al. 1987; Mapes et al. 2010a), suggesting that Cretaceous species shared some taphonomic traits with extant taxa, such as a necroplanktonic drift phase and extensive encrustation after

death with minimal in vivo encrustation. The differences observed in *C. perstriatum* from different localities illustrate that encrusting faunas can be affected by not only the palebiological, paleoecological, and taphonomic pathway of the basibiont but also by slight discrepancies in environmental parameters.

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