

An Early Cretaceous sponge meadow from the Neuquén Basin, west-central Argentina: unsuspected hosts of a dynamic sclerobiont community

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ABSTRACT: Sponges, especially Calcarea, are minor components of benthic associations, especially during the Mesozoic. In the Lower Cretaceous of the Neuquén Basin, small calcareous sponges have been found building a small monospecific meadow. It is restricted to a marlstone lens-shaped bed in a quiet outer-ramp setting in the Cerro Marucho Locality (Picún Leufú depocentre), above a shell bed of small exogyrid oysters; oysters and sponges were the only preserved macrobenthic faunal elements. Individual sponges were small, under 4 cm high, and presented a sub-cylindrical morphology with one or more rounded, apical osculi, many inhalant openings and triactine spicules. Specimens studied here were assigned to *Endostoma* sp. aff. *Endostoma nodosa*. These sponges are quite commonly encrusted by exogyrid oysters, serpulids, sabellids, agglutinating foraminifers and cyclostome bryozoans. Overgrowths among sclerobionts were common, though no undoubtedly *in vivo* interaction has been recorded. Disarticulated left oyster valves were frequently bioclaustrated by the sponges, showing that *in vivo* settlement upon sponges was common. Many oysters settled in the periphery of the osculum suggesting a commensal relationship. The study of this sponge meadow and its sclerobiont community allowed the identification of different stages of ecological succession. The pioneer stage was characterised by sponge settlement on oyster valves, within an otherwise soft consistency bottom. High sedimentation or high nutrient inputs, either individually or in combination, could explain the great abundance of oysters. During the climax stage, sponges thrived and harboured several sclerobiont taxa, developing a relatively dynamic palaeocommunity. Finally, an intensification in either sedimentation rates or nutrient input (or both) past the tolerable threshold for sponges may have been the cause(s) of the meadow's demise. *Endostoma* and similar forms were up to now reported mostly from the Jurassic and Cretaceous of Europe as accessory builders, or as accompanying fauna in reefal settings. This new record shows that in rare occasions they could form low-relief meadows on their own.



KEY WORDS: Agrio Formation, bioclaustration, biotic interactions, Calcarea, commensalism, *Endostoma*, Porifera, sponge build-up.

Fossil sponges have a complicated taxonomy that has fundamental issues yet to be resolved, for example: relationships among main sponge clades are still uncertain, and fossil and recent classification proposals proved difficult to integrate – some morphological grades occur across different orders (e.g., Wood 1990; Senowbari-Daryan & García-Bellido 2002; Finks & Rigby 2004; Pisera 2006; Vacelet *et al.* 2010). Many species are difficult to classify without thorough observation of very specific traits, some of which require extensive sectioning of specimens and scanning electron microscope (SEM) imaging (Wood 1990; Díaz & Rützler 2001). In the last few decades many advances have been made for extant sponges, through DNA sequencing analyses and cladistic approaches (e.g., Morrow & Cárdenas 2015). Fossil sponges are even more difficult to identify as bios-tratinomy and diagenesis often obliterate or alter diagnostic

skeletal features (Wood 1990; Pisera 2006; Wulff 2006). Thus, the fossil record is strongly biased towards sponges with a rigid mineralised skeleton (Pisera 2006). The plasticity of sponge growth is another factor that complicates taxonomic assignment of fossils, as the same taxon can vary substantially in shape among different environmental settings (e.g., Palumbi 1984; Loh & Pawlik 2009; Ávila & Ortega Bastida 2014). In addition, fossil sponges are truly rare in some rocks and time intervals (Pisera 2006).

However, the various ecological functions of sponges and their importance have been acknowledged in the literature on both fossil and extant forms (e.g., Wood 1990; Díaz & Rützler 2001; Wulff 2006; Bell 2008). Since the Cambrian, sponges have been reef-builders with different taxonomic groups dominating this niche over the Phanerozoic (see Brunton & Dixon 1994;

Pisera 2006; Wulff 2016; Maldonado *et al.* 2017). From the Mesozoic onwards, sponges became important binders as well as playing parts in stabilisation, consolidation and regeneration of reef frames (Bell 2008; Wulff 2016). In deeper settings, hexactinellid mounds and reefs persist even today, and they represent biodiversity hotspots in such environments (Kauffman *et al.* 2000; Maldonado *et al.* 2017). Recent sponges are also important components of mangroves and seagrass meadows (e.g., Diaz 2012; Ávila & Ortega Bastida 2014; Maldonado *et al.* 2017). Boring sponges play a significant part in carbonate cycling by breaking up calcareous materials and clasts (Rützler 1975; Achlatis *et al.* 2017). Sponge communities have an impact on the water column as well (benthic-pelagic coupling), playing important roles in the carbon, nitrogen, oxygen and silica cycles (see Bell 2008) and maintaining water clarity (Wulff 2016); they also contribute significantly to the removal of bacteria and other microorganisms through their filtering activity (Diaz & Rützler 2001; Bell 2008). They provide nourishment for many different types of consumers (see Wulff 2006; Maldonado *et al.* 2017). A great variety of single-celled autotrophs and heterotrophs dwell within sponge tissues (see Wulff 2006; Taylor *et al.* 2007, for an overview). In addition, sponges often establish remarkably diverse symbiotic associations with a variety of algae, invertebrates (including crustaceans, bryozoans, polychaetes, ophiuroids, cnidarians and molluscs) and fishes (Wulff 2006, 2016 and citations therein). Besides they may also host a diverse sclerobiont fauna, resulting in increased local benthic diversity (e.g., Gundrum 1979; Wilson *et al.* 2008, 2010).

Despite their importance, studies on fossil sponges that focus on their ecological roles are generally rare (Pisera 2006), particularly for Mesozoic sponges (e.g., Palmer & Fürsich 1981; Fürsich & Werner 1991; Werner *et al.* 1994; Leinfelder 1992). Lithistid and hexactinellid sponge-dominated reefs were quite common during the Jurassic–Cretaceous, and thus are extensively studied (see Maldonado *et al.* 2015, and citations therein). Sponges also took part in other types of reefs or mounds; for some examples consult Palmer & Fürsich (1981), Fürsich & Werner (1991), Leinfelder (1992), Kauffman *et al.* (2000), Svennevig & Surlyk (2019) and Bonuso *et al.* (2020). Most studies deal with Jurassic or Late Cretaceous occurrences centred mostly in Europe, with few mentions of Early Cretaceous records.

Argentinian fossil sponges are quite common and abundant in Palaeozoic successions (e.g., Carrera 1997a, b, 2003; Beresi 2007; Beresi & Rigby 2013; Carrera *et al.* 2018), but Mesozoic records are scarce (e.g., Afşar *et al.* 2014). A remarkable exception is that of the Oxfordian La Manga Formation reefal structure, which bears a moderately diverse siliceous sponge assemblage, that occurs in the mainly coral-built structure (Beresi 2007). In the Lower Cretaceous Agrio Formation (AF) fossil sponges have been mentioned or figured but never studied in detail. Small sponges are usually found attached to ramose coral colonies in shallow water coral patch-reefs and coral meadows (e.g., Lazo *et al.* 2005; Garberoglio *et al.* 2013; Luci *et al.* 2015; Garberoglio 2019); alternatively loose siliceous spicules have been described from thin sections of fine grained carbonates from distal marine settings (see Sagasti & Ballent 2002). In addition, borings on mollusc shells and corals, usually referred to clionid sponges were described (see Garberoglio *et al.* 2013; Garberoglio 2019; Toscano *et al.* 2021). In this paper a newly discovered sponge meadow from the AF is reported for the first time. The objectives of the present paper are as follows: (a) to describe and identify these sponges to the lowest taxonomic level possible; (b) to analyse their sclerobiont community, including sclerobiont taxa identification, interactions among them and with the sponges and other palaeoecological metrics; and (c) to interpret the sponge assemblage in palaeoecological terms along with its

associated palaeoenvironment, and reconstruct the sponge meadow establishment, climax and demise.

1. Geological setting of the sponge-bearing bed

The Neuquén Basin, located in west-central Argentina, extends through most of the Neuquén and Mendoza provinces along the Andean foothills, between 32° and 40° SL (Fig. 1). During most of Jurassic and Early Cretaceous times it was a retro-arc basin with a gentle thermal subsidence regime. Oceanic waters penetrated from the Pacific Ocean through a volcanic arc to the west and formed a large marine epicontinental embayment. During the Early Cretaceous the basin was located not far from its current position, roughly between 28° and 36° SL (Somoza 2011), a mid-latitude location at the boundary between the tropical and subtropical belts.

The materials studied here come from the Picún Leufú depocentre, which developed in the southern region of the basin, between the Huincul High to the north and the North Patagonian Massif to the south (Fig. 1). The Huincul High, an east–west oriented morphostructural feature, was proved to be an ancient positive element developed since Early Jurassic times prior to the main Andean contractional cycle that started in the Late Cretaceous (Ramos *et al.* 2011; Naipauer *et al.* 2012). This topographic high was at times a true division between the northern and southern regions of the basin, especially during times of relative sea level fall, but during transgressive episodes, marine waters drowned it and both regions became partially connected. It is within this southern depocentre that the studied sponge meadow was recorded in the AF.

The AF, defined by Weaver (1931), is a well-known unit because of its abundant and diverse marine fossil content and also because it is a reservoir unit of interest for oil exploitation. It was deposited from early Valanginian to latest Hauterivian times based on a refined ammonoid biostratigraphy which has been correlated to the European Standard Ammonoid Zonation and constrained by precise radioisotopic dates (see Aguirre-Urreta *et al.* 2007, 2017, 2019). The unit comprises three members: the lower Pilmatué Member; the middle Avilé Member; and the upper Agua de la Mula Member (Weaver 1931; Leanza *et al.* 2001). The upper and lower members are marine, representing inner to outer ramp settings with abundant benthic fauna (e.g., Lazo 2007a). In the Picún Leufú depocentre, the unit overlies the Bajada Colorada Formation and underlies the La Amarga Formation, and the Avilé Member is not recorded. The unit is well exposed at several localities that are easily correlated among each other due to an abundant and diverse macrofossil and microfossil content (see Musacchio & Simeoni 2008; Cataldo & Lazo 2012; Luci & Lazo 2015). In terms of facies, the unit is composed mainly of carbonate shales alternating with shell beds, skeletal sandstones, packstones and grainstones (di Paola 1990).

The studied sponges were collected at Cerro Marucho (S 39°25.71'; W70°10.173'). This locality lies on a prominent hill next to National Road 40, some 60 km south of Zapala City, Neuquén Province. Here, the AF is well exposed, and a detailed sedimentary log of 127 m was made (Fig. 2; see also Leanza & Hugo 1997; Musacchio & Simeoni 2008; Lescano & Concheyro 2014). The sponge-bearing level was recorded within the *Hoplitocrioceras gentilii* Zone of Early Hauterivian age, that in turn has been correlated with the *Lyticoceras nodosoplicatum* Mediterranean Standard Zone (see Aguirre-Urreta *et al.* 2007; Reboulet *et al.* 2014).

The studied sponge bed corresponds to a single lenticular bed of poorly consolidated grey marlstone of 1.8 m of maximum thickness and 20 m of maximum width along strike. This lens is embedded in a 30-m-thick continuous interval of tabular

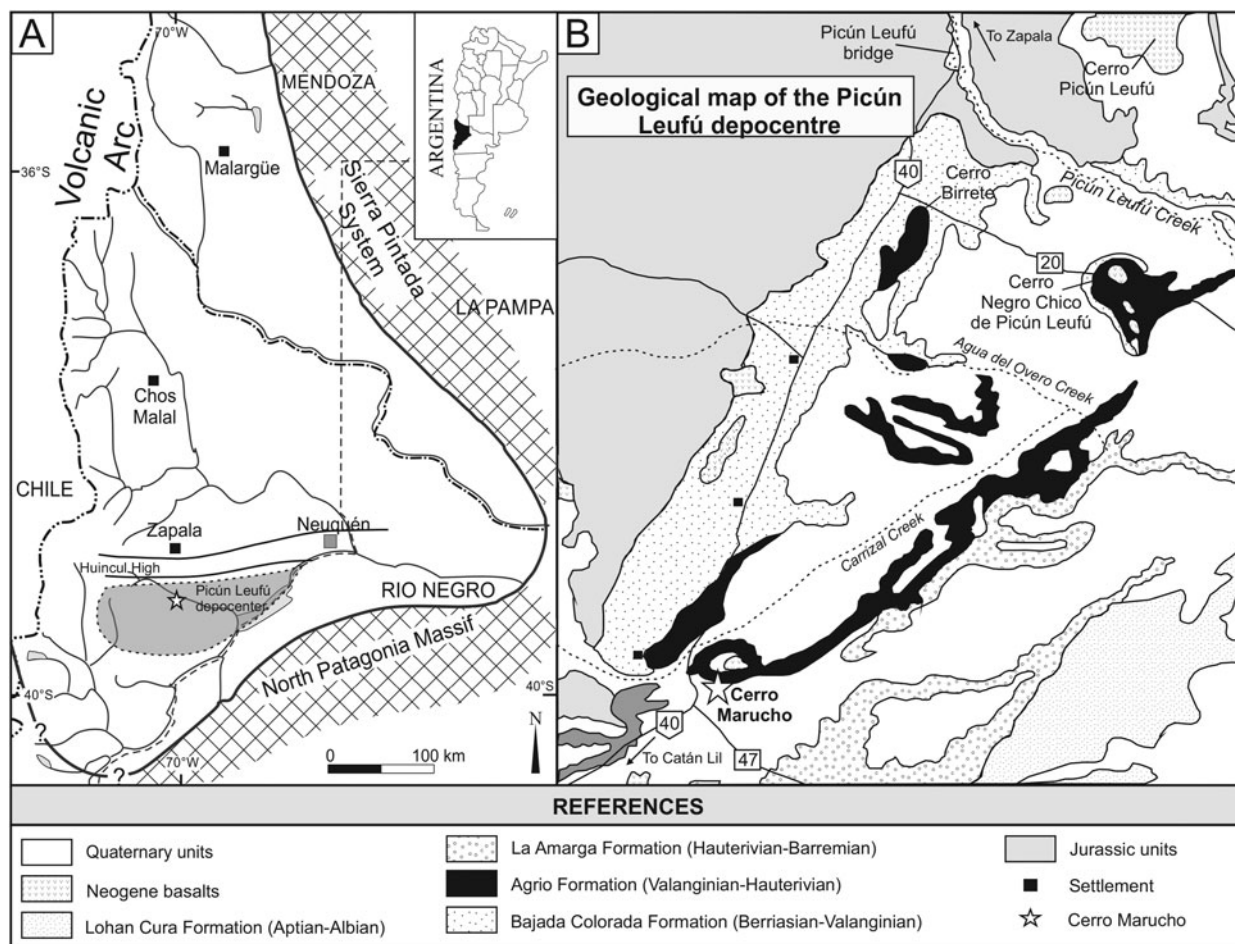


Figure 1 (a) Map showing the former location and shape of the Neuquén Basin for the Early Cretaceous, and the main (north) and Picún Leufú (south) depocentres separated by the Huincul High. (b) Geological map of the study area, with the main outcropping units.

grey shales with abundant ammonoids lying parallel to the bedding planes (Fig. 2). The lens contains abundant sponges, loosely packed (no contact among bioclasts). At its base is an oyster shell bed composed of small cementing *Ceratostreon* exogyrid oysters, that grades upwards into sponge-bearing marls. Sponge specimens are placed mostly above the oyster shell bed: a gradual increase in sponge abundance was detected towards the top. Abrasion and/or rounding were negligible for both sponges and oysters. Sponges and oysters were oriented parallel to bedding in cross-section and randomly in a plane view. No other benthic macrofauna was observed, except for the sclerobionts harboured by the sponges (see section 3). Base contact was sharp and top contact gradational. No sedimentary structures were recorded and both surfaces that limit the lenticular sponge-bearing bed cannot be traced laterally beyond the lens, that is, they have no great local, much less regional importance. Thus, the lens is a very local, within facies occurrence, as both below and above it, grey shales with scattered ammonites occur. This is also supported by the fact that the sponge bed was not recorded in nearby localities such as Cerro Birrete and Cerro Negro Chico de Picún Leufú. A distal low energy ramp setting is envisaged with a predominance of settling of suspended fine-grained carbonates.

The sponges are interpreted to have formed a low-relief, low-diversity meadow of rare outcrop occurrence. For this definition we followed Aretz (2010) who defined a series of terms based on coral build-ups in which colonisation of the seafloor varied between high-diversity dense populations and impoverished occurrences.

2. Materials and methods

Sponges were collected *in situ* from the sponge-bearing level at Cerro Marucho along its field exposition. A total of 137 specimens were examined in detail. They are all deposited in the Museo Olsacher (Zapala City, Neuquén, Argentina) under repository number MOZ-Pi 12114.1-137 (suffix number indicates an individual specimen's number). Finks & Rigby (2004) and Senowbari-Daryan *et al.* (2020) were followed in the taxonomic section. For general sponge terminology, Webby *et al.* (2010) were followed. Some specimens were sectioned and polished along the transversal and longitudinal planes in order to observe their inner structure.

Most specimens are terminal branch fragments (with the apical osculum preserved); only six specimens are complete. However, it was evident in field observations that fragmentation was recent, and not caused by extensive reworking of the materials. For all specimens, maximum preserved length and width were measured with a digital caliper.

Prior to data collection, sponges were washed under running water with a brush; care was taken that this did not affect (efface or remove) the more delicate sclerobionts by checking on the sponges under a binocular stereomicroscope (up to 50X; Leica EZ5) before and after washing. Little sediment remained attached to the sponges, so there was no need for further cleaning by mechanical means. All cleaned and dried specimens were observed under binocular stereomicroscope and sclerobiont presence/absence data were recorded for each sponge specimen. Interactions among sclerobionts and/or sclerobionts–basibiont were also

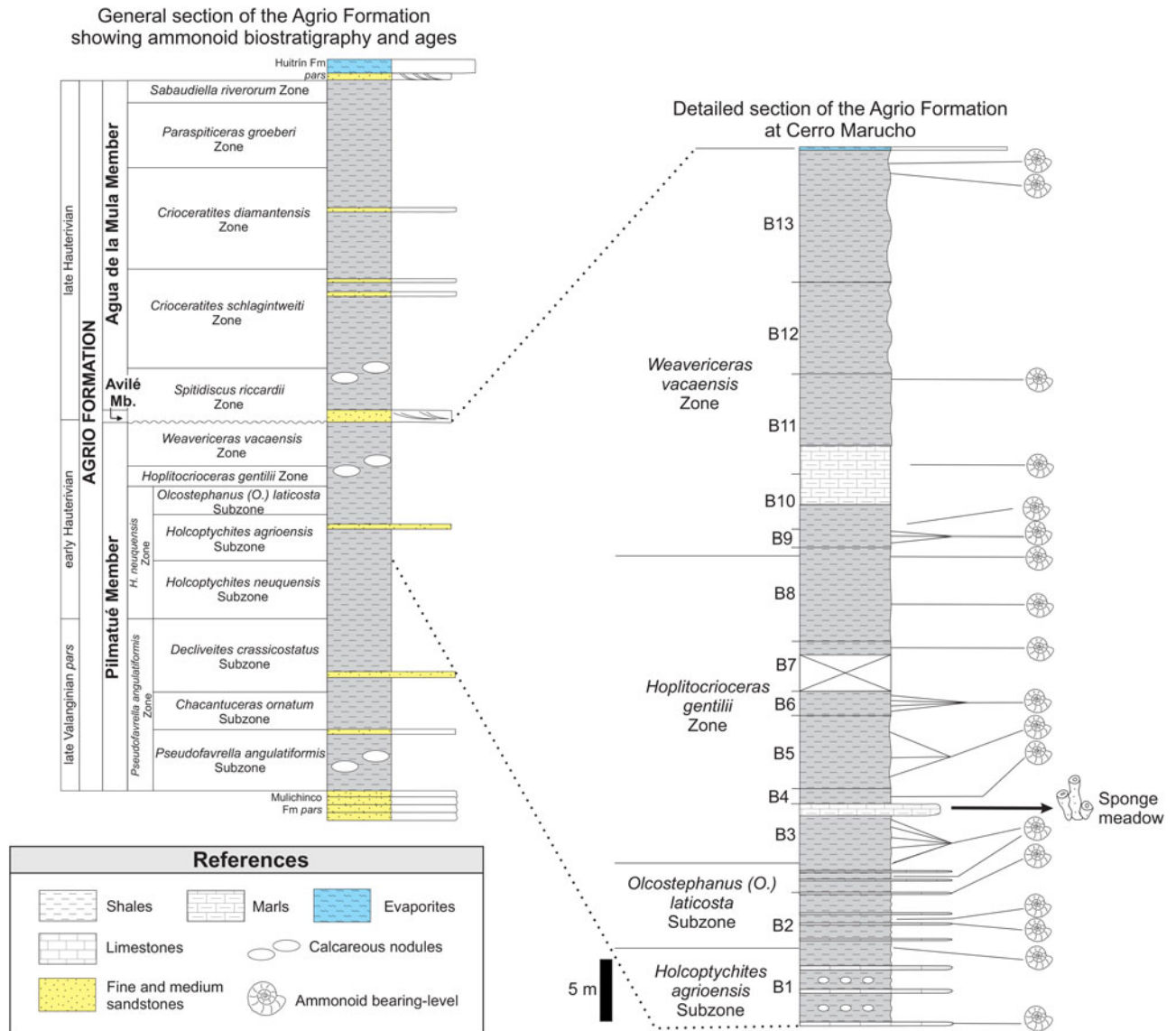


Figure 2 Measured section at Cerro Marucho. To the left, a generalised stratigraphic column of the Agrio Formation is shown; to the right, the partial section of the Pilmatúé Member measured in Cerro Marucho is depicted, with the sponge meadow level indicated by an arrow.

recorded. Sponges lacking sclerobionts were also accounted for. When present, markings on the sponge skeleton were also recognised. When preserved, the substrate that sponges had settled upon was also recorded. Four specimens (MOZ-Pi 12114.14, 12114.17, 12114.22 and 12114.51) were examined using a SEM for imaging and energy dispersive spectroscopy (EDS) analysis.

Overall richness of sclerobiont taxa was calculated for the whole sponge sample, as well as percentage of sponges presenting at least one sclerobiont. In addition, maximum richness per sponge specimen was also calculated. Number of sponges with a given sclerobiont taxon, and the corresponding percentage over the total number of sponges were calculated; these metrics provide information on dispersion of sclerobiont taxa across available sponge substrates regardless of the abundance of each individual sclerobiont taxon. Richness of sclerobionts per sponge was then plotted against sponge maximum length and width, to search for patterns in number of sclerobiont taxa with respect to sponge size. However, since most specimens are fragmentary, these data must be interpreted with caution. Finally, overall trends in sclerobiont location with respect to any preserved anatomical landmarks in sponge specimens (e.g., osculum, growth direction, ridges and inter-branch spaces in sponges, etc.) were recorded qualitatively.

Three specimens were subject to longitudinal cutting in order to observe whether sclerobionts had been bioimmured by the sponge. The specimens selected for cutting showed distinctive morphologies (for example, ridges that had a corkscrew shape over the sponge) that were suggestive of serpulid overgrowth by the sponge.

3. Systematic palaeontology

Class Calcareo Bowerbank 1864

Order Stellispongiida Finks & Rigby 2004

Family Endostomatidae Finks & Rigby 2004

Genus Endostoma Roemer 1864

Type species: Scyphia foraminosa Goldfuss 1829. Posterior designation by de Laubenfels (1955).

Diagnosis: Conical-cylindrical, simple but occasionally basally conjoined, small sponges. Deep, central inner tube. Exhalant channels entering the cloaca sub-horizontally, occurring on top surface as radial grooves converging on the osculum. Additional channels essentially in intertrabecular spaces. Lower

part may be covered by an imperforate dermal layer. Fibres conformed by very slender, bundled triradiates; paratangential dermal triradiates and tetradiares may be present or not (modified from Roemer 1864; Hinde 1884; Finks & Rigby 2004).

Remarks: The genus was created by Roemer (1864) to group simple, cylindrical sponges with an inner tube (axial spongocoel) and large, lateral openings, from the Cretaceous of Germany. He also created *Polyendostoma*, which included *Endostoma*-like sponges that grew joined at the base. Later, Zittel (1878) erected *Corynella* to include simple, thick-walled, sometimes joined at the base, cylindrical, globular or clavate sponges of Triassic–Late Cretaceous age and assigned six Triassic, 18 Jurassic and 11 Cretaceous species to *Corynella*; among the latter were the then existing species of *Endostoma* and *Polyendostoma*, now junior synonyms of *Corynella*.

Later Hinde (1883) revised *Corynella*, adding further details to Zittel's (1878) diagnosis and describing 15 species in varying detail from the Triassic–Cretaceous of several places over Europe; later on, he added five species from the Jurassic of England to the genus (Hinde 1893). As in Zittel (1878), he included *Endostoma* within *Corynella*. Shortly after the revision of *Corynella*, Hinde (1884) appointed *Scyphia foraminosa* Goldfuss 1829 as the type species of *Corynella*.

Hinde (1893) erected the genus *Peronidella*, which differs from *Corynella* in lacking a radial canal system. However, as the development of the channel system can be very variable in *Corynella* (ranging from nearly inexistent or limited to the basal portion of the sponge, to clearly present), it is not a reliable diagnostic character.

Deci *et al.* (1968) separated the Triassic forms from the north of Italy, based on their spherulitic microstructure and grouped them together in the genus *Precorynella*. Much later, Rigby & Senowbari-Daryan (1996) grouped the Permian and Triassic species lacking spicules in the genus *Permocorynella*. Thus, only Jurassic–Cretaceous species remained within *Corynella*.

Finks & Rigby (2004) recognised *Corynella* Zittel as a junior synonym of *Endostoma* Roemer, on the basis of both genera sharing the type species. *Endostoma* was thus redefined as a genus comprising only Jurassic and Cretaceous species.

Recently Senowbari-Daryan *et al.* (2020) described three species of *Endostoma* (one new) and gave a list of valid species of the genus, but their list contains some mistakes in names and dates. The revised list is as follows: *Endostoma bullata* (Étallon 1860); *Endostoma clava* (Oppliger 1929); *Endostoma costata* (Stahl 1824); *Endostoma cribrata* (Hinde 1893); *Endostoma divisa* (Müller 1984); *Endostoma intermedia* (Münster 1829); *Endostoma langtonensis* (Hinde 1893); *Endostoma madreporata* (Quenstedt 1876–78); *Endostoma nodosa* (Keeping 1883); *Endostoma parva* (Étallon 1859); *Endostoma perplexa* (Quenstedt 1876–78); *Endostoma polonica* (Hurcewicz 1975); *Endostoma quenstedti* (Zittel 1878); *Endostoma stellata* Senowbari-Daryan *et al.* 2020; and *Endostoma stolata* (Zittel 1878).

The only other genus within the family Endostomatidae, *Raphidonema* Hinde, has a similar structure but is cup-shaped (Finks & Rigby 2004), so it can be easily distinguished from *Endostoma*.

Discussion: Most authors citing *Endostoma* (or more commonly, *Corynella*) made no descriptions and published no pictures, and mentions are usually at the genus level. Thus, a thorough revision of species and occurrences is necessary, though this is out of the scope of the present work.

To our knowledge, no analyses have been made on the mineral skeleton of *Endostoma*, but the genus *Barroisia* Munier-Chalmas (also a Jurassic–Cretaceous calcareous sponge) has a similar structure to *Endostoma* and was found to bear triactine spicules embedded in a calcareous matrix, and according to some authors (Reid 1968; Masse & Termier 1992) these spicules could be

siliceous. However, the finding of siliceous materials within their skeletons does not necessarily imply that these sponges secreted siliceous spicules. This could have alternative explanations, for example, incorporation of foreign materials (some extant sponges incorporate loose spicules into their structure); also, infiltration of siliceous spicules belonging to the boring genus *Entobia* may occur (Reid 1968). Thus, the ability of these sponges to secrete siliceous spicules is still not conclusively proven.

Palaeoecological remarks: Discussions of the palaeoecology of the genus in the literature are limited; there is agreement that these sponges are small (up to a few centimetres in height) and, as with most sponges, they tend to prefer low-energy, relatively deep settings and hard substrates (see section 5 for further details).

Endostoma sp. aff. nodosa (Keeping 1883)

Figs 3, 4

Materials: Sponge materials comprise 137 specimens, listed under repository number MOZ-Pi 12114.1–137. All are from one single bed, *Hoplitocrioceras gentilii* ammonoid Zone, Early Hauterivian, AF, Cerro Marucho, Neuquén, Argentina.

Description: Small specimens are either club shaped, globular or sub-cylindrical; branching specimens are sub-cylindrical (Fig. 3). Most fragments are longer than wide. Mean preserved length is 24.02 mm (minimum = 11.52; maximum = 44.47). Mean preserved width is 16.93 (minimum = 8.69; maximum = 48.62). Rounded osculum, of 1–2 mm in diameter, at the top. Most specimens are isolated, but some are tubes conjoined by their bases, or bundles of short tubes starting from a common base (Fig. 3a, e–g). Some specimens retain the dermal layer, but in most of them it is slightly weathered or recrystallised, showing the reticulated arrangement of the non-spicular skeleton, made of fibres which show a very fine lamellar structure. Some scattered triactine spicules can be observed. Slightly weathered surface pores are formed by bundled triactine spicules. An axial canal, of about the same diameter as the osculum, extends from it to almost the base of the sponges (Fig. 4a). EDS analysis showed two distinct peaks corresponding to calcium carbonate and silica – when targeting the matrix the maximum peak is on calcium, while in the skeleton the main peak is on silicon.

Occurrence. AF, *Hoplitocrioceras gentilii* Zone, Lower Hauterivian, Cerro Marucho, Neuquén Province, Argentina.

Discussion: '*Corynella*' *nodosa* was described by Keeping (1883) as a more or less pyramidal to rarely cylindrical species, attached by a broad base; sessile, or mounted upon a short neck. Sponge walls are very thick, composed of a uniform, coarse vermiculate tissue, leaving only a narrow cylindrical central cloaca. A system of lateral canals opens into the central cloaca but is imperfectly developed. Osculum terminal, central. A simple smooth area forms the terminal cone around the osculum, but below this the surface is raised into prominent, coarse knobs and foldings. No measurements were given, but specimens depicted on the Sedgwick Museum's website (<http://www.sedgwickmuseum.org/index.php?page=collections>) where the materials are deposited allowed some size estimations (diameter less than 1 cm); Keeping's paratypes, specimens SM 26242, 26244, 26245 and 26248 (repository numbers) can be assigned to this species. Unfortunately, the holotype is not figured.

Hurcewicz (1975, p. 237) described specimens assigned to '*Corynella*' *nodosa* as follows: 'solitary, subcylindrical, slender, gradually thinning out to the form of a short hypophare ended with small projections. Wall surface equal, without cortex, with transversal growth rings. Osculum 1.75–2.10 mm in diameter, with rounded margins, situated in depression.'. Hurcewicz (1975) illustrated specimens that are more elongated than those

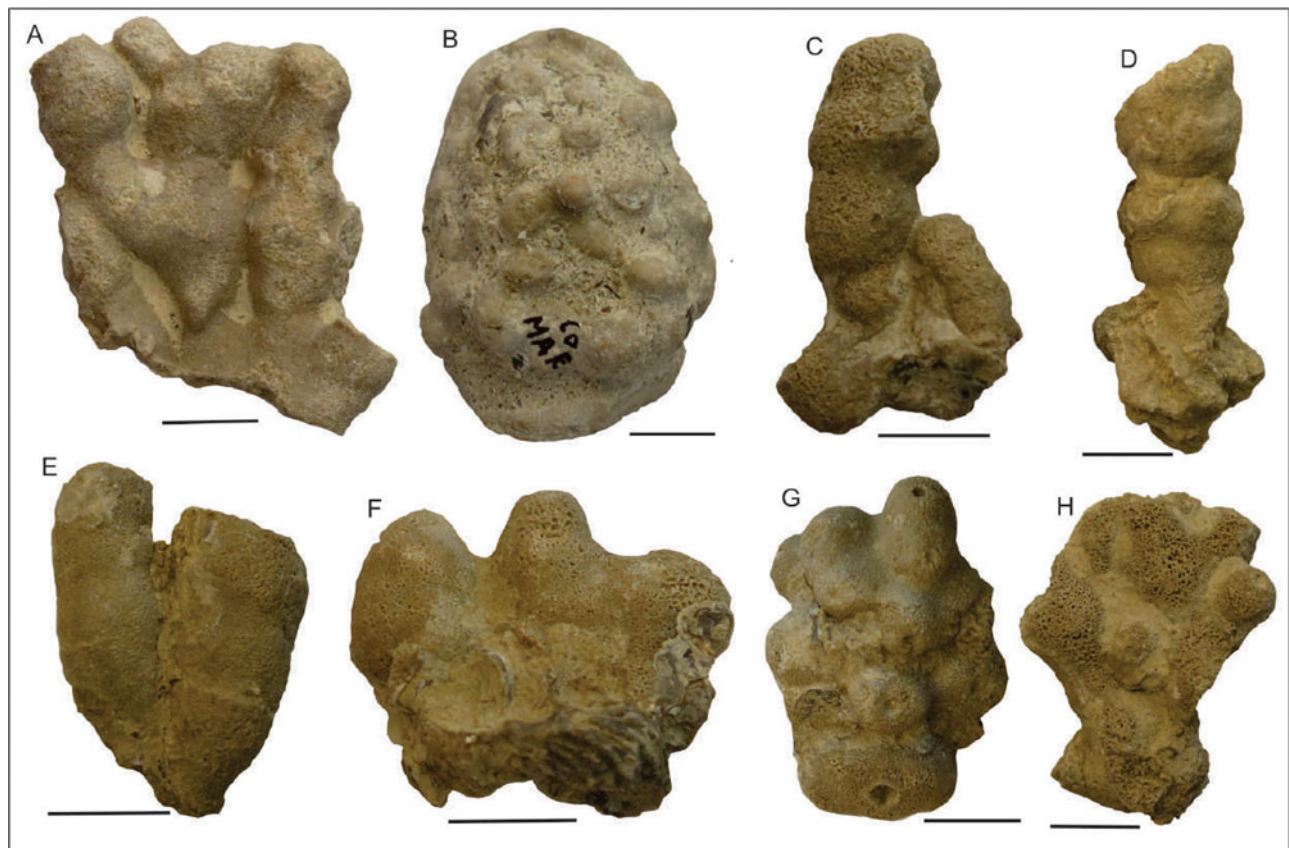


Figure 3 Overall morphology of *Endostoma* sp. aff. *nodosa* MOZ-Pi 12114. (a) Lateral view of a group of tubes joined by their bases (specimen 12114.77). (b) Top view of specimen 12114.130 with short globular projections. (c) Lateral view of a finger-like ramose specimen 12114.12. (d) Lateral view of an isolated tube (specimen 12114.2). (e) Lateral view of two tubes united at the base (specimen 12114.79). (f) Lateral view of specimen 12114.105 growing over *Ceratostreon* sp. oysters and showing globular projections. (g) Top view of specimen 12114.106 with globular projections. (h) Top view of specimen 12114.76 with finger-like and globular projections. Scale bars: 5 mm.

of Keeping (1883), and they closely resemble the materials studied here. On the basis of all characters shared by our materials and those described by other authors, we assign these sponges to *Endostoma* aff. *nodosa*. An open nomenclature treatment is preferred due to geographical and temporal distance between previous records and ours.

The specimens studied herein can be easily differentiated from *E. bullata* (Étallon 1860), *E. clava* (Opplinger 1929), *E. costata* (Stahl 1824), *E. intermedia* (Münster 1829), *E. langtonensis* (Hinde 1893), *E. madreporata* (Quenstedt 1879-78), *E. parva* (Étallon 1859), *E. perplexa* (Quenstedt 1879-78), *E. polonica* (Hurcewicz 1975), *E. quendstedti* (Zittel 1880), *E. stellata* Senowbari-Daryan *et al.* 2020 and *E. stolata* (Zittel 1878) on the basis of differences in size and shape. *Endostoma cribrata* (Hinde 1893) resembles the specimens studied here in some respects but differs from them in having larger osculi and forming colonies of lower relief and smooth outer walls.

Two of our specimens (numbers MOZ-Pi 12114.20 and 12114.106) have slightly wider diameters (14 mm) and slightly bigger osculi (3 mm) than the rest, thus resembling *E. divisa* (Müller 1984), from the Tithonian of Germany; but one of them (MOZ-Pi 12114.106) is part of a bundle of short tubes with a common base, the others being noticeably smaller, so we interpret that those measurements remain within the natural variability of the species.

4. Sponge sclerobiont community analysis

Considering all 137 specimens, only 11 bore no sclerobionts, thus 91.97% of sponges were encrusted by at least one sclerobiont. Overall minimum (see below) sclerobiont richness is nine, comprising exogyrid oysters, cyclostome bryozoans, sabellid and

serpulid polychaetes and agglutinating foraminifers (Figs 5, 6). Some serpulids were undetermined as their preservation prevented generic identification; these specimens are preserved as ‘half-tubes’, because their upper halves have been naturally eroded or dissolved away (Fig. 5d, e); these were not included in the richness metric, since they could either correspond to the already identified serpulid taxa, or else, correspond to entirely different taxa. Thus, the measured richness is considered as a minimum value.

Table 1 lists the general metrics on presence–absence data for sponges. Oysters were the most widespread across sponges, followed by undetermined serpulids and foraminifers. Two bryozoan taxa and one serpulid taxon were also quite common on sponges, with the remaining sclerobiont taxa being found in less than 10% of sponge specimens (Fig. 7a). Minimum richness per sponge specimen is one sclerobiont taxon, and maximum richness is seven sclerobiont taxa (mean is 2.53 taxa per sponge specimen; Figure 7b). Figure 7c represents richness of sclerobionts per sponge, distributed according to the size of the latter. It shows that while larger sponge fragments host a larger number of sclerobiont taxa, smaller sponges can also quite commonly do so too. Considering that most specimens are actually sponge fragments, richness per sponge specimen may have been higher.

Interactions were common among sclerobionts. Table 2 lists the 19 pairs of interactions recorded on the sponges, with a total of 34 occurrences. Here it must be remarked that some of them may be considered as possibly redundant, as they involve undetermined serpulids and thus may be the same serpulid taxa represented among well-preserved tubes. Correcting for these possible redundancies, 17 pairs of interaction were recorded among sclerobionts. They cannot be unequivocally regarded as *in vivo* interactions because no skeletal modification is evident in any of the participants; in addition, many

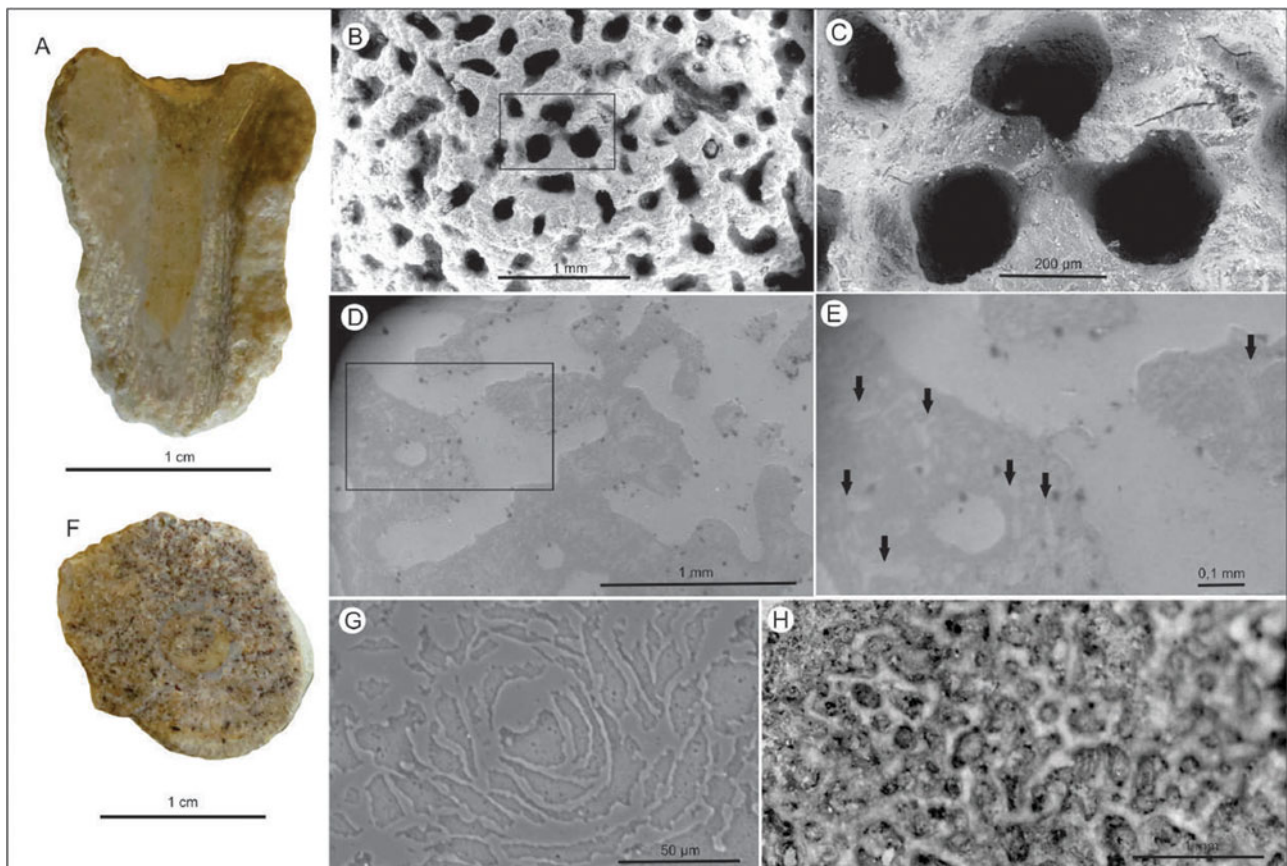


Figure 4 Sectioned specimens of *Endostoma* sp. aff. *nodosa* MOZ-Pi 12114. (a) Polished longitudinal section, showing the axial canal. (b) Lateral view of the weathered surface, showing the non-spicular skeleton. (c) Detail of rectangle in (b). (d) Polished section showing details of the skeleton. (e) Detail of rectangle in (d), arrows point to scattered triactine spicules. (f) Transversal polished section of a tube, showing the axial canal. (g) Polished section showing the arrangement of the fibres. (h) Lateral view displaying the system of inhalant pores showing a triactine arrangement.

interactions took place over disarticulated left oyster valves, or involved overgrowth of serpulid tubes by bryozoans, but away from the tube's aperture. Some overgrowths involve up to four different taxa settling upon each other. In many cases, large serpulids were almost completely covered by the cyclostome bryozoan *Idmonea?* sp.

The most common interactions consist of (clearly *post mortem*) overgrowth of disarticulated left-oyster valves by cyclostome bryozoans (Table 2). Interactions show that no sclerobiont taxon consistently overgrew others. Individual frequencies of occurrence of each interaction pair are low; only for seven pairs was more than one occurrence recorded, and the maximum occurrence for a single pair is five. All interactions for which more than one occurrence was recorded involve bryozoans overgrowing serpulids, oysters, foraminifers and other bryozoans, and foraminifers overgrowing the cyclostome *Idmonea?* sp. The pair *Idmonea?*-*Berenicea?* overgrew each other with an almost equal amount of occurrences, and no skeletal modifications were recorded on their zoaria that can prove without question that this happened *in vivo*.

Interactions were also recorded between the basibiont sponges and oysters; 53 sponge specimens presented one or more oyster valves that had been partially bioclaustrated by the sponge skeleton (Fig. 5a, f, h). They represent 38.69% of the total amount of sponge specimens and 51.96% of sponges bearing oyster sclerobionts. Thus, oyster bioclaustration was a quite common occurrence; furthermore, this is a minimum estimate as more oyster valves may have suffered complete bioclaustration and are thus undetectable unless a section of the sponge specimen is made. These bioclaustrated oysters consist in left valves only.

In addition, 20 sponge fragments presented markings on their skeletons. They represent varied morphologies (Fig. 5b, d, i), the

margins of which are frequently distinct. They are placed in the middle part of the branches rather than in their upper ends.

Finally, some trends were observed occasionally in a few sclerobiont taxa, regarding their orientation and/ or placing with respect to the sponge's skeleton. Oysters are commonly found in the immediate proximity of the osculum. Some of these were actually bioclaustrated by the sponge. Occasionally, bryozoans were also growing in the immediate proximity of the osculum. Serpulids are sometimes aligned to the sponge's growth axis, and in a few sponges, large serpulid tubes formed a loop that made at least a whole turn around a sponge's branch. Other serpulids grew below an expanded fold or crest of the sponge.

5. Discussion

5.1. Comparison of *Endostoma* sp. sclerobiont community with other study cases from the AF and interpretation of the sclerobiont community

Endostoma sp. is by far the smallest basibiont studied so far from the AF. Substrate size can impact the richness of a sclerobiont fauna (e.g., Osman 1977; Keough 1984; Alexander & Scharpf 1990), but richness in *Endostoma* sp. is comparable to that of much larger molluscs (see Table 3), especially as it is a minimum value given the incomplete preservation of most serpulid tubes. In addition, the sclerobiont community in these sponges is taxonomically very similar to that of molluscs: all taxa found in *Endostoma* sp. are common sclerobionts in various other invertebrate shells, reinforcing the hypothesis that these sclerobiont taxa were quite capable of settling upon very different basibionts, corresponding also to varying settings. In addition, oysters are also

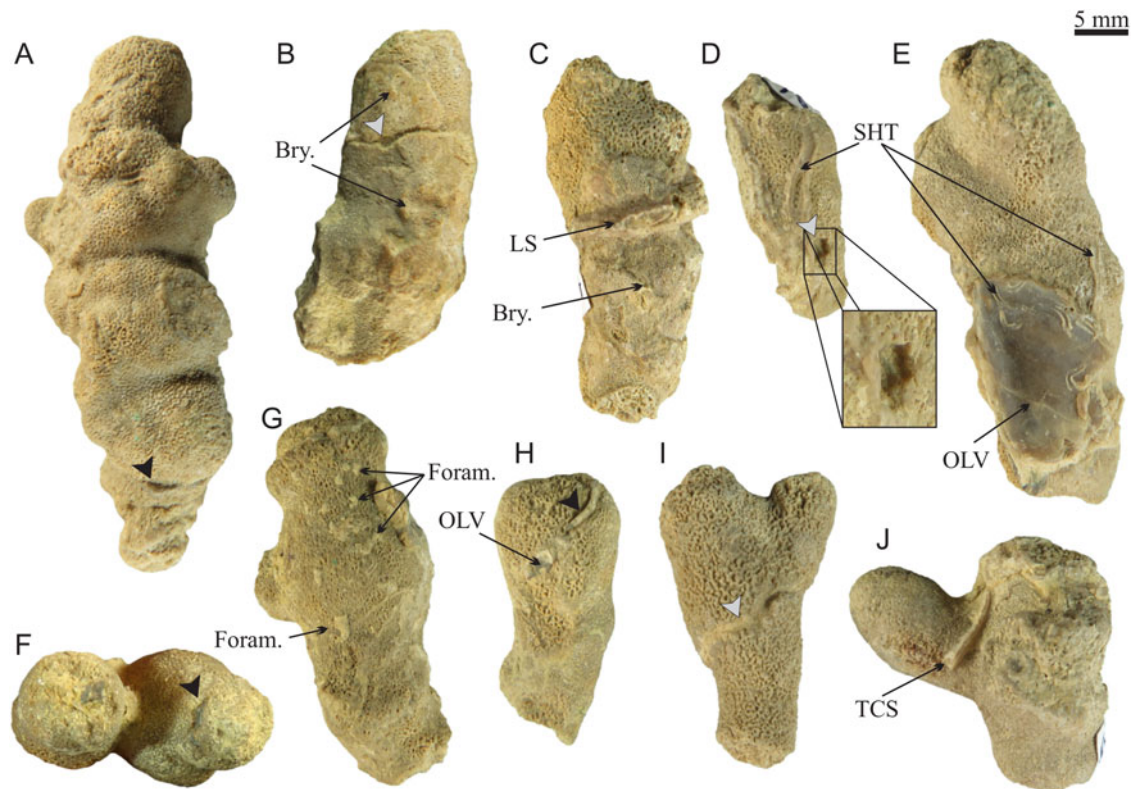


Figure 5 Sclerobiont fauna in *Endostoma* sp. aff. *nodosa* MOZ-Pi 12114. (a) Lateral view of specimen 12114.8, showing lateral buds and abundant inhalant openings. Towards the lower end, a partially bioimmured left oyster valve can be distinguished. (b) Specimen 12114.14 in lateral view, showing encrusting bryozoans and an irregular transversal mark (see detail in Fig. 6). (c) Specimen 12114.17 with a large serpulid (*Propomatoceros*) partially overgrown by two bryozoan taxa (see detail in Fig. 6). (d) Small branch fragment (specimen 12114.62) showing the ‘half-tube’ serpulid preservation and a marking of irregular shape. (e) Lateral view of specimen 12114.81 showing a large oyster left valve encrusted by small serpulids preserved as half-tubes. (f) Upper view of specimen 12114.80 showing bioimmured oyster by the osculum. (g) Lateral view of specimen 12114.64, encrusted by agglutinated foraminifers. (h) Lateral view of specimen 12114.33 showing partially bioimmured oyster left valve. (i) Lateral view of specimen 12114.82 showing an irregular mark. (j) Small, branched specimen (number 12114.91) with a tricarinate serpulid growing at the base of the branch. Black arrowheads point to partially bioimmured left oyster valves; grey arrowheads indicate markings on the sponge skeleton. Abbreviations: Bry = bryozoans; Foram. = foraminifers; LS = large serpulid (genus *Propomatoceros*); OLV = disarticulated, cemented oyster left valve; SHT = serpulid ‘half-tube’ preservation; TCS = tricarinate serpulid (genus *Mucroserpula*). Scale bar: 5 mm.

always the most common sclerobiont taxon, which has been attributed to its persistent high abundance in the Neuquén Sea and their pioneer role in the exploitation of organic hard substrates (Toscano *et al.* 2018; Luci *et al.* 2019).

A feature observed in *Endostoma* sp. that is not common among mollusc basibionts and their sclerobiont communities is the presence of four bryozoan taxa. In most molluscs, only the ubiquitous ‘*Berenicea*’ is found. The exception is the large epifaunal pectinid *Prohinnites*, in which four cyclostome taxa were recorded. *Prohinnites*, also from the Pilmatué Member of the AF, is abundant only in the Picún Leufú depocentre of the Neuquén Basin (though scarce, fragmentary records may be found in the Mendoza sector of the basin, and even more rarely in central Neuquén; see Fig. 1), as is *Endostoma* sp. It has been suggested that the more calcareous nature of the sedimentation in this area of the basin may have been better tolerated by bryozoans than the mixed carbonate–siliciclastic sedimentary input typical of the central part of the basin (see Luci & Lazo 2015). The recording of the same trend in a second study lends further support to this hypothesis. Both basibionts also have the highest number of interaction pairs among sclerobiont taxa and the highest number of sclerobiont–sclerobiont interaction occurrences. Both were also the most commonly encrusted, with over 90% of specimens having at least one sclerobiont.

However, *Prohinnites* valves were large and thick, offering stable settlement substrates, while *Endostoma* sp. only reached a few centimetres high and offered a much smaller surface for attachment. Thus, *Prohinnites* was commonly and extensively

encrusted because it offered a long-lasting, stable substrate. In contrast, the common colonisation of small *Endostoma* sp. by sclerobionts may be reflecting a lack of other available substrates in the immediate area; in contrast, *Prohinnites* was accompanied by abundant benthic fauna, so even though it was an attractive option for settlement, it was not the only one. In addition, the upwards growth direction of *Endostoma* sp. was taken advantage of by several sclerobionts, such as serpulids that commonly grew along the sponge vertical axis; this is also suggestive of *in vivo* settlement of some serpulids at least. Also, serpulids growing in this manner could also have been taking advantage of the sponge’s exhalant flows. Vertical growth is an advantageous factor for sclerobionts that bivalves can rarely provide. The irregular morphology of the sponge, with its crests and ridges, also provided a somewhat more sheltered habitat in its undersurfaces, that were taken advantage of by foraminifers and small serpulids. The scarcity of other substrates for settlement is likely the reason why overgrowths among sclerobionts, even if *post mortem*, are much more common in *Endostoma* sp. than in molluscs, even those located in shallower, more densely populated settings such as *Prohinnites*, and also than those that endured a much more prolonged time of exposure, such as the cephalopods.

Few studies have reported the presence of sclerobionts on fossil sponges, and most of these examples deal with Palaeozoic occurrences (see Gundrum 1979; Carrera 2000 for a short summary). Apart from calcareous tubes of uncertain affinity, other common Palaeozoic sclerobionts on sponges included bryozoans, brachiopods, acrothoracic barnacles, tabulate and rugose corals,

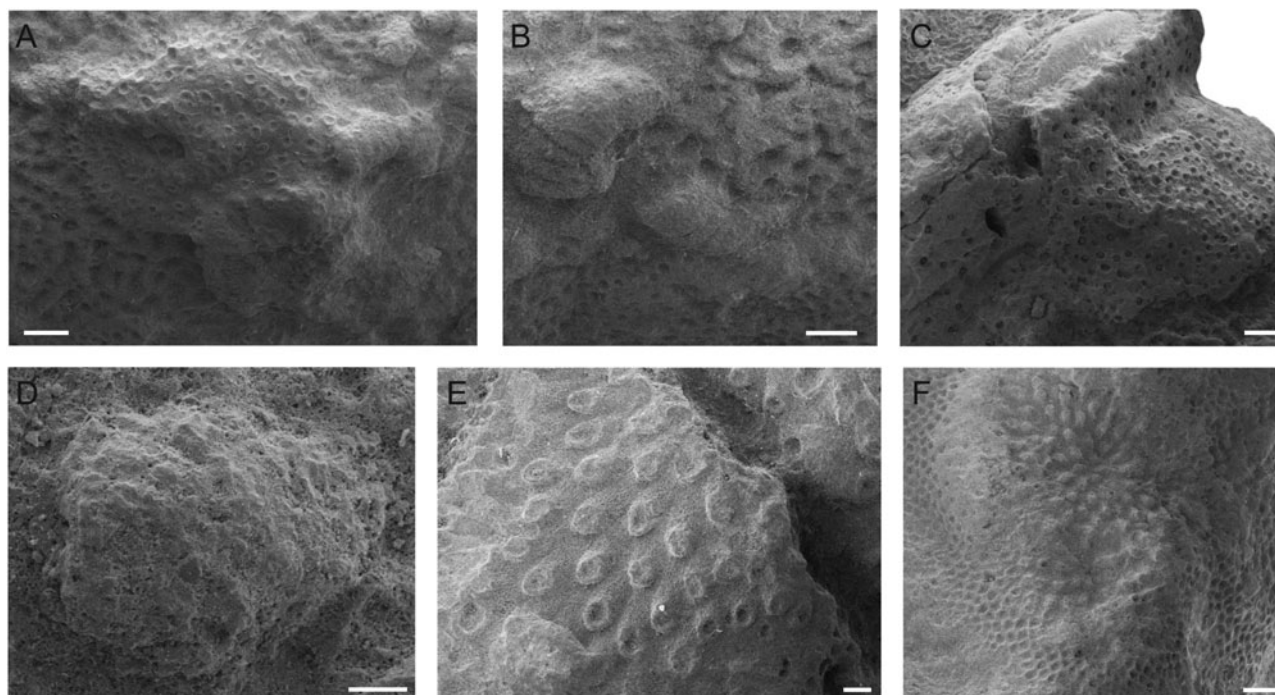


Figure 6. Scanning electron microscope pictures of sclerobionts in *Endostoma* sp. aff. *nodosa* MOZ-Pi 12114. (a) '*Berenicea*' sp. to the right, partially overgrowing foraminifers. Specimen 12114.22. (b, d) Detail of agglutinating foraminifers (both in specimen 12114.22). (c) Detail of specimen 12114.17 (see Fig. 5) showing encrusting *Propomatoceros* partially overgrown by *Idmonea*? sp. (e) Detail of specimen 12114.14, showing encrusting '*Berenicea*' and detail of the mark on the sponge and bryozoan skeleton. (f) Detail of a *Neuquenopora* colony in specimen 12114.22. See Table 1 for sclerobiont identification. Scale bars: 500 μ m.

pelmatozoans, foraminifers and other sponges (Gundrum 1979; Palmer & Fürsich 1981; Carrera 2000; Taylor & Wilson 2003). Mesozoic sclerobionts on sponges include bivalves, serpulids, brachiopods, sponges, bryozoans, corals, foraminifers, algal and microbial crusts (Palmer & Fürsich 1981; Fürsich & Werner 1991; Leinfelder 1992). Thus, the sclerobionts found in *Endostoma* sp. from the Neuquén Basin are, in taxonomic terms, in agreement with the known sclerobionts on sponges from the fossil record. This sclerobiont community is rather typical of other known Cretaceous examples (see Taylor & Wilson 2003 and references there, for an overview). The oldest known bioimmuration (Taylor 1990) is from the Ordovician of the United States, and involves the preservation of several soft-bodied and hard-bodied invertebrates on the underside of bryozoans. There are not many examples of bioimmuration of invertebrates by sponges (but see Carrera 2000; Cónsole-Gonella & Marquillas 2014), so this could be the oldest known record of bioclaustration by sponges.

Table 1 Presence–absence data of sclerobiont on sponges.

		# sponges	% sponges
Exogyrid oysters	<i>Cerastreon</i>	102	74.45
	Agglutinated foraminifers	40	29.20
Serpulid polychaetes	<i>Mucroserpula</i>	3	2.9
	<i>Propomatoceros</i>	26	18.8
	Undet. Serpulid	42	30.6
Sabellid polychaetes	<i>Glomerula</i>	12	8.6
Cyclostome bryozoans	<i>Berenicea</i>	37	27.1
	<i>Idmonea</i>	23	16.9
	<i>Proboscinoopora</i> ?	1	0.3
	<i>Neuquenopora</i>	2	1.46

'# sponges' represents the number of sponges bearing at least one individual of a given sclerobiont taxon. '% sponges' lists the percentage of sponges (over the total) that corresponds to the previous figures.

The term bioclaustration (Taylor 1990) has been used in a flexible way here (see section 4), since though it refers to the complete overgrowth of a soft-bodied organism by the skeleton of another, preserving its shape as a hollow mould, the process is very similar to the case of complete encasing of the skeleton (or part of it) of an organism by that of another. The common presence of bioclaustrated oysters indicates that *in vivo* settlement of sclerobionts was common, at least in the case of oysters, and that they were not harmful for the sponge. It is likely that sponges were not strongly affected by sclerobiont settlement due to the numerous inhalant openings in their skeleton. In fact, the finding of oysters as the sole preserved settlement substrates for sponges strongly suggests that in Cerro Marucho these two species established a positive feedback loop between them, in which they served as settlement substrate for each other in soft-bottom settings in which other invertebrate taxa were apparently incapable of inhabiting. Moreover, oysters sometimes seem to have taken advantage of the exhaling currents of *Endostoma* sp., as suggested by the common bioclaustration of oyster valves next to the osculum. Thus, oysters not only took advantage of the skeletons of the sponges for settlement, but also occasionally established a commensal relationship with them. This likely had little effect on *Endostoma* sp., as the filtering process performed by the sponge remained mostly unaltered, except for the covering of some inhalant openings. But, as stated above, the latter were very numerous, and eventually, following the oyster's death and disarticulation, the sponge managed to engulf the left oyster valves, which were the largest sclerobionts and thus the ones that covered the most pores. By overgrowing them, the sponge eventually recovered the inhalant surface covered by the oyster's left valves. It is curious that no other sclerobionts have been found at least partially bioclaustrated by the sponges. Serpulids, sabellids and foraminifers were perhaps ignored by the sponge due to their tubes covering smaller areas than oyster valves, and thus clogging fewer inhalant openings at a given section of the sponge skeleton. Though large serpulids may, as a whole,

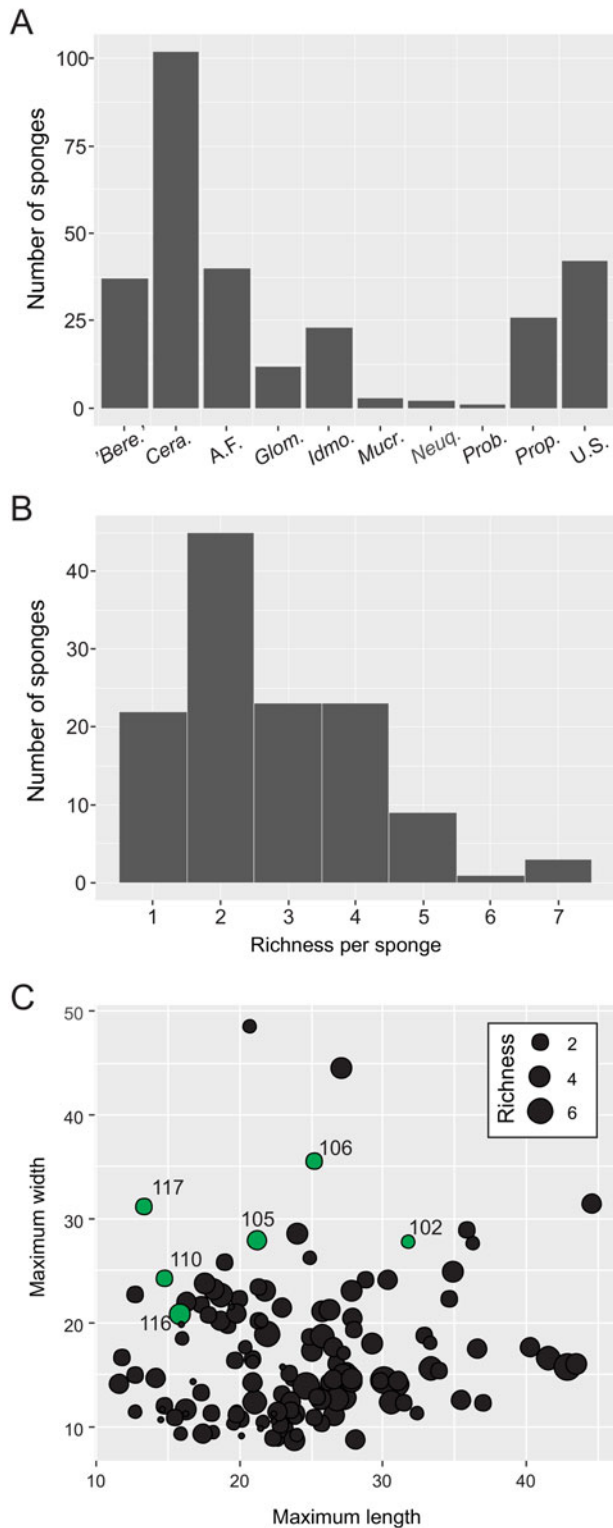


Figure 7. Statistical results of the sclerobiont fauna on *Endostoma* sp. aff. *E. nodosa*. (a) Bar plot showing the number of sponges bearing at least one specimen of a given sclerobiont taxon. Taxon names are shortened to their first four letters; see Table 1 for full names. (b) Bar plot showing the number of sponges with a given value of sclerobiont richness. (c) Plot of maximum width versus maximum height of sponges. Dot size represents richness of sclerobionts in each sponge. Green dots represent complete sponge specimens. Abbreviations: A.F. = agglutinated foraminifers; U.S. = undetermined serpulids.

have covered more openings than small oysters, these clogged inhalant openings are distributed across the sponge branch, while those covered by oysters are concentrated on their settlement spot. Bryozoans did occasionally cover quite a large area

Table 2 Interaction pairs among sclerobiont taxa.

Interaction pair	Occurrences
<i>Idmoneal/Berenicea</i>	2
<i>Propomatoceros/Ceratostreon</i>	1
<i>Idmoneal/undetermined serpulid</i>	3
<i>Propomatoceros/Idmonea</i>	1
<i>Idmoneal/Ceratostreon</i>	4
<i>Ceratostreon/Berenicea</i>	1
<i>Bereniceal/Ceratostreon</i>	5
<i>Bereniceal/foraminifer</i>	3
<i>Bereniceal/Idmonea</i>	3
<i>Neuquenoporal/Berenicea</i>	1
<i>Neuquenoporal/Idmonea</i>	1
<i>undetermined serpulid/Berenicea</i>	1
<i>Mucroserpulal/Berenicea</i>	1
<i>Glomerulal/Idmonea</i>	1
<i>Idmoneal/Propomatoceros</i>	1
<i>Foraminifer/Idmonea</i>	2
<i>Bereniceal/undetermined serpulid</i>	1
<i>Undetermined serpulid/Ceratostreon</i>	1
<i>Idmoneal/foraminifer</i>	1
Total	34

The taxon to the left represents the overgrowing organism; to the right the overgrown taxon. Occurrences represents the number of times each interaction was observed.

on sponges but seem to have remained undisturbed. These cyclostome taxa show no defensive structures, so it is unlikely that they defended themselves against the sponge. It is possible that the sponge was capable of overgrowing dead sclerobionts only, thus left oyster valves were the most common bioclaustrated ones.

The markings on the sponge's skeletons are difficult to interpret. Though some of them have morphologies that suggest manipulation by possible predators, or at least breakage (Fig. 5b, i), these morphologies are highly irregular and differ among specimens; not two markings are alike. Possible predators recorded elsewhere in the *Hoplitocrioceras gentilii* Zone of the AF include lobsters (Aguirre-Urreta 1989; Andrada *et al.* 2022). Durophagous fishes have also been recorded in the AF (e.g., Bocchino 1977; Gouiric-Cavalli *et al.* 2019). Thus, possible predators are known to have dwelt in the Neuquén Basin during the accumulation of the AF, but it is still difficult to confirm any of them as predators for the sponges.

Some other markings, however, are not suggestive of breakage (Fig. 5d), but represent small areas of the sponge skeleton where growth was apparently temporarily interrupted. At least some of these markings may correspond to the sponges encountering other sponges or their sclerobionts and growing around these foreign objects, resulting in their partial bioclaustration. Another possibility is that soft-bodied sclerobionts had established themselves at these sites but were subsequently overgrown by the sponges. This is an interesting possibility as it is highly unlikely that the presence of soft-bodied sclerobionts would be recorded on mollusc shells, but the capability of the sponges to overgrow these sclerobionts could allow these soft-bodied organisms to be recorded as traces. However, with the data available up to now no further inferences can be made in order to confidently settle the matter. Thus, the issue of their origin remains open.

5.2. Life history of the sponge meadow

The sponge meadow reported here is of special interest for comparison with the previously described benthic communities of the AF as it represents the maximum development and abundance of sponges in the unit. Sponges, very similar to the ones described here but much smaller in size, have been recorded

Table 3 Comparison of *Endostoma* sp. aff. *nodosa* sclerobiont fauna with those of several molluscs from the Pilmatué Member.

	Nautilids ¹	Globose ammonites ³	Compressed ammonites ³	Pectinid <i>Prohimmites</i> ²	Trigonoids ⁴	<i>Endostoma</i> (this paper)
Environment	Inner–outer ramp		Mid-outer ramp	Inner ramp	Mid ramp	Outer ramp
Transport	High–moderate, nekroplanktic drift			Low–moderate, paraautochthonous associations		
Richness	9	8	3	14	13	9
% encrusted basibionts	60.5	58.46	59.65	92.7	36.66	91.97%
Interaction pairs	6	5	0	16	2	19
Number of interactions	12	6	0	37	3	34

For further details on these, see ¹Luci & Cichowolski (2014); ²Luci & Lazo (2015); ^{3,4}Luci *et al.* (2016, 2019).

attached to ramose coral colonies in a few stratigraphic levels of the AF (Lazo *et al.* 2005; Garberoglio 2019). So, even as sclerobionts, sponges are rare in the unit, because corals appear only at discrete levels scattered across the AF, comprising either coral meadows or patch-reefs. The situation of Mesozoic sponge meadows outside the Neuquén Basin will be considered further in the Discussion, Section 5.3. But within the AF, sponges are absent from benthic communities except for this meadow and their presence as sclerobionts on corals.

The sponge meadow is restricted stratigraphically and geographically. It is recorded only in the locality of Cerro Marucho, despite the surveying efforts carried out in several nearby localities where the same levels are exposed (see for example localities in Cataldo & Lazo 2012; Luci & Lazo 2015). Its lenticular shape and limited vertical development, together with the small size of the sponges, suggests that the conditions for their settlement were quite limited in space and time.

The history of the sponge meadow can be reconstructed as follows. In a soft-bottom setting within the outer ramp, oysters were the only benthic dwellers locally at this particular time within the *H. gentilii* Zone. Benthic fauna were already scarce, as below the sponge meadow only an oyster shell bed is recorded. *Ceratostreon* oysters had a facultative reclining life habit which in addition to their small size and thin shells would have prevented them from sinking in the soft, muddy bottoms, allowing early colonisation. Oyster mass occurrences are not rare in the Early Cretaceous AF and are often formed in outer ramp settings (Toscano & Lazo 2020). In some cases, they have been associated with increased nutrient input conditions and/or relatively increased sedimentation rates (Toscano *et al.* 2018). They may be traced almost basin-wide, and replace the usual benthic communities composed by a variety of bivalves, gastropods and to a minor extent, decapods, echinoderms and other invertebrates (see, for example, Lazo *et al.* 2005; Lazo 2007b). Thus, conditions in this interval in the Cerro Marucho locality were already indicative of an environmental setting that did not allow the typical benthic macrofaunal association of the AF to thrive, before the sponge meadow established itself.

Sponges took advantage of abundant oyster valves to settle themselves and thrived on this otherwise soft bottom for some time (pioneer stage; Fig. 8a). Sponges were then encrusted by oysters, which in turn provided, at their death, additional valves for further sponge colonisation. Oysters were the early settlers/pioneers as sclerobionts because they were already present in the sea bottom. Oysters were then followed by sabellids, serpulids, foraminifers and bryozoans which often overgrew each other (climax stage) and were not, apparently, bioclaustated by the sponges, probably due to their covering fewer inhalant openings (Fig. 8b, c). Sclerobionts most likely settled preferentially on sponges due to their higher elevation above the substrate

than the oysters. Bryozoans occasionally covered serpulid tubes, most likely causing no harm had the serpulids still been alive, as long as openings were not obliterated. Bryozoans are often the overgrowing organisms in sclerobiont–sclerobiont interactions, but this may be because they were late settlers or because they are the only colonial organisms among sclerobionts, and thus more easily able to overgrow older, dead or inert skeletal parts of other sclerobiont taxa.

After a fairly short time, the sponge meadow perished (Fig. 8d). Though sponges are fragmented and not preserved in life position, no evidence of storm events was recorded in the field. One possible cause for the demise of this low-relief community could be increased sedimentation. A lack of oxygen within the first centimetres of the water column would imply extraordinary palaeoenvironmental changes of which there are no indication. High rates of sedimentation coupled with an elevated nutrient input were factors already in place as suggested by the high abundance of reclining oysters at the base of the sponge-bearing bed. An intensification in either sedimentation rates or nutrient input (or both) may have been the cause(s) of the meadow's demise. Sponges have been reported to tolerate higher sedimentation rates than other benthic taxa (see section 5.3) but being filter feeding animals they are still incapable of enduring sedimentation beyond a given threshold. The optimal conditions for sponge development existed only for a short period of time, and after conditions changed, the benthic fauna did not immediately flourish, since only ammonites are found in the interval above the sponge-bearing level.

5.3. Similar Mesozoic occurrences worldwide

The Mesozoic record of *Calcarea* is very sparse, and more so when it concerns forms similar to *Endostoma* sp. as the main benthic elements constituting sponge meadows or build-ups. Most known cases are from the Jurassic of Europe, especially from the Kimmeridgian of Portugal (Fürsich & Werner 1991; Leinfelder 1992; Werner *et al.* 1994). Several *Endostoma* species have been mentioned as forming 'moderately large' communities in some 'sheltered parts of the basin' in the Oxfordian of Poland, as reported by Hurcewicz (1975). However, this paper focused on the taxonomy of sponges, and thus the author did not elaborate much further on the ecological function and environmental setting of these sponges. Also, Reitner (1989) mentioned sponges communities containing *Endostoma* from the Aptian Faringdon 'Sponge Gravels' of England and Aptian–Albian coralline sponge communities from Spain. The role of *Endostoma* was not specified.

Palmer & Fürsich (1981) reported sponge patch reefs to bioherms with *Endostoma* as accessory frame builders from the Upper Bathonian of France. The environmental interpretation for these build-ups was a relatively shallow setting, below fair-

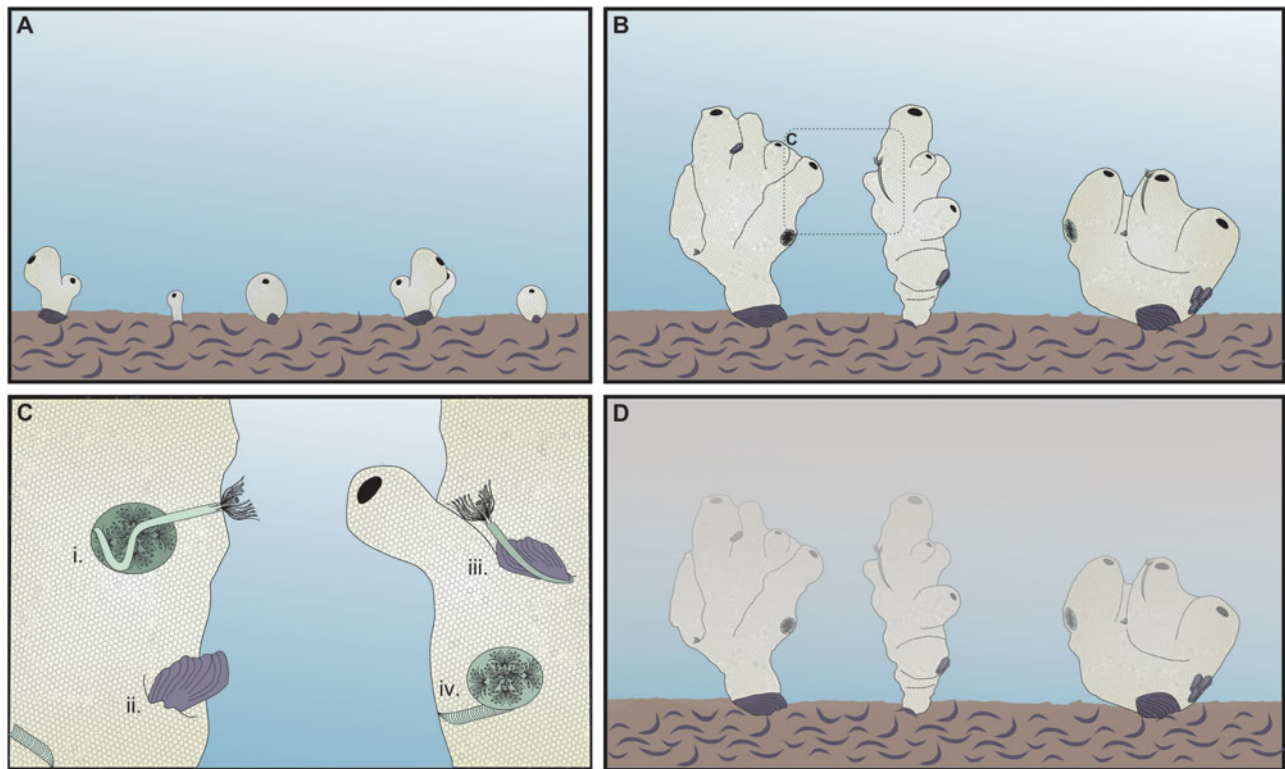


Figure 8. Succession sequence of *Endostoma* sp. aff. *nodosa* meadow. (a) Initially, within a quiet, soft bottom and probably exaerobic setting, with relatively high sedimentation rate and nutrient input, oysters were the sole organisms able to thrive. Their valves provided hard substrate (taphonomic feedback) in an otherwise sterile bottom, which was eventually exploited by *Endostoma* sp. aff. *nodosa*, giving way to the pioneer stage of the meadow. During this stage, sponges were on their early growth stages. (b) With time, sponges grew considerably and a dynamic sclerobiont community developed on them, representing the climax stage of the meadow. Oysters were early settlers, followed by sabellids, serpulids, foraminifers and bryozoans, which, in turn, often overgrew each other. (c) Detail of the sclerobiont community that developed on *E. aff. nodosa*. Several interactions between the sclerobionts and with the sponges were recorded (see also Table 2). (i) Serpulid overgrowing a ‘*Berenicea*’ sp. colony; (ii) *Ceratostreon* sp. left valve bioimmured by *E. sp. aff. E. nodosa*; (iii) serpulid overgrowing *Ceratostreon* sp. left valve; (iv) ‘*Berenicea*’ sp. colony overgrowing an agglutinating foraminifer. (d) Shortly after the climax stage, the meadow perished. An intensification in sedimentation rate and/or nutrient input beyond a threshold manageable for the sponges may have been the cause(s) of their demise.

weather wave-base but above storm wave-base, within the lower photic zone. Fürsich & Werner (1991) described low sponge–coral meadows from the Kimmeridgian of Portugal, in which *Endostoma* was a part of the frame-builder association. This association was interpreted as belonging to a shallow fully marine environment, with low sedimentation rates and moderate to low energy levels punctuated by occasional high energy events. Fürsich & Werner (1991) noted an increase in sponge abundance in detriment of corals towards the south-east, which they attributed to an increment in turbidity in that direction; sponges may have been able to cope with it better than corals. In addition, they noted that occasionally, greater influxes of fine-grained particles took place that probably prevented corals and sponges’ growth.

Complex coral reefs from the Kimmeridgian of Portugal had several coralline sponges as possible accessory frame builders, including *Endostoma* in a high-energy setting above fair-weather wave base (Leinfelder 1992). Also, from the Kimmeridgian of Portugal and Germany, *Endostoma* was reported within lenticular crinoid–coral mounds, hexactinellid and other siliceous sponge meadows, in which it did not play an important role (Werner *et al.* 1994). The inferred environmental setting was a fully marine, low-energy and low-sedimentation outer slope. Werner *et al.* (1994) drew a conclusion that is of relevance here: an increase of siliceous and calcareous sponges at the expense of corals could be caused by a slight increase in sedimentation, nutrients, or lowered oxygenation. Thus, sedimentation and nutrient input are reported as factors for which sponges may have increased tolerance as compared to other benthic fauna (especially other reef builders) but they may, under extreme conditions, hinder their development also.

Clearly the development of a low-relief, monospecific sponge meadow in Cerro Marucho corresponds with geographically and temporally limited, very specific conditions that allowed the sponges, a rare and marginal component of benthic faunas along the AF and other reported examples, to colonise the sea bottom as the main, and almost sole, benthic component, along with small *Ceratostreon* oysters. This is a previously unreported mode of occurrence of *Endostoma* sp. and similar sponges, the first for the Cretaceous outside the Tethyan Realm, and could draw attention upon other similar examples previously unnoticed.

6. Conclusions

This is the first record of calcareous sponges belonging to *Endostoma* for the Neuquén Basin and adds to the few known reports outside the Tethyan Realm. Despite usually being described as accessory builders or even accessory components of different types of build-ups, *Endostoma* could construct short-lived, low diversity, low relief meadows on quiet settings in association with small oysters. Sponges also housed a quite diverse sclerobiont community in an otherwise soft bottom. These sponges were quite capable of overgrowing sclerobiont oysters, which proves that at least some of the recorded encrustation took place *in vivo*. Some sclerobionts’ growth direction and placement were also suggestive of live interaction with the basibiont sponge. Oysters and some serpulids may thus have established a commensal relationship with *Endostoma*. This example adds to the knowledge about the genus’ palaeoecology by presenting a hitherto unknown role for small calcareous sponges.

7. Acknowledgements

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9. Competing interests

None.

10. References

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