



Coral-dominated communities from the Jurassic of Argentina: an overview

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ABSTRACT

This paper is a synthesis of the knowledge on the Jurassic coral-dominated communities of Argentina, providing novel information for some of them. Scleractinian corals were scarce during the Hettangian-Sinemurian but were frequent and diverse during the Pliensbachian. Three main communities are recognized for this last age: the earliest Pliensbachian Puesto Araya reef (Mendoza Province), the late Early to early Late Pliensbachian Piedra Pintada coral meadow (Neuquén Province), and the Late Pliensbachian to earliest Toarcian patches from Chubut Basin. After the end-Pliensbachian and Early Toarcian biotic crises, scleractinian corals reappeared in the Jurassic basins of Argentina in the latest Aalenian to Early Bajocian. By this last age they present high diversity, probably generating meadows. There are also some Callovian coral records spread throughout the Neuquén Basin. During the Oxfordian, coral-dominated communities reached their maximum development in the Jurassic of Argentina. A large coral reef of 13 km of lateral extension was described for Bardas Blancas (Mendoza Province), recognizing different zones within it. Coral meadows were described at Coihue Co and Covunco, while small patches developed at Las Lajas (Neuquén Province). Finally, during the Tithonian, coral meadows developed at Picún Leufú (Neuquén Province), and some corals were recorded in Mallín Cotidiano (Chubut Province, Austral Basin). The general trends observed for corals in Argentina (diversity peaks during the Pliensbachian and Bajocian, severe reduction during the Toarcian, the Oxfordian bioconstruction optimum) match the 'global' trends based mostly on the records from the Northern Hemisphere. These communities also bear great relevance in palaeoenvironmental interpretations, indicating shallow and well-lit marine environments.

Keywords: Scleractinia, Neuquén Basin, Chubut Basin, Austral Basin, reef, bioherm.

RESUMEN

Comunidades dominadas por corales del Jurásico de Argentina: una revisión general.

Este trabajo procura sintetizar el conocimiento de las comunidades dominadas por corales del Jurásico de Argentina, aportando información inédita para algunas de ellas. Los corales escleractinios fueron escasos durante el Hettangiano-Sinemuriano, pero se volvieron frecuentes y variados durante el Pliensbachiano. Tres comunidades principales fueron reconocidas durante esta edad: el arrecife de Puesto Araya (Mendoza) del Pliensbachiano Temprano más temprano, la pradera coralina de Piedra Pintada (Neuquén), del Pliensbachiano Temprano tardío al Pliensbachiano Tardío más temprano, y parches del Pliensbachiano Tardío al Toarciano más temprano de la Cuenca de Chubut. Después de las crisis bióticas de fines del Pliensbachiano y del Toarciano más temprano, los corales escleractinios reaparecieron en las cuencas jurásicas de la Argentina en el Aaleniano más tardío a Bajociano Temprano. Durante esta última edad muestran una gran diversidad, probablemente generando praderas coralinas. Hay también registros callovianos dispersos en la Cuenca Neuquina. Durante el Oxfordiano las comunidades coralinas alcanzaron su máximo desarrollo para

el Jurásico de Argentina. Un arrecife de 13 km de extensión fue descrito para Bardas Blancas (Mendoza), reconociéndose en ella diferentes zonas. En Coihue Co y Covunco se describieron praderas coralinas, mientras que en Las Lajas (Neuquén) se desarrollaron pequeños parches. Finalmente, durante el Tithoniano se desarrollaron praderas coralinas en Picún Leufú (Neuquén), y se registraron algunos corales en mallín Cotidiano (Chubut, Cuenca Austral). Las tendencias generales observadas para los corales de Argentina (los picos de diversidad durante el Pliensbachiano y el Bajociano, la drástica reducción durante el Toarciano, el óptimo de desarrollo de las bioconstrucciones durante el Oxfordiano) coinciden con las tendencias «globales» definidas mayormente sobre registros del hemisferio norte. Estas comunidades presentan también una gran importancia en la interpretación paleoambiental, indicando ambientes marinos someros y bien iluminados.

Palabras clave: Scleractinia, cuenca Neuquina, cuenca de Chubut, cuenca Austral, arrecife, biohermo

INTRODUCTION

Scleractinian corals appeared in the fossil record during the Anisian, but from then to the early Norian they represented minor components of reef environments. After a burst of taxonomic turnover in the Norian (Roniewicz 2011) both corals and sphinctozoan sponges began to dominate these environments (Stanley 2003). The Late Triassic sponge- and coral-dominated reefs were severely affected by the Triassic/Jurassic biological crisis (Stanley 2001, Flügel 2002, Lathuilière and Marchal 2009). The disruption of these environments was caused by a first-order extinction event that selectively affected reef communities more intensely than other benthonic communities (Kiessling et al. 2007).

Much of the Early Jurassic is marked by an eclipse interval of 5 to 8 million years with a global reduction in carbonate deposition and a virtual absence of reef-building (Stanley 2001, 2003, Pandolfi and Kiessling 2014). The few coral taxa surviving from the Triassic generated the scarce Hettangian–Sinemurian coral reefs (Leinfelder et al. 2002), some of them reaching relatively high palaeolatitudes (see Stanley and McRoberts 1993, Leinfelder et al. 2002, Kiessling et al. 2009, Lathuilière and Marchal 2009, Boivin et al. 2018). During Pliensbachian times, solitary coral diversity reached a peak, but this diversity increase was interrupted by a new extinction at the end of the stage (considered as a first-order crisis for Scleractinia) and a significant reef collapse (Lathuilière and Marchal 2009, Vasseur et al. 2021). As a consequence, corals suffered a taxonomic reorganization, with the loss of all Triassic holdover taxa and the appearance of many new genera and species that became dominant in later Jurassic times (Stanley 2003, Vasseur et al. 2021).

At the beginning of the Middle Jurassic, reefs were driven back to possibly one single reef domain in Morocco (Leinfelder

et al. 2002), but during the Bajocian coral diversity increased in conjunction with the development of a new global reefal event, well documented in the Tethys (Stanley 2001, Lathuilière and Marchal 2009). Reef-building genera became more numerous and cosmopolitan, though species distribution allows for the recognition of several distinct basins (Beauvais 1984). From the Bathonian to the early Oxfordian a cooling trend developed, marked by the disappearance of coral reefs from relatively high latitudes in North America and Europe, and a slight reduction in the number of genera (Beauvais 1984), though coral-dominated communities were still frequent.

Favourable conditions for reef development reappeared in the middle Oxfordian and reefs began to expand all over the world, with coral reefs reaching relatively high latitudes once again (Beauvais 1984, Leinfelder et al. 2002). The development of a global east-west current system aided considerably in the global distribution of corals (Leinfelder et al. 2002), and by Oxfordian–Kimmeridgian times between 130 and 150 genera were recorded with major new groups (Beauvais 1984, Leinfelder et al. 2002).

Loss of habitats triggered a reduction of coral reef sites during the Early Tithonian, and from the mid-Tithonian onwards, the falling global sea level dramatically accelerated the withdrawal of reefs in most areas (Leinfelder et al. 2002).

Jurassic reef corals were most likely zooxanthellate, though not as efficient as modern ones (Leinfelder 2001), probably encompassing two adaptive strategies: 1) the adaptation to terrigenous settings, triggering partial adaptation towards turbidity and siltation stress; and 2) the adaptation to truly oligotrophic tropical intra-ocean settings (Leinfelder et al. 2002). The first strategy, nonetheless, was largely wiped out by the demise of such marginal settings owing to the Late Jurassic–Berriasian sea-level drop, while the second strategy might have provided the nucleus for further colonization of

oligotrophic environments, leading to the modern reefs (Leinfelder et al. 2002). This view has been questioned, nonetheless, since during the Neogene, a moment of increase in reef development, there is also an important proportion of reefs in marginal and/or siliciclastic settings, even larger than the proportion of Jurassic reefs in this kind of settings (Kießling 2002, Dimitrijević et al. 2024). In any case, these variations highlight the need for caution when comparing reefs in the geological record with their modern counterparts (Leinfelder 2001).

This global picture is focused mostly on the Northern Hemisphere, particularly on the Tethys and North America, with scarce examples of coral-dominated communities from South America. This paper aims to provide, as an update of current research on the subject, a comprehensive overview of the present state of knowledge about previously less known coral-dominated communities from southern hemisphere mid-palaeolatitude epeiric seas, such as the Neuquén, Chubut and Austral basins in western Argentina, together with some new information by the authors from various localities and ages. A comprehensive synthesis, including palaeoecological and palaeobiogeographical implications, is also provided.

Descriptive terminology. It follows the usage among fossil Scleractinia researchers as established in the Treatise on Invertebrate Paleontology (Wells 1956) and still currently applied (e.g., Budd and Stolarski 2009, Löser 2024).

Both corallite arrangement and general shape of the corallum were considered when characterizing coral associations, as they provide different palaeoecological information. Corallite arrangement (or corallite integration) has been usually related to the inference of zooxanthellae symbiosis, with higher levels of integration considered as one of the indications of the presence of zooxanthellae (Nose and Leinfelder 1997, Gill et al. 2004, Kießling and Kocsis 2015, Tornabene et al. 2017, Kolodziej et al. 2018), and is related to the ability of the colony for sediment clearance (Ricci et al. 2018). It also provides systematic information, as it is crucial for the determination of the genera (Löser 2024).

Corallum shape, on the other hand, is usually related to environmental variables such as hydrodynamic energy, sedimentation rates and sunlight incidence (Chappell 1980, Insalaco et al. 1997, Stanley and Lipps 2011, Ricci et al. 2018), being variable even within the same species. Colonial coralla can be branching (independent of the corallite arrangement); massive, if they form more or less thick masses or heads; foliaceous, if they form thin, expanding, overlapping sheets with a small basal attachment; and platy, if they have a thin, flattened, sheet-like form. Within the branching morphologies, three main types can be differentiated: caespitose, repre-

sented by small colonies (up to 25 cm high and 40 cm basal diameter) with fine branches (0.5 cm to 1.5 cm diameter) of variable packing, without a main axis and with domical outline; corymbose, represented by large colonies (up to 1.8 m high and 2 m basal diameter) with branches of constant diameter (3 cm) and loosely arranged, without a main axis and with elliptical to domical outline; and arborescent, represented by large colonies (up to 1.8 m high and 2 m basal diameter) with a main axis (up to 15 cm wide) and loosely arranged branches (up to 5 cm at their base) decreasing in diameter towards the apex (for more detailed description and measures see Hoqui 2022).

Also, the descriptive terminology of Insalaco (1998) for coral-bearing beds was applied, recognizing six styles of growth fabric development depending on the growth form of the corals generating the bulk of the deposits (over 60% of the coral skeletal volume). Pillarstones (dense or sparse) are constituted by branching morphologies; platestones are dominated by platy corals; sheetstones are generated by very thin and laterally expanded colonies; domestones are constituted mostly by massive morphologies; and mixstones are related to varied morphologies, none of them representing more than 60% of coral skeletons.

The term 'meadow' is used in this paper to refer to coral communities of scattered coralla (separated by sediment) without making upwards-growing buildups but with wide lateral development (see Fürsich and Werner 1991, Melnikova and Roniewicz 2012). On the other hand, the use of the term 'reef' refers to rocky bodies generated by in situ high calcium carbonate production, as a direct or indirect result of the aggregation and cementation of sessile epibenthic marine organisms capable of thriving in energetic environments and developing a structure with positive topographic relief on the seafloor (James and Bourque 1992, Wood 2001). This structure is laterally constrained by surrounding sediments that are linked to it in its genesis.

Also, and particularly to describe the reef facies in the Bardas Blancas area, arbitrary categories were generated according to the size of the structures that make up the reef complex. The reef is divided into zones or components; these are, in increasing order of size: colonies, patches and pseudobarriers (Hoqui 2022). The minimum component of this classification is the individual colony (never larger than 2.5 m in diameter). This is followed by patches that originate because more than one colony grows at a distance of less than 2.5 m. Each patch can be singled out and measured and may exceed ten metres in lateral extent and up to ten metres in thickness. When more than one patch grows in close proximity, we use the term pseudobarrier, its size can reach up to 100 m in

horizontal extent and exceed ten metres in height.

Repositories and institutional abbreviations. Specimens examined are housed in the following repositories: IANIGLA-PI = Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, Mendoza, Argentina; MCF-PIPH = Museo Municipal Carmen Funes, Plaza Huinca, Argentina; MLP = División Paleozoología Invertebrados, Museo de Ciencias Naturales de La Plata, La Plata, Argentina; MOZ-PI = Museo Provincial de Ciencias Naturales “Dr. Prof. Juan A. Olsacher”, Zapala, Argentina; and MPEF-PI, Museo Paleontológico Egidio Feruglio, Chubut, Argentina. Further specimens examined are housed in: CPBA = Geology Department, Universidad de Buenos Aires, Buenos Aires, Argentina; SIRAME-SEGEMAR and DNGM= Dirección Nacional de Geología y Minería, Buenos Aires, Argentina.

GEOLOGICAL SETTING

Marine Jurassic in Argentina developed in three main basins: Neuquén, Chubut and Austral basins; coral-dominated communities were reported in all of them, though it is in Neuquén Basin where they developed more frequently (Fig. 1).

The Neuquén Basin is located to the east of the Andes, between 32°S and 40°S (Howell et al. 2005) and it encompasses most of the Jurassic stages in marine facies (Fig. 1). Its development began with a rifting phase that lasted from the Middle Triassic to the Sinemurian (Ramos 1992, Manceda and Figueroa 1995), which led to the evolution of a series of narrow and isolated depocentres (Uliana and Biddle 1988, Legarreta and Uliana 1996). Marine sedimentation began in southern Mendoza Province (Fig. 2) by Late Triassic times (Riccardi et al. 1988). After it, a sag stage (late Early Sinemurian to Toarcian) developed, causing the coalescence during the late Sinemurian-Pliensbachian of the initial depocentres and the enlargement of the area under marine influence (Legarreta and Gulisano 1989, Legarreta and Uliana 1996, see Fig. 2). From this time on, until the Early Cretaceous, it developed as a back-arc basin related to circum-Pacific convergence (Legarreta and Uliana 1996, Howell et al. 2005). According to Groeber (1946) a major sedimentary cycle (his ‘*ciclo Jurásico*’) developed until Oxfordian-Kimmeridgian, with the closure to marine sedimentation; as a consequence, no marine sediments were deposited during the Kimmeridgian (Fig. 1). During the Tithonian marine sedimentation resumed, marking the beginning of a new sedimentary cycle (‘*ciclo Andico*’). Tithonian sediments are currently included in the Mendoza Group (Groeber 1946, Digregorio and Uliana 1980, Ric-

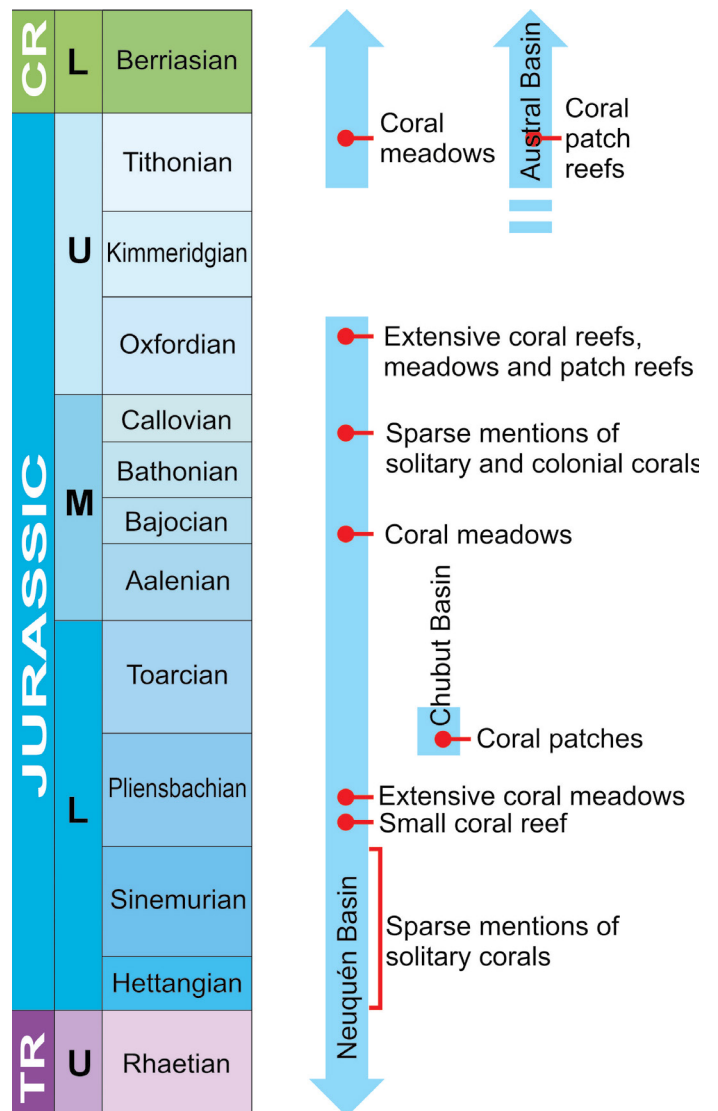


Figure 1. General development of the Jurassic basins in Argentina and stratigraphic position of the coral-dominated communities discussed in the text. Light blue stripes indicate the temporal ranges of marine sedimentation.

cardi 1988).

The Chubut Basin is a NNW-SSE elongated depocentre, lying unconformably over late Palaeozoic rocks, with marine beds deposited during a short time interval from Pliensbachian to Early Toarcian (Riccardi 2008a, 2008b, see also Fig. 1). Both marine and continental sedimentary deposits of Early Jurassic age, crop out mainly in the western region of the Chubut Province, central-northern Santa Cruz Province, and southwestern Río Negro Province (from 41°00'S to 44°30'S, Fig. 2) (Suárez and Márquez 2007). The sedimentary succession of the Chubut Basin accumulated under an extensional tectonic regime (Lizuaín 1999, Uliana and Legarreta 1999), starting with continental deposits overlain by shallow marine and continental successions. These marine beds normally in-

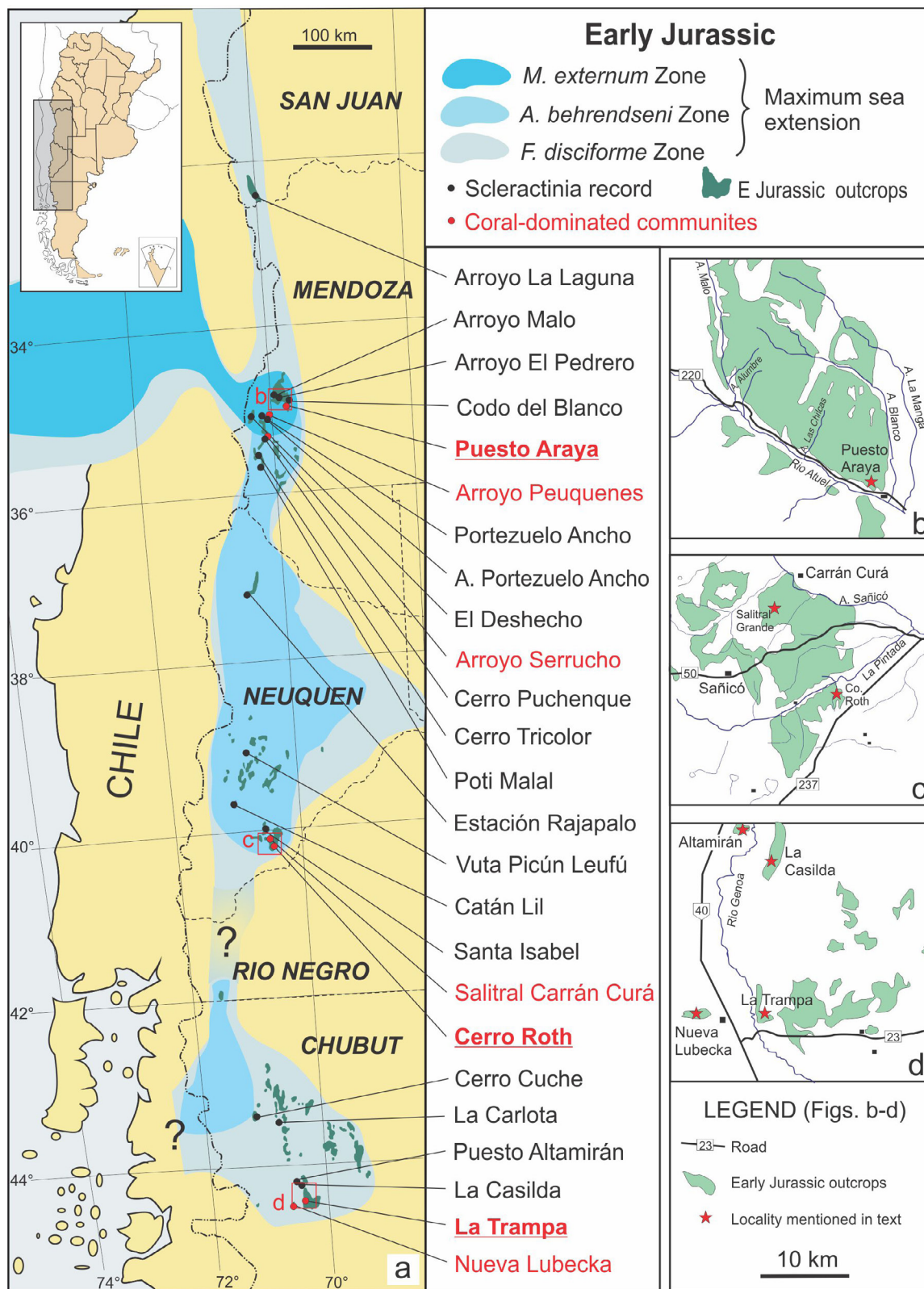


Figure 2. Early Jurassic location maps. a. Map of western Argentina showing the maximum extension of the sea during the Early Jurassic at different times (modified from Legarreta and Uliana 1996, and Vicente 2005), and the location of Early Jurassic scleractinian records (based on data from previously known records and new ones from the authors). The localities with known coral-dominated communities are in red, those described in the text are underlined. b-d. Location sketch maps of the examples discussed in the text. b. Puesto Araya in the upper Atuel river region, Mendoza Province. c. Cerro Roth and Salitral Grande de Carrán Curá in the Piedra Pintada region, Neuquén Province. d. La Trampa and Nueva Lubecka in the Genoa river region, Chubut Province.

terfinger with continental facies, mainly pyroclastic, to the east (Franchi et al. 1989).

The Austral Basin was a retro-arc marine basin developing between the Late Jurassic and the Early Cenozoic, in southwestern Patagonia and Tierra del Fuego Island; in Argentina it encompasses western Tierra del Fuego and Santa Cruz provinces, and southwestern Chubut Province (Suárez et al. 2009, Cuitiño et al. 2019). The Jurassic outcrops belong to the rift stage of sedimentation, with the marine transgression developing over grabens and half-grabens on a Middle-Upper Jurassic volcanic basement (Suárez et al. 2009, Cuitiño et al. 2019). Towards the north of the basin (southwestern Chubut Province), marine sedimentation began in small inner retro-arc and intra-arc depocentres, developed in a volcanic context (Folguera and Iannizzotto 2004), most likely during the Tithonian (Olivero 1987, Bucur et al. 2009, Aguirre-Urreta et al. 2022, Fig. 1).

JURASSIC CORAL COMMUNITIES FROM ARGENTINA

The published information on Jurassic corals from this part of the world is limited and scattered; the oldest references for Argentina date from late in the 19th century: Behrendsen (1891) mentioned *Montlivaltia?* from Portezuelo Ancho, Mendoza. Later Jaworski (1915), Gerth (1925, 1926, 1928), and Weaver (1931) described solitary and colonial coral species from several localities in the Neuquén Basin. More recent papers deal with diverse aspects of the coral communities, their evolution and palaeoenvironment (Damborenea et al. 1975, Morsch 1986, Matheos and Morsch 1990, Lanés and Morsch 1998, Massaferro et al. 1998, Palma et al. 2007, 2009, Echevarría et al. 2017, 2024, Hoqui et al. 2019). Unfortunately, despite their increasing records, taxonomic studies are few (Gerth 1926, 1928, Weaver 1931, Morsch 1990, 1991, 1996, 2001, Hoqui et al. 2019), in part due to the deficient preservation of the available specimens. A list of the systematic identifications compiled from the literature is provided (Table 1).

This section will be arranged by age, from oldest to youngest records, and divided by geochronologic epochs. For each time interval, the most relevant references are summarized and complemented by field observations by the authors.

Early Jurassic

Hettangian-Sinemurian

As elsewhere in the world, scleractinians were scarce in Hettangian and Sinemurian beds in the Neuquén Basin; only solitary corals were recorded in the Puesto Araya Formation

in southern Mendoza, mostly as rare occurrences in a recurrent biofacies dominated by diverse pectinoid and limoid bivalves (Damborenea and Manceñido 2005). The specimens were discussed and figured by Echevarría et al. (2017, p. 73, fig. 4). Most of the materials so far available are preserved as moulds; hence, precise systematic assignments are not possible, but these Hettangian and Sinemurian corals are morphologically rather uniform (simple discoidal coralla) and low in diversity, likely representing only one or two taxa. As discussed by Echevarría et al. (2017), some of them strongly resemble the species *Haimeicyclus haimeii* (Chapuis and Dewalque 1853), known from Hettangian–Sinemurian strata of Europe.

Pliensbachian

The impoverished picture described for Hettangian and Sinemurian drastically changed by Early Pliensbachian times, when coral records became more common throughout the Neuquén Basin (Fig. 2.a). Solitary corallum shapes were more diverse and colonial scleractinians were first recorded for the Jurassic in the basin (Echevarría et al. 2017, figs. 5-6) and soon diversified. These corals usually contributed to various benthonic macroinvertebrate associations, but only in some cases they dominated their communities, in localities spanning a wide palaeolatitudinal range. We will focus on three different time points, each of them developing a particular coral-dominated community: (a) Early Pliensbachian *Meridicerases externum* Zone, with a reef in southern Mendoza Province, (b) late Early Pliensbachian *Austromorphites behrendseni* Zone, with coral meadows in southern Neuquén Province, and (c) Late Pliensbachian–Early Toarcian *Fanninoceras disciforme*–*Tenuicostatum* Zones, with coral patches in Chubut Province (Chubut Basin).

There is a general trend for coral-dominated communities to shift southwards throughout the Pliensbachian (Echevarría et al. 2023); this trend seems to accompany the southward advancement of the epeiric sea (Fig. 2.a). This may represent a facies progradation, with the main coral communities occupying a similar environment throughout the marine transgression. It is also worth bearing in mind that this trend may be related to the northward displacement of the whole basin postulated by palaeomagnetic studies (Iglesia-Llanos et al. 2006).

(a) *Meridicerases externum* Zone - The marine transgression was restricted to the south of Mendoza Province during the Early Pliensbachian (Fig. 2.a). In the Atuel River region (Fig. 2.b), the Puesto Araya Formation crops out, with siliciclastic deposits indicating a storm-dominated shelf, evolving from a wave-dominated estuary to a turbidity-current-influenced outer shelf (Lanés 2005). Close to the locality of Puesto Araya (Fig. 2.b), on the slope of a hill just north of the road (Fig. 3.a)

Table 1. Coral taxa from Argentina recognized by the different authors at different moments during the Jurassic. Continues on next page.

Time slice	Taxa	References	Localities (maps in Figs. 2, 8)	Age
Late Jurassic	<i>Eocolumastrea octaviae</i> (Prever 1909)	Garberoglio et al. 2023	Picún Leufú (Neuquén)	Late Tithonian
	<i>Stelidioseris columbaris</i> (Scott and Aleman 1984)	Garberoglio et al. 2023	Picún Leufú (Neuquén)	Late Tithonian
	<i>Stelidioseris</i> sp.	Aguirre-Urreta et al. 2022, fig. 9.a-b	Mallín Cotidiano (Chubut)	Tithonian
	<i>Stephanastrea</i> sp.	Beresi et al. 2017, fig. 8e-f	Covunco (Neuquén)	Oxfordian
	<i>Etallonasteria</i> cf. <i>minima</i> (Étallon in Thurmann and Étallon 1864)	Palma et al. 2009: fig. 7c; Hoqui et al. 2019: fig. 8	Bardas Blancas (Mendoza); Covunco (Neuquén)	Oxfordian
	<i>Stelidioseris</i> sp.	Palma et al. 2009: fig. 7a-b; Beresi et al. 2017, fig. 8c-d; Hoqui et al. 2019: fig. 6-7	Bardas Blancas, Coihue Co (Mendoza); Lajas, Covunco (Neuquén)	Oxfordian
	<i>Australoseris radialis</i> Morsch 1990	Morsch 1990: pl. 1, 4-5, pl. 2, fig.1-5	Bardas Blancas, Coihue co (Mendoza); Covunco, Lajas, Sierra Vaca Muerta (Neuquén)	Oxfordian
Middle Jurassic	<i>Montlivaltia andina</i> Gerth 1928 (aff. <i>kobyi</i> Beauvais 1966 in Morsch 1996)	Gerth 1928: pl. 2, fig. 3, 3a; Weaver 1931: pl. 11, fig. 1-5; Morsch 1996: pl. 87, fig. 4a-b	Ayo Los Molles, Los Pozones, Chacaico (Neuquén)	Callovian
	" <i>Convexastrea</i> " <i>weaveri</i> Gerth 1928	Gerth 1928: pl. 2, fig. 5; Weaver 1931: pl. 11, fig. 9; Morsch 1996: pl. 83, fig. 2a-d, t-fig. 3	7 km NW Co Picún Leufú, Los Pozones (Neuquén)	Callovian
	<i>Convexastreopsis caracolensis</i> (Steinmann 1881)	Gerth 1928; Weaver 1931; Morsch 1996: pl. 88, fig. 1a-c	7 km NW Co Picun Leufú, Los Pozones (Neuquén)	Callovian
	<i>Convexastraea</i> sp.	Weaver 1931, pl. 11, fig. 12	Ayo Los Molles (Neuquén)	Callovian
	<i>Neuquinosmilia lospozonenensis</i> Morsch 1991	Morsch 1991, pl. 1, fig. 1-7, pl. 2, fig. 1-4, pl. 3, fig. 1-5, pl. 4, 3-7; 1996: pl. 87, fig. 1a-b	Los Pozones (Neuquén)	Bajocian? Callovian?
	? <i>Stephanastrea ramulifera</i> Étallon (in Thurmann and Étallon) 1864	Morsch 1996: pl. 83, fig. 1a-e	Los Pozones (Neuquén)	Bajocian? Callovian?
	<i>Mapucheastrea andina</i> Morsch 1996	Morsch 1996: pl. 89, fig. 1a-d, t-fig. 11	Barda Negra S, Los Pozones (Neuquén)	Bajocian - Callovian?
	<i>Araucanastrea minuscula</i> Morsch 1996	Morsch 1996: pl. 84, fig. 1a-e; t-fig. 2	Barda Negra S (Neuquén)	Early Bajocian
	<i>Araucanastrea majuscula</i> Morsch 1996	Morsch 1996: pl. 84, fig. 2a-c	Barda Negra S (Neuquén)	Early Bajocian
	<i>Garateastrea bardanegrensis</i> Morsch 1996	Morsch 1996: pl. 85, fig. 1a-f, t-fig. 4-7	Barda Negra S (Neuquén)	Early Bajocian
	<i>Kobyastraea louisae</i> Morsch 1996	Morsch 1996: pl. 86, fig. 1a-e, fig. 8-9	Barda Negra S (Neuquén)	Early Bajocian
	<i>Astraraea</i> cf. <i>fungiformis</i> Beauvais (in Negus and Beauvais) 1979	Morsch 1996: pl. 89, fig. 2a-c	Barda Negra S (Neuquén)	Early Bajocian
	<i>Pseudocoeniopsis</i> cf. <i>wintoni</i> (Wells 1933)	Morsch 1996: pl. 86, fig. 2a-c	Barda Negra S (Neuquén)	Early Bajocian
	<i>Convexastreopsis</i> sp.	Morsch 1996: pl. 88, fig. 2a-b	Barda Negra S (Neuquén)	Early Bajocian
	<i>Cyathophylloids delabechei</i> (Milne-Edwards and Haime 1851)	Morsch 1996: pl. 87, fig. 3a-c	Barda Negra S (Neuquén)	Early Bajocian
	<i>Neuquinosmilia gerthi</i> Morsch 1996	Morsch 1996: pl. 87, fig. 2a-c, t-fig. 10	Barda Negra S (Neuquén)	Early Bajocian
Scleractinia indet.	Álvarez 1997: fig.30.c-d	La Ramada (San Juan)	Early Bajocian	

some beds corresponding to a small coral reef (Puesto Araya reef) were recognized in the *Meridiceras externum* Zone. These beds were already mentioned by previous authors (Lanés and Morsch 1998, Morsch 2001) and described in detail by Echevarría et al. (2024). The general logged section in which these beds are included (Fig. 3.b) shows tidal-dominated deposits towards the base, followed by storm and fair-weather deposits fining and thinning upwards (Lanés 2005).

To better understand the development of Puesto Araya reef, Echevarría et al. (2024) logged five sections distribut-

ed along a north-south transect (Fig. 3.c). The reef crops out with a lateral extension of more than 130 metres (though the outcrops are covered southwards, and the reef was, most likely, more extensive) and has a vertical development of up to 6 metres. Coral diversity is low; Morsch (2001) recognized three coral taxa from the Puesto Araya section: the solitary *Styllophyllopsis?* cf. *victoriae* (Duncan 1868) which appears in great abundance in beds a few metres below the reef, the phaceloid *Phacelostylophyllum* cf. *peruvianum* (Wells 1953) (Fig. 4.a-b) and the cerioid *Meandrostylis?* *jaworskii* (Gerth

Table 1 cont. Coral taxa from Argentina recognized by the different authors at different moments during the Jurassic.

	<i>Cyathophora decamera</i> Gerth 1928	Gerth 1928: pl. 2, fig. 4; Weaver 1931: pl. 11, fig. 8	N Catán Lil (Neuquén)	Pliensbachian?
	<i>Stylophyllopsis?</i> cf. <i>victoriae</i> (Duncan 1868)	Gerth 1928; Weaver 1931; Carral Tolosa 1942: pl. 1, fig. 1; Morsch 2001: fig. 2.1; Ferrari and Bessone 2015: fig. 3.Y; Aguirre-Urreta et al., 2022, fig. 3d, 3i	Puesto Araya (Mendoza); Cerro Roth (Neuquén); La Casilda, Nueva Lubecka, La Trampa (Chubut)	Pliensbachian
	<i>Phacelostylophyllum</i> cf. <i>peruvianum</i> (Wells 1953)	Morsch 2001: fig. 2.2	Puesto Araya (Mendoza)	Early Pliensbachian
	<i>Meandrostylis?</i> <i>jaworskii</i> (Gerth 1926)	Gerth 1926: pl. 4, fig. 24; Morsch 2001: fig. 3.3	Cerro Puchenque, Puesto Araya (Mendoza)	Pliensbachian
	<i>Collignonastrea?</i> sp.	Damborenea 2002, pl. 11, fig. 13	Cerro Roth (Neuquén)	Pliensbachian
	<i>Distichomeandra</i> cf. <i>austriaca</i> (Frech 1890)	Morsch 2001: fig. 4.2	Santa Isabel, Cerro Roth (Neuquén)	Pliensbachian
	<i>Retiophyllia?</i> sp.	Morsch 2001: fig. 2.3	Cerro Roth (Neuquén)	Pliensbachian
Early Jurassic	Scleractinia indet. (solitary, discoidal)	Echevarría et al. 2017: fig. 5.1-4	Portezuelo Ancho; Codo del Blanco (Mendoza)	Pliensbachian
	Scleractinia indet. (solitary, patellate)	Echevarría et al. 2017: fig. 5.8-10	Arroyo Peuquenes, A. Pzo Ancho (Mendoza)	Pliensbachian
	Scleractinia indet. (solitary, cylindrical)	Echevarría et al. 2017: fig. 5.20-22	Arroyo Serrucho (Mendoza)	Early Pliensbachian
	Scleractinia indet. (solitary, turbinate)	Echevarría et al. 2017: fig. 5.11, 5.15-16	A. Pzo Ancho (Mendoza)	Pliensbachian
	<i>Stylophyllopsis?</i> cf. <i>victoriae</i> (Duncan 1868)	Echevarría et al. 2017: fig. 5.12-14, 5.19	A. Pzo Ancho; Co La Brea (Mendoza)	Pliensbachian
	Scleractinia indet. (solitary, trocoid/ceratoid)	Echevarría et al. 2017: fig. 5.17-18	A. Pzo Ancho (Mendoza)	Early Pliensbachian
	Scleractinia indet. (colonial, phaceloid)	Echevarría et al. 2017: fig. 6.1-4	Puesto Araya (Mendoza)	Early Pliensbachian
	cf. <i>Meandrostylis?</i> <i>jaworskii</i> (Gerth 1926)	Echevarría et al. 2017: fig. 6.5-7	Puesto Araya (Mendoza)	Early Pliensbachian
	cf. <i>Haimeicyclus haime</i> (Chapuis and Dewalque 1853)	Echevarría et al. 2017: fig. 4	Arroyo Malo (Mendoza)	Hettangian-Sinemurian

1926) (Fig. 4.c-d).

A clear vertical succession could be recognized, identifying the main developmental stages defined by Walker and Alberstadt (1975), but these stages were recurrent sometimes, implying that allogenic environmental fluctuations were partly responsible for this kind of succession, as highlighted by some authors (see Mewis and Kiessling 2013).

At least two, but most likely three, phases could be recognized. The first phase begins with a conspicuous colonization stage, represented by pillarstones (Fig. 3.c) of phaceloid colonies in life position (Fig. 4.a-b). Scarce cerioid colonies may appear associated with this stage, as well as bivalves of varied life habits (epibyssate, endobyssate, even occasionally burrowers); echinoid spines were recovered from micropalaeontological samples. In vertical succession, these beds are followed by a rudstone to floatstone of resedimented phaceloid colonies with a similar taxonomic composition, suggesting an increase in hydrodynamic energy. In turn, this structure is covered by siliciclastic sediments, indicating the demise of an initial community (Fig. 3.c).

The second phase begins with similar beds (Fig. 3.c), though a stabilization stage could be recognized at some points as a floatstone of mollusc shells below the colonization pillarstones (Fig. 3.c). A diversification stage was recognized after the colonization one, marked by a platestone of platy to tabular cerioid colonies in life position (Fig. 3.c), associated with abundant cementing fauna (oysters and serpulids) and other reef crevice dwellers; phaceloid colonies are scarce at this stage. These beds were interpreted as a response to low siliciclastic sedimentation and relatively high hydrodynamic stress (Echevarría et al. 2024): a shell debris matrix alternates with platy and laterally extended cerioid colonies, revealing the fast growth of the scleractinians and of the whole structure. The flat colonies were better adapted to the increasing environmental energy, being resedimented only on rare occasions.

The following beds suggest an environmental change, and hence a third phase, with lower hydrodynamic energy. A widely developed mixstone, with low-domal cerioid as well as phaceloid colonies in life position, can be found with a very di-

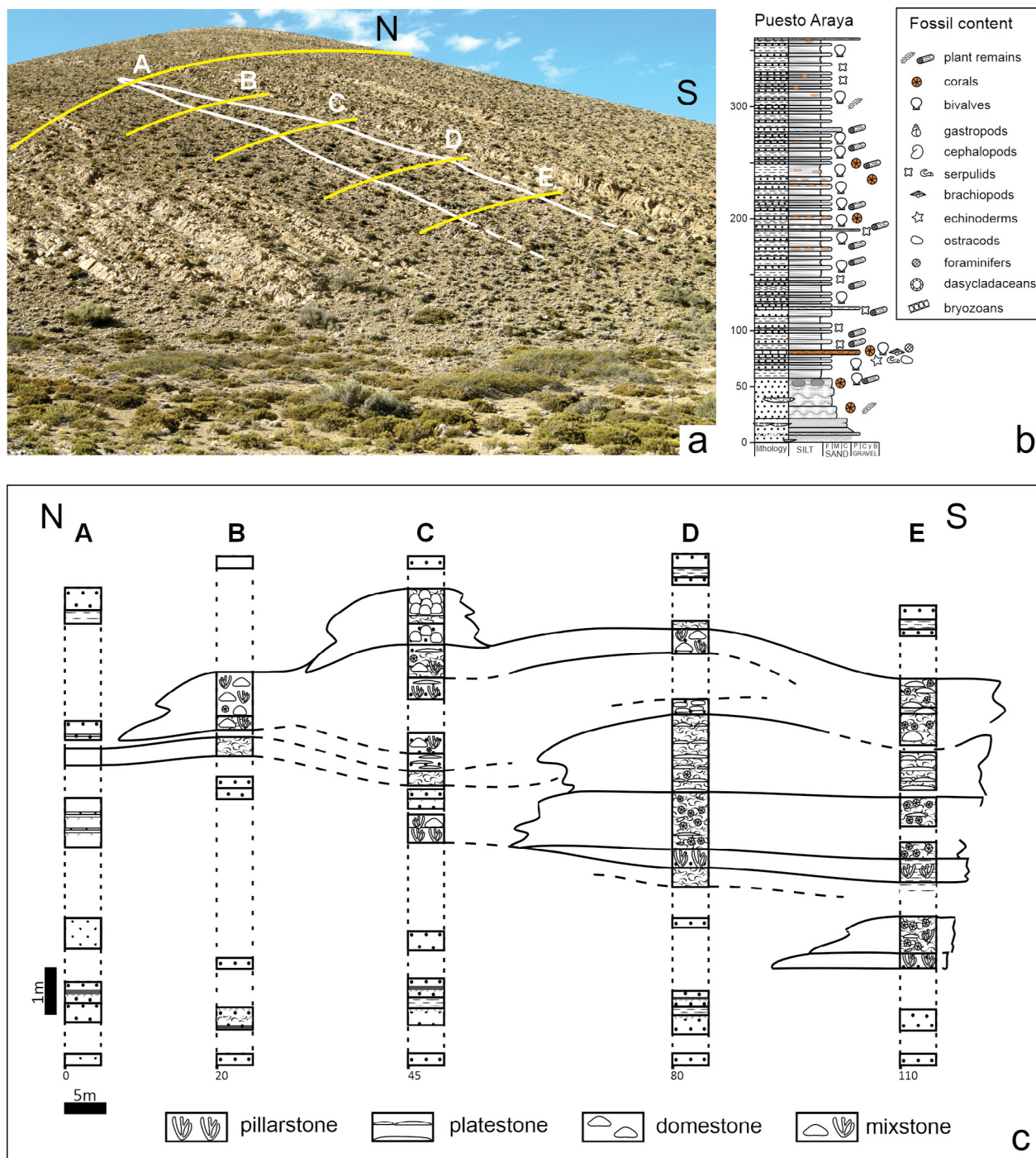


Figure 3. Coral reef outcrops at Puesto Araya, Río Atuel area, Mendoza Province. a. General view of the outcrops at Puesto Araya, taken from south-west to north-east, white line: coral beds, long yellow line: location of the measured main section (b), short yellow lines: location of the supplementary sections (c). b. Simplified measured section (logged at long yellow line in a), showing the location of the coral bed and other isolated occurrences of scleractinian corals. c. The five logged sections indicated in (a) covering the Puesto Araya reef (simplified from Echevarría et al. 2024).

verse associated fauna (byssate, crevice dweller and cementing bivalves, serpulids, echinoids, holothuroids). The morphology of cerioid colonies, together with the phaceloid colonies in life position, may imply a decrease in hydrodynamic energy and an increase in siliciclastic sedimentation (Echevarría et al. 2024). At this point, the relatively loose arrangement of

coralla suggests that this extensive structure was more like a meadow than a true framework. However, towards the north, a low-diversity domestone of densely-packed hemispherical cerioid colonies suggests a small reef front, exposed to high hydrodynamic energy, hinting to an allogenic domination stage (Walker and Alberstadt 1975).

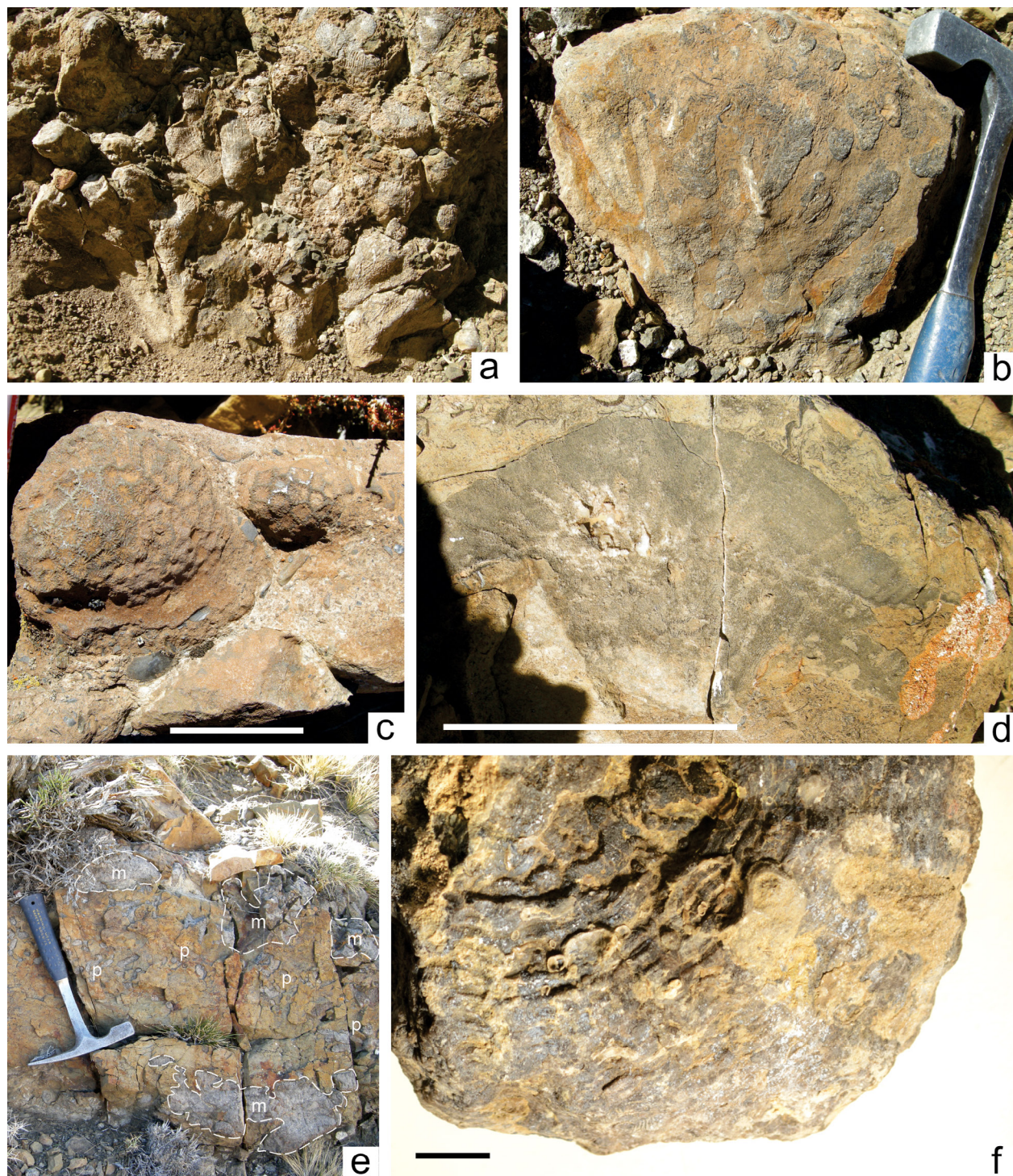


Figure 4. Field photographs showing some features of the coral reef at Puesto Araya and its fauna. a-b. Pillarstones of the colonization stage, with phaceloid colonies in life position, rock hammer length 28 cm. c. Calical view of a cerioid colony in life position, scale 50 mm. d. A fungiform cerioid colony showing jagged margins and episodes of sediment overgrowth, scale 100mm. e. General view of the mixstone and the alternation of morphologies (massive colonies at the base and top [m] and phaceloid branching colonies in the middle [p]), rock hammer length 28 cm. f. Detail of a massive cerioid colony showing the encrusted epitheca (non calyciferous surface), mostly bivalves and small thecidellinid brachiopod shells (IANIGLA-PI 3467), scale 10 mm.

Phaceloid and cerioid colonies in life position may alternate vertically (Fig. 4.e). Encrustation and bioerosion are scarce (though present) pointing to a brief residence time; despite the difficulty of finding preserved epithecas, some

examples with attached cementing bivalves and thecidellinid brachiopods were recovered (Fig. 4.f). The jagged margins of cerioid colonies (Fig. 4.d) and vertical overgrowth also point to rapid burial (most likely by storm deposits).

Microfossil associations appear dominated by Nodosariata foraminifers (vaginulinids, ichthyolariids, and nodosariids), with few ostracods (cypridoids, cytherelloids, and cytheroids); considering the foraminifer morphogroups in the successive stages of the reef, there is a strong diversification during the development of the mixstone (Harguindeguy et al. 2023, Echevarría et al. 2024).

(b) *Austromorphites behrendseni* Zone - By this moment the Neuquén Basin extended considerably (Fig. 2.a), favouring the development of coral communities in different environments. In the south of Mendoza Province (north of the basin), scattered small patches (1–10 metres) of cerioid colonies and/or the hypercalcified sponge *Andenipora liasica* Gerth 1926 were identified at Arroyo Peuquenes. A small patch (3 metres of extension) of cerioid colonies with frequent *Andenipora* towards the periphery was identified at Puesto Araya.

It is towards the south of the basin (southern Neuquén Province, Fig. 2.a) that coral-dominated communities reached a major development, generating an extensive coral meadow. The Early Jurassic beds of the Piedra Pintada Formation bear a great diversity of invertebrate faunas, known since the beginning of the 20th century (Roth 1902, Burckhardt 1902). Damborenea et al. (1975) recognized and characterized several biofacies in these shallow marine deposits, and the coral beds (their sub-biofacies A2) were then tentatively referred to as biostromes. In this broad area, coral-dominated beds occur at several localities. According to Morsch (2001), both coral diversity and corallite arrangement disparity are higher than in the Puesto Araya reef previously described, with solitary [*Styllophyloopsis?* cf. *victoriae* (Duncan 1868), *Myriophyllum* sp.], phaceloid (*Retiophyllia?* sp.), cerioid [*Distichomeandra* cf. *austriaca* (Frech 1890), *Microphyllia* cf. *flemingi* (Milne-Edwards and Haime 1851)] and cerio-meandroid (*Goldfussastrea?* cf. *toarciensis* Beauvais 1986) corallite arrangements. Nevertheless, the poor preservation of these scleractinians hinders accurate systematic identifications, and further taxa may be present, including forms with thamnasterioid corallite arrangements (Damborenea et al. 1975). Regarding corallum shape, phaceloid coralla represent the branching forms, while the more integrated colonies develop massive habits.

At Cerro Roth (Fig. 2.c), the coral bed is well-exposed in laterally continuous outcrops on the western slope of a couple of low hills (Cerro Roth and Cerro Roth Sur, Fig. 5.a), and can be followed laterally (Fig. 5.b). Along this line, observations and collections were focused on 13 points (A-M from south to north). The whole section logged at this locality (Fig. 5.c) is mainly siliciclastic, mostly sandstone and mudstone beds, with interbedded tuffaceous sandstones and tuffs towards the top. Solitary corals occur at several levels, together with diverse

bivalves, gastropods, brachiopods and crinoid ossicles, but at about 100 m from the base of the measured section, there is an extensive coral-dominated bed which can be tracked laterally for at least 1 km. The coral bed thickness varies between 0.80 and 1.30 m.

Below this bed, a limestone of remobilised bivalve shells was recognized, probably acting as a stabilization stage for the later development of corals. Towards the south, (Fig. 5.b, d), the bed shows a growth fabric mainly built by calcareous skeletons of a variety of solitary (Fig. 6.e) and especially colonial scleractinians, with most of the coralla preserved in life position. The base of the coral bed is usually built by a thick, dense mass of phaceloid colonies in life position (pillarstone), which may be locally followed by isolated, or groups of, tabular, fungiform, and hemispherical massive cerioid and thamnasterioid colonies, also found in life position (locally domestone, Fig. 6.a-b). This phaceloid to massive corals succession can occupy the whole bed thickness, or this sequence of growing fabric styles may be repeated vertically within the bed (Fig. 6.b). Laterally the growth fabric style continuity is not uniform, the coral bed may also show just one of these growth fabric styles or a mixture of them.

The non-calificiferous epithecias of tabular and fungiform corals of this bed are heavily encrusted by a variety of cementing organisms: bivalves, serpulids, bryozoans and brachiopods, in addition to bearing diverse etchings and borings (Fig. 6.d). Less frequently, some of these organisms may encrust solitary (turbinate to subcylindrical corallites) calcificiferous surfaces (Fig. 6.c) or shells. Encrusting bivalves include ostreids and *Atreta* sp. The distribution and orientation of the *Atreta* shells indicate that the substrates were living organisms (Damborenea 2002, p. 98-99, text-fig. 47, pl. 11, figs. 13a-b) and that there was enough time for at least five successive generations of the cemented bivalves to grow upon the same coral epitheca. Manceñido and Damborenea (1991) recorded a couple of generations of thecideid brachiopods (*Ancorellina ageri* Manceñido and Damborenea 1991) encrusting the same under surfaces (see Fig. 6.d), stressing that these sciaphilous, rugophilic cemented epibionts were most probably warm-water cryptic dwellers. The abundance of shade-loving encrusters and borings, as well as the successive generations of encrusters on the same surface, are indicative of meagre sediment supply.

The hypercalcified sponge *Andenipora liasica* Gerth 1926, echinoid spines and plates, some gastropods, and crevice dweller byssate and cemented bivalves are also very abundant in, if not exclusive of, these southern outcrops of the bed. These may be found in situ in crevices among the coral branches and suggest a certain degree of superstratal growth

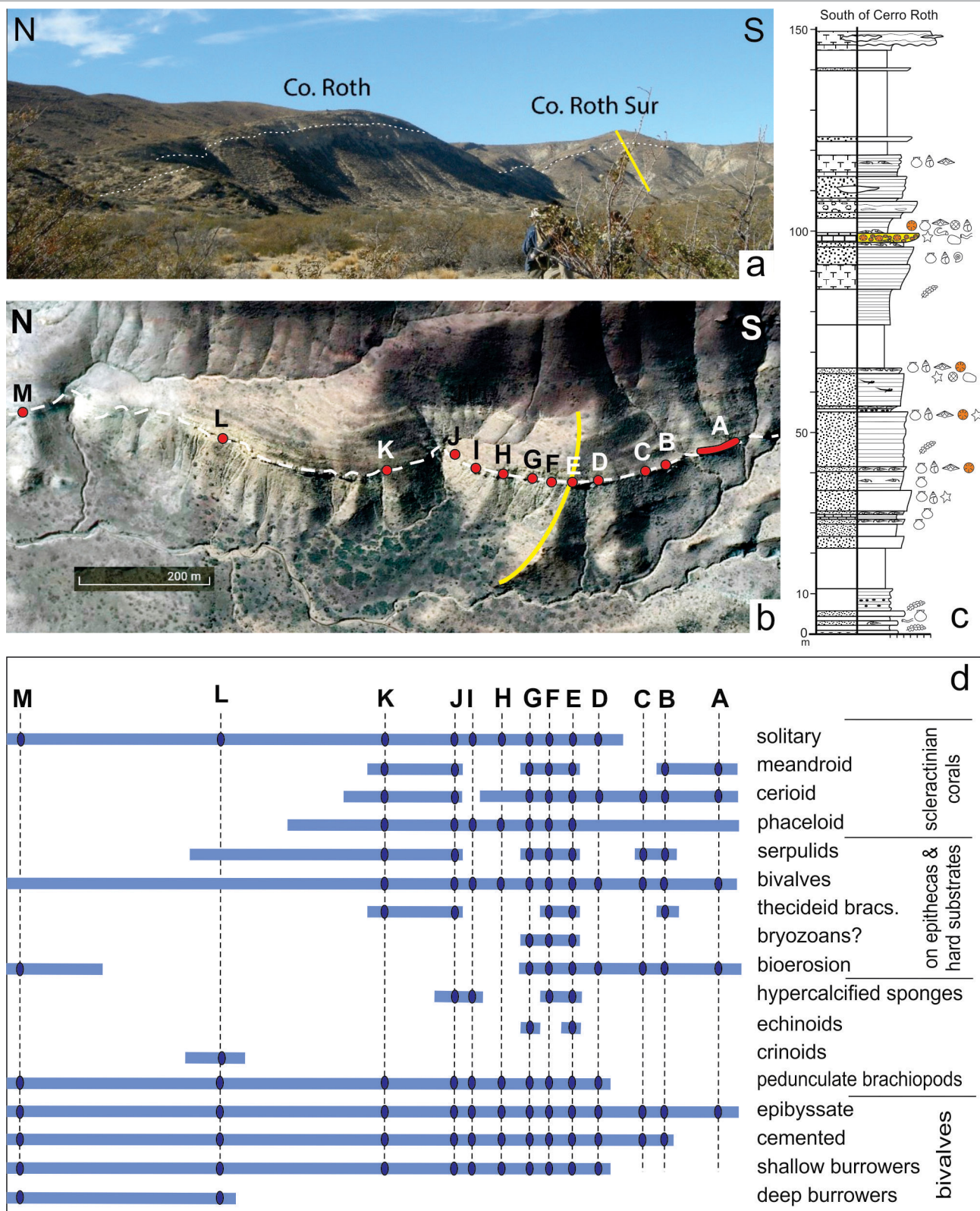


Figure 5. Coral-dominated bed at Cerro Roth, Piedra Pintada area, Neuquén Province. a. General view of the outcrops at Cerro Roth and Cerro Roth South, taken from west to east, broken white line: coral bed, yellow line: location of the measured section (c). b. Plan view (based on Google Earth image) of the same area showing the N (to the left)-S (to the right) extension of the outcrops of the coral bed (white dashes) and the observation points along it (red dots, A to M from South to North). c. Simplified measured section (logged at yellow line in a and b, including point "E" in b), showing the location of the coral bed and preceding isolated occurrences of scleractinian corals; fossil content as in Fig. 3. d. General distribution of macroinvertebrate groups along the north-south outcrops of the coral bed at the observation points indicated in b (see discussion in text).

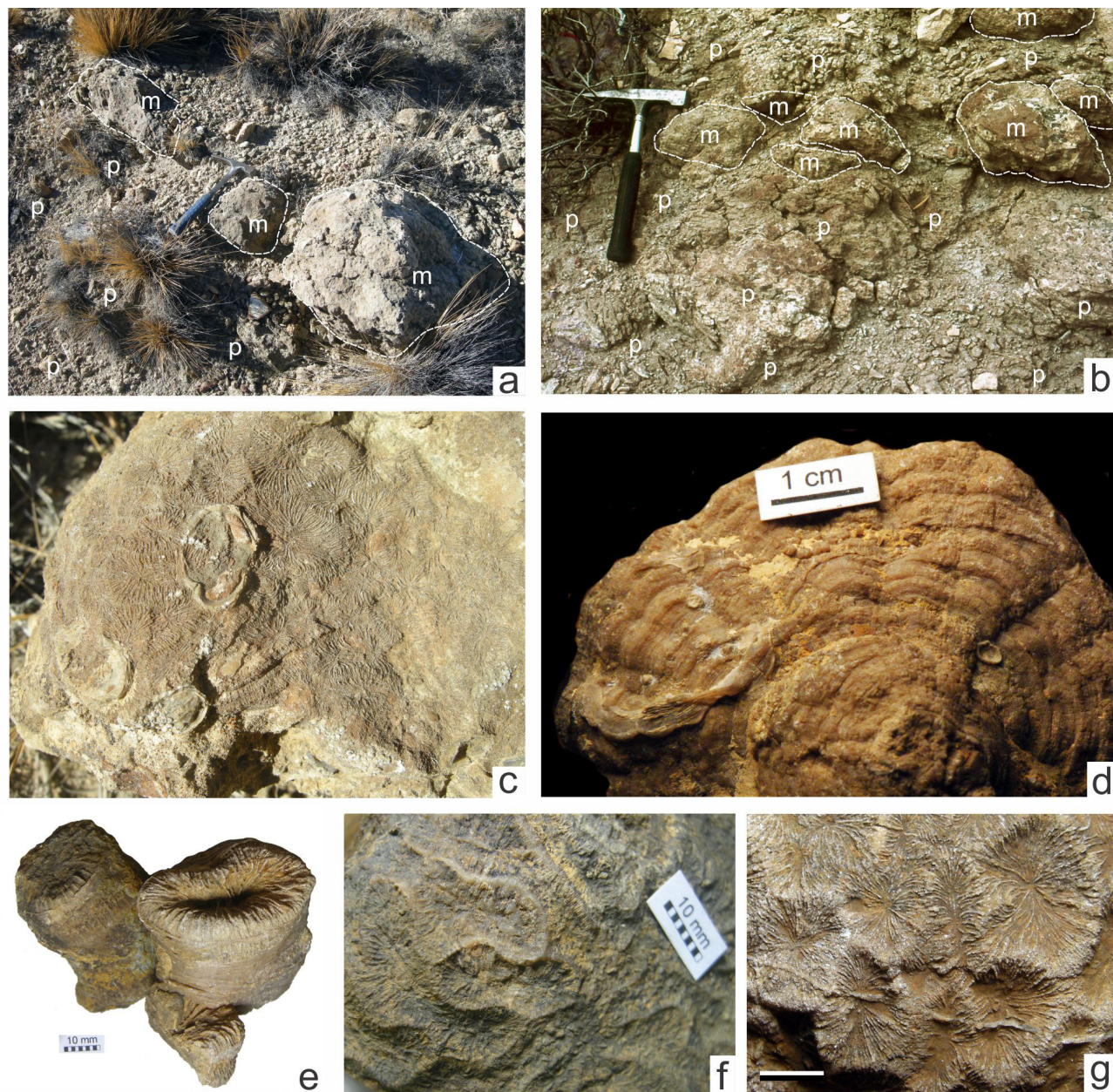


Figure 6. Field photographs showing some features of the coral-dominated bed at Cerro Roth and its fauna. a. General view of the bed near point “C”, showing the density of the mixstone frame and the growing sequence (pillarstone of phaceloid colonies at the base [p], domestone of massive colonies at the top [m]), rock hammer length 28 cm. b. Detail of mixstone bed at point “H”, showing a repetition of the coral growing sequence (p-m, p-m), rock hammer length 28 cm. c. Massive colony in life position at point “A”, with the thamnasterioid calical surface encrusted by cemented bivalves. d. A fungi-form colony showing the encrusted epitheca (non calical surface), small thecideid brachiopod shells and oysters (MLP 24470). e. Cylindrical-throchoid solitary corallites from point “E” (MCF-PIPH 653a). f. Detail of the surface of a massive cerio-meandroid colony from point “F” (MLP 36580). g. Detail of the surface of a massive colony from point “E” (MCF-PIPH 653b), scale 10 mm. See relative location of observation points in Fig. 5.

fabric genesis. All these invertebrate groups are usual dwellers in circumscribed biofacies corresponding to coral meadows.

On the other hand, towards the northern part of the bed, colonial corals become very rare, although solitary corals are still present, and occasionally bear encrusters and bioerosion. There, the accompanying fauna includes a large variety of shallow burrower bivalves and even occasional deep burrowers.

Microfossil samples were taken at the main log trace (point “E”, Fig. 5.b) and were studied by Ballent (1987), who

described *Nodosariata* foraminifers (vaginulinids and polymorphinids) and ostracods (cypridoids, pontocypridoids, and cytherelloids).

In the nearby locality of Salitral Carrán Curá (Fig. 2.c), two successive coral-dominated beds were recorded (see section in Damborenea 1987, p. 49, t-fig. 5), with comparable features and faunal content as the Cerro Roth beds. A similar coral fauna was described by Morsch (2001) from Estancia Santa Isabel (Fig. 2.a), about 12 km NW of Carrán Curá (see

section in Damborenea 1987, p. 47, t-fig. 5). These records show that those coral meadows were widespread over a wide area with rather uniform palaeoenvironmental conditions of probably low energy, shallow water depth and well-illuminated substrates.

(c) *Fanninoceras disciforme*–*Tenuicostatum* Zones - During the Late Pliensbachian to early Toarcian, the epeiric sea extended further south, encroaching on the Chubut Basin (Fig. 2.a). Fossil corals were reported from a few localities in western Chubut Province along the Río Genoa area (Fig. 2.d): Puesto Altamirán (Feruglio 1934), Nueva Lubecka and La Trampa (Carral Tolosa 1942), La Casilda (Ferrari and Bessone 2015); and farther north, in Aguada La Carlota (Manceñido and Damborenea 1991) and Cerro Cucho (Massaferro et al. 1998, Massaferro 2001). Abundant solitary corals and massive cerioid colonies are known from Lomadas Occidentales just west of Nueva Lubecka (Carral Tolosa 1942), but outcrops are very poor and the geometry of the coral-bearing beds is hardly discernible.

Instead, at La Trampa, the hills on the opposite side of the Genoa valley (Fig. 2.d), outcrops are better exposed, and small coral patches were recognized by the authors in the lower part of the Mulanguiñeo Formation (*Fanninoceras disciforme*–*Tenuicostatum* Zones), about 25 m above the local base of the unit (Fig. 7.a-b). These patches are around 1 m thick and a few metres long, and bear very abundant massive and large cerioid coral colonies preserved in life position, associated with trochoid solitary corals (Fig. 7.c-d). The growth fabric style appears to be a domestone. The coral epithecas are ill-preserved so encrusters and borings are lacking (or very few).

Unfortunately, the preservation of the coral skeletons is very poor, and they have not been systematically revised; the colonial corals were referred to *Isastrea* sp. by Feruglio (1934), and the solitary ones were identified as *Montlivaultia* [sic] cf. *victoriae* Duncan 1868 (see Carral Tolosa 1942, pl. 1, fig. 1; Aguirre Urreta et al. 2022, fig. 3.d, i) (Table 1, Fig. 7 c-d).

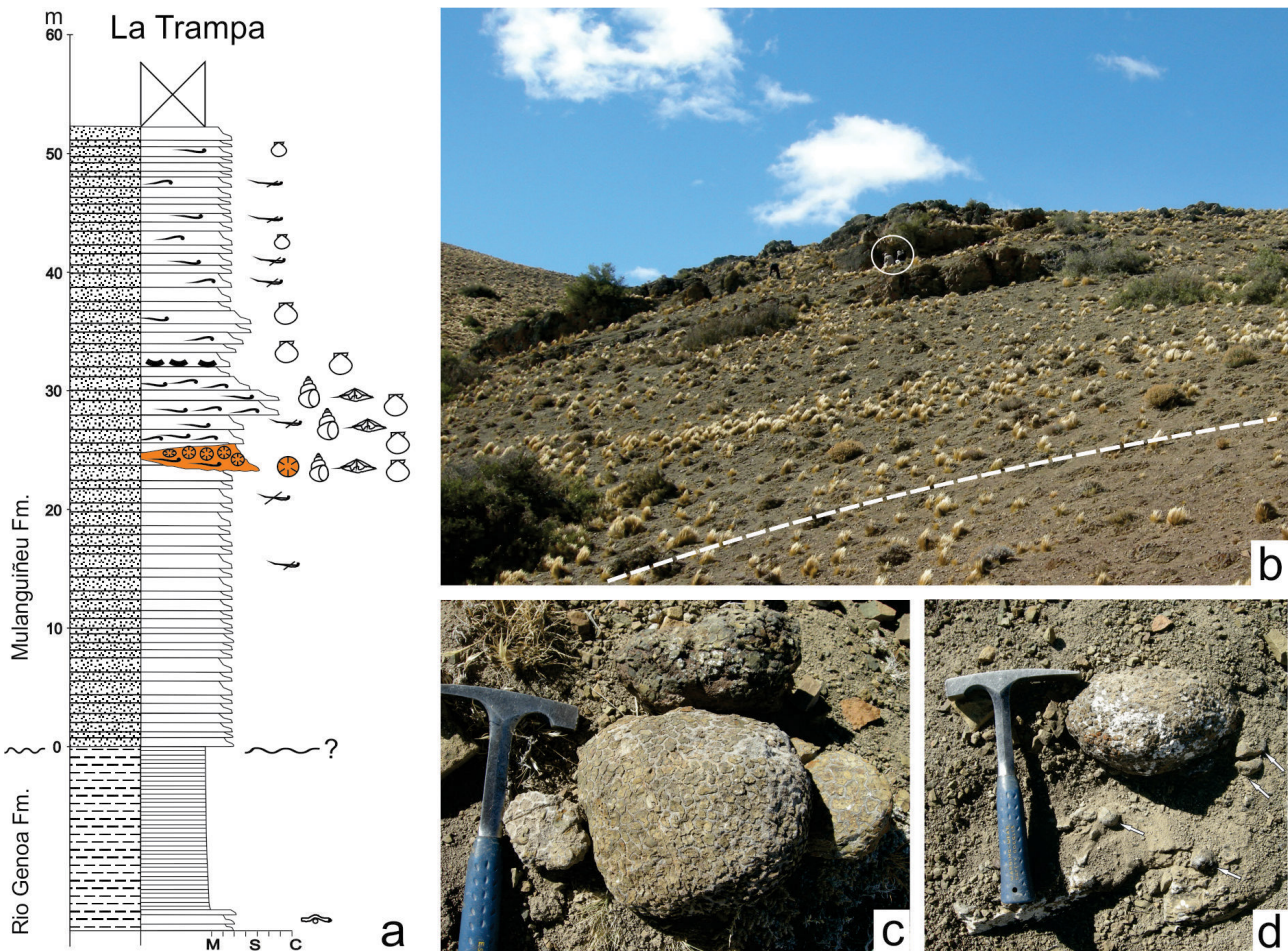


Figure 7. Coral patches at La Trampa, western Chubut Province. a. Simplified log of section; fossil content as in Fig. 3. b. General view of lower part of section; broken line approximately at the base of the Early Jurassic beds; white circle: persons for scale at level of the coral patches. c. Domestone, massive cerioid colonies from top of coral patch, rock hammer length 28 cm. d. Domestone, section of coral patch bed; white arrows point to solitary corals; massive cerioid colony in life position on top, rock hammer length 28 cm.

Middle Jurassic

In San Juan Province (Cordón de la Ramada, Fig. 8.a), Álvarez (1997) mentioned some cerioid-thamnasterioid colonial corals associated with ammonites of late Aalenian to earliest Bajocian age. Yet, the Bajocian diversification of scleractinians is better reflected in the lower coral association (early Bajocian) of the Lajas Formation (or even its transition to Los Molles Formation) from central Neuquén Province, showing the highest alpha diversity of coral communities from the Jurassic of Argentina described so far (Table 1). From lower Bajocian deposits at south of Barda Negra (=Paso del Carro Quebrado, Fig. 8.d), Morsch (1996) described ten species distributed in nine genera, with varied corallite arrangements, such as: plocoid [*Pseudocoeniopsis* cf. *wintoni* (Wells 1933)], cerioid (*Araucanastrea minuscula* Morsch 1996, *A. majuscula* Morsch 1996, *Garateastrea bardanegrensis* Morsch 1996, *Mapucheastrea andina* Morsch 1996), thamnasterioid (*Kobyastrea louisae* Morsch 1996, *Astraraea* cf. *fungiformis* Beauvais in Negus and Beauvais 1979) and meandroid (*Complexastreopsis* sp.), as well as different solitary morphologies [*Cyathophylliopsis delabechei* (Milne-Edwards and Haime 1851), *Neuquinosmia gerthi* Morsch 1996]. Massive morphologies were identified for most of the colonial coralla, with scarce laminar morphologies in *A.* cf. *fungiformis*, while the solitary forms were mostly of low height (discoïdal, cupolate or short cylindrical). These taxa occur in fine- to coarse-grained calcareous sandstones. Similar associations are likely to occur in the lower Bajocian from the Chacaico-Charahuilla area, as well (Volkheimer 1973). Despite their diversity, none of these localities shows unmistakable reefal structures, perhaps attaining patchy thickets very locally (scarce coralline biostromes, according to Volkheimer 1973). Associated fauna shows great diversity, with bivalves, gastropods and some brachiopods, bryozoans, echinoderms and serpulids. This variety of morphologies and diversity of species and genera suggests that a coral meadow may have developed in the area.

On the other hand, another set of coral occurrences has been reported from a couple of areas in central Neuquén Province (the vicinities of Los Molles-Chacaico and of Los Pozones, Weaver 1931, see Fig. 8.d), and northern Neuquén Province (Vega de la Veranada, Groeber et al. 1953, Stipanovic 1965, Fig. 8.a). The coral assemblage from brown bioclastic sandstones of variable grain size, in central Neuquén Province, appears characterized by fewer genera/species, including conspicuous solitary *Montlivaltia* aff. *kobyi* Beauvais 1966, plus cerioid "*Convexastrea*" *weaveri* Gerth 1928 and meandroid *Complexastreopsis caracolensis* (Steinmann 1881). Notice that members of this association have

been usually regarded as Callovian (Weaver 1931, Stipanovic, 1965, Volkheimer 1973), though allegedly early Bajocian by Morsch (1996). The arcose beds from Vega de la Veranada, bearing "*Convexastrea*" *weaveri* Gerth 1928, correspond to upper terms of the Lajas Formation being early Callovian in age (Gulisano and Gutiérrez-Pleimling 1995). Corallite arrangement corresponds mainly to cerioid colonies (Fig. 9) and some discoid to cupolate solitary forms. However, proper reefs have not been recognized so far.

Likewise, in San Juan Province (Cordón de La Ramada, Fig. 8.a), at the top of the Patillos Formation (probably Callovian in age), both solitary and colonial corals have been found. Some of these are large, massive coralla with large corallites of cerioid arrangement; yet bioconstructions or coral-dominated beds have not been described so far (pers. obs.).

From this general background, it seems clear that the Middle Jurassic of Argentina still requires a thorough assessment of its coral-dominated communities, being a promising field for future studies.

Late Jurassic

During this lapse of time, two main intervals with well-developed coral-dominated communities were recognized in western Argentina: the late Middle Oxfordian, with the coral bioconstructions of La Manga Formation; and the Tithonian, with the well-developed coral communities of the Picún Leufú and Cotidiano formations (Fig. 1).

Late Middle Oxfordian - *Perisphinctes-Araucanites* Zone

Coral-dominated beds and reefs can be recognized within deposits of La Manga Formation at several localities in the Neuquén Basin. In this paper, coral communities from Bardas Blancas, Coihue Co (both in southern Mendoza Province, Fig. 8.b), Cuchillo Curá and Covunco (both in Neuquén Province, Fig. 8.c) will be described. Although among the coral-bearing beds present in these localities there is a great disparity in thickness, shape and extension, they share a low alpha diversity of corals. At least four genera (*Stelidioseris*, *Australoseris*, *Etallonasteria* and *Stephanastrea*) were recognized (Morsch 1990, Beresi et al. 2017, Hoqui et al. 2019); however, estimates of diversity based on a taxonomic list may be seriously biased because most of the fossil samples belonging to this time interval show poor overall preservation, showing at least four taphonomic grades, of which three show loss or deformation of diagnostic characters necessary for systematic assignments (Hoqui et al. 2019). Corallum growth forms can be branched (caespitose, corymbose and arborescent), platy and domal. The corallite arrangement is usually plocoid

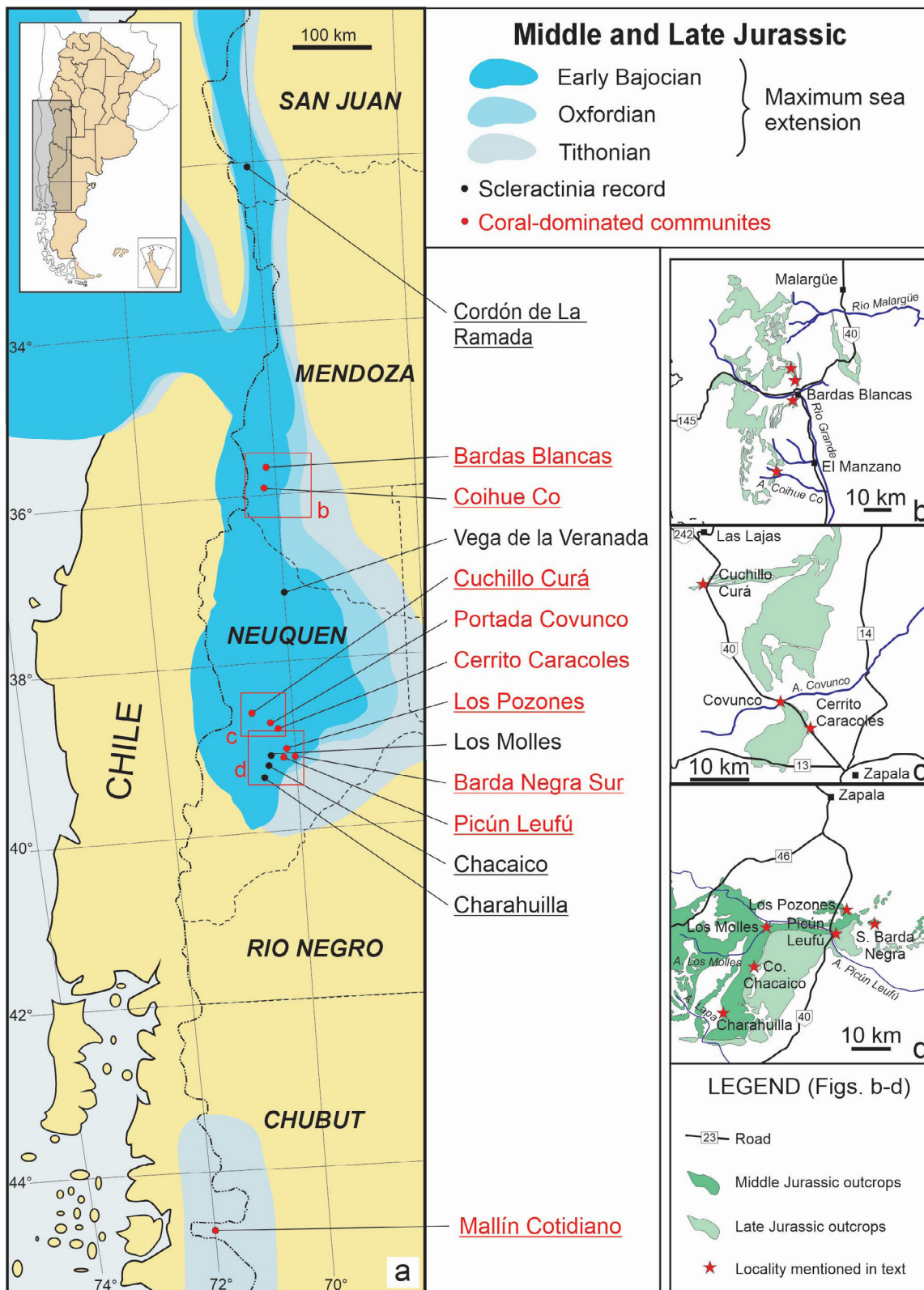


Figure 8. Middle and Late Jurassic location maps. a. Map of western Argentina showing the maximum extension of the sea during the Jurassic at different times (modified from Legarreta and Uliana 1996, and Suárez et al. 2009), and the location of Middle and Late Jurassic scleractinian records (based on data from previously known records and new ones from the authors). The localities with known coral-dominated communities are in red, those described in the text are underlined. b-d. Location sketch maps of the examples discussed in the text. b. Late Jurassic localities Coihue Co and Bardas Blancas in southern Mendoza Province. c. Late Jurassic localities Cerrito Caracoles, Covunco and Cuchillo Curá, central Neuquén Province. d. Middle Jurassic localities in central Neuquén Province (Los Pozones, South of Barda Negra, Los Molles, Cerro Chacaico) and Picún Leufú (Late Jurassic).

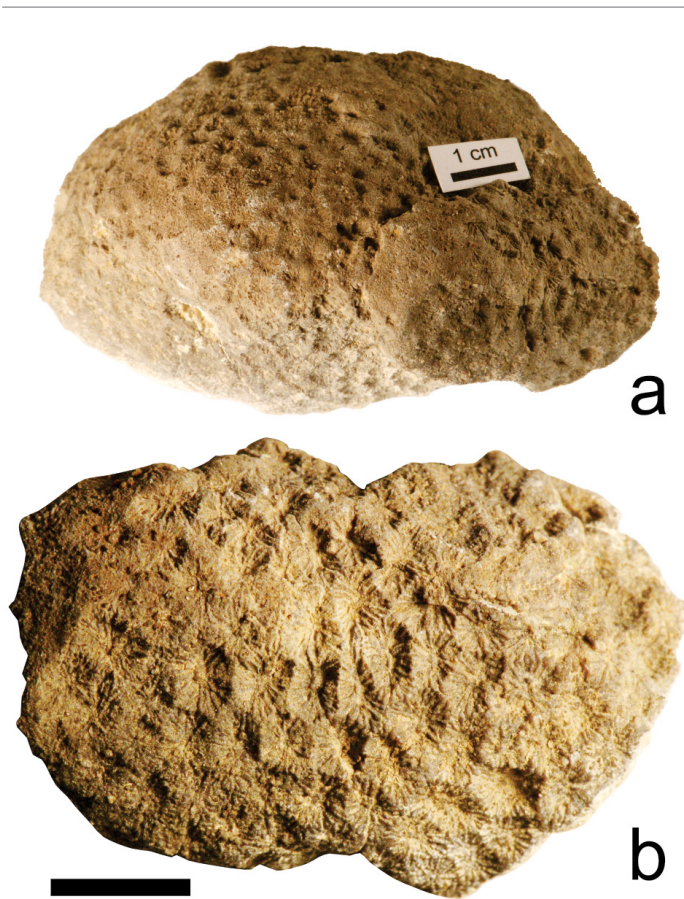


Figure 9. “*Convexastrea*” *weaveri* Gerth 1928 cerioid corallum from the Middle Jurassic (Early Callovian) locality Vega de la Veranada (MLP 36579). a. General morphology. b. Detail of calical surface. Scale 10 mm.

to cerioid with very small calices in the branched colonies and thamnastero-meandroid with calices up to 1 cm in diameter in the platy and domal forms.

Three main types of coral-dominated communities were identified in La Manga Formation for the late Middle Oxfordian (Fig.10): (a) coral meadows of platy corals with dense or sparse fabric (usually associated with mobile substrates e.g., oolitic or calcareous sand banks); these are no more than 40 cm thick, although the lateral extension can be tens of metres (tabular strata); (b) small reef patches of domal section, not exceeding 2 m in thickness, show at least two types of growth forms: platy and branched (either caespitose or corymbose) colonies, although in many cases globose and arborescent forms can also be recognized; (c) large patches that can amalgamate and generate pseudo-barriers; in this case, all the associated growth types may be recognized in the same biocenosis or they can replace each other in the same beds (ecological succession).

The largest expression of coral reefs (in areal extension and thickness) so far known from the Neuquén Basin occurs

at Bardas Blancas. It has been studied from at least two approaches, i.e., its stratigraphic meaning in a stratigraphic/sequential context and its palaeoecological complexity (Palma et al. 2009, 2020, Hoqui 2022). At this locality, the reef deposits crop out more than 13 km from north to south (Fig. 8.d) and reach 20 m in thickness in one particular section (Fig. 10.a-b).

This reef can be divided into a core reef zone, a back reef zone and a frontal reef zone (Hoqui 2022). Each of these zones is characterized by morphofunctional coral associations. The back reef has densely packed corymbose colonies associated with platy and caespitose colonies. The reef core shows a progression from associations with small platy and branching corals to associations dominated by large globose colonies and arborescent forms, reflecting an increase in hydrodynamic energy (Hoqui 2022). Finally, the front reef is characterized by patches and isolated colonies of platy corals that may sometimes be surrounded by caespitose forms (Hoqui 2022). Below the reef deposits, tabular beds dominated by platy colonies can be recognized; these layers represent coral meadows which, in their arrangement and composition, resemble the associations of the front reef that follow them (Fig.10.b). This type of association reflects particular ecological dynamics where a mobile substrate (above the storm surge line) can only be colonized by platy colonies that by modifying the physical conditions of their environment, due to their growth, allow the recruitment of other morphologies (e.g. caespitose forms).

In Coihue Co, about 40 km south of Bardas Blancas (Fig. 8.d), there is an alternation of oopeloidal bioclastic storm deposits (packstone-grainstone up to 40 cm thick) and platy coral packstone/floatstone (up to 50 cm thick each) representing coral meadows (Fig. 10.c). At this locality, more than 20 cycles of alternation (corals/packstone-grainstones) could be recognized at the base of the La Manga Formation (Fig. 10.d).

Similar associations developed in Covunco (Neuquén Province), in the first metres of the logged section. Nonetheless, dome-shaped patches up to ten metres in lateral extension and two metres in thickness developed above such beds. These patches are characterized by two morphologies, almost equally abundant (Hoqui 2022): either platy colonies similar to those represented in the underlying beds, or else, branching colonies with very loosely packed, corymbose forms (Fig. 11). The corymbose forms recognized mainly in Covunco show a large vertical development and a much wider spacing or separation among branches than in specimens with this type of growth from other localities. Based on the inferences by Beresi et al. (2017) about the sedimentation rate at this locality, it can be assumed that the corymbose forms,

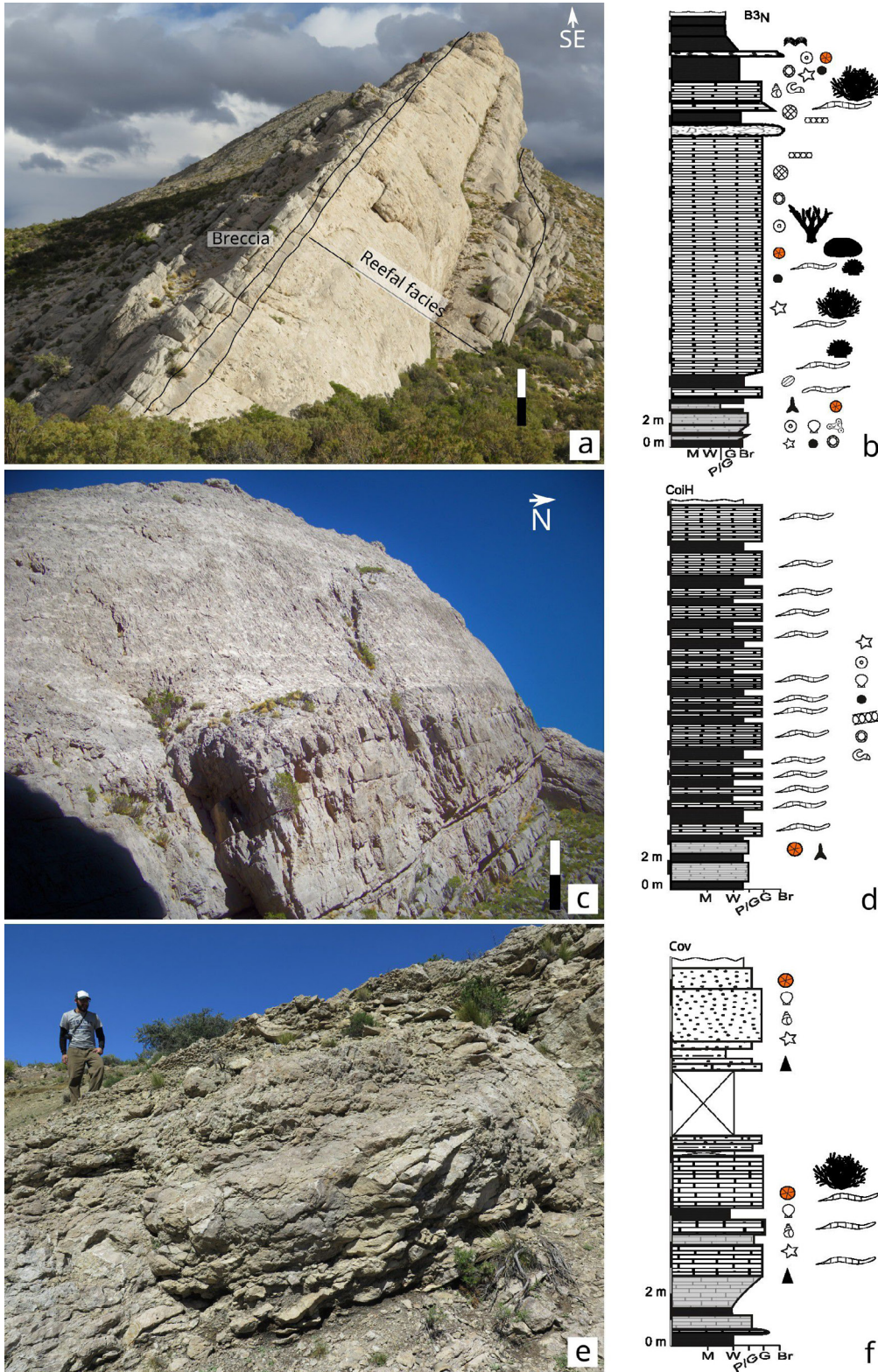


Figure 10. Middle Oxfordian coral-dominated communities from La Manga Formation. a-b. Coral-dominated beds from Bardas Blancas (see location at Fig. 8.b). a. Reefal deposits at Bardas Blancas (B3N, see Hoqui, 2022 for further explanation), note the significant vertical trend of the reefal facies; scale 5 m. b. Log of coral-dominated part of La Manga deposits; fossil content as in Fig. 3. c-d. Coral-dominated beds from Coihue Co (see location at Fig. 8.b). c. Intercalation of coral dominated deposits (coral meadows) and bioclastic wackestone/packstone mainly at the base of La Manga Formation; scale 5 m. d. Log of coral-dominated part of La Manga deposits; fossil content as in Fig. 3. e-f. Coral-dominated beds from Covunco (see location at Fig. 8.c). e. Field photograph showing patches generated by platy coralla associated with corymbose forms at the top of deposits. f. Log of coral-dominated part of La Manga deposits, note the transition from carbonatic deposits to siliciclastic ones at the top; fossil content as in Fig. 3.

- Legends**
- | | | | |
|-----------------|----------------------|------------|------------------------------------|
| Coral limestone | Packstone/grainstone | Covered | Calcareous sandstones |
| Karstic breccia | Wackestone/packstone | Marls | Siliciclastic Packstone/grainstone |
| Ooids | Pellets | Intraclast | Siliciclastics |
| Stromatolites | Section limits | | |

- Corals**
- | | |
|-------------|--|
| Arborescent | |
| Corymbose | |
| Caespitose | |
| Domal | |
| Platy | |

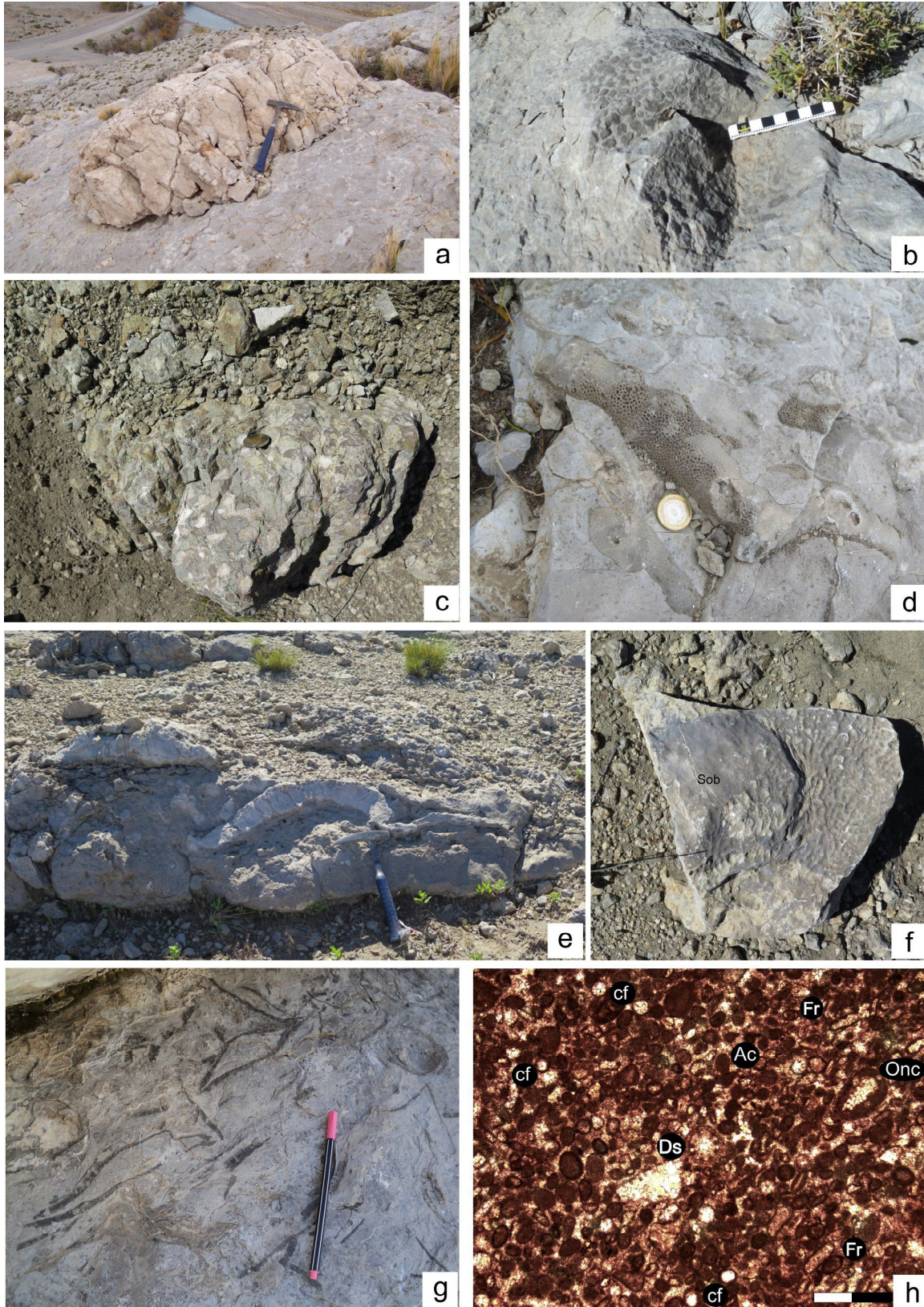


Figure 11. Coral growth forms at Oxfordian deposits. a. Globose colony, rock hammer length 28 cm. b. Caespitose colony. c. Fragment of corymbose colony, coin diameter 24.5 mm. d. Branch of arborescent colony, coin diameter 24.5 mm. e. Platy colony, rock hammer 28 cm long. f. Platy colony with knobs or overgrowth (Sob). g. Bioclastic wackestone/packstone with large articulated bivalves, marker length 16.8 cm. h. Microphotograph of bioclastic wackestone/packstone in g: Ds reproductive organs of *Dasycladales* (*Terquemella* spp.); cf calcispheres; Fr foraminifers; Onc oncoids; Ac *Acicularia*, scale 0.5 mm.

with plocoid corallite arrangement (*Stelidioseris*) played the same environmental role as the phaceloid forms in Early Jurassic examples. They developed in slightly agitated but somewhat turbid waters (either due to sedimentary input or resuspension of sediments), being able to cope with relatively high sedimentation rates.

In the Cuchillo Curá provincial protected area (south of Las Lajas, central Neuquén Province, Fig. 8.c) the bioconstructions are very different from those mentioned above. In this case, they are small clusters (1 m high and 80 cm in diame-

ter) of small discoidal *Stelidioseris* sp. colonies with columnar projections and a plocoid corallite arrangement though with very narrow coenosteum and hence appearing cerioid. The colonies do not exceed 1-15 cm in diameter and the columnar projections never exceed 1 cm in diameter and 5 cm in height. Interestingly, the growth of these bioconstructions occurred in environments where the oolitic fabric was optimal, indicating that the environmental energy was high to very high. As a result, the bioconstructions are made up of this single morphological type. These discoidal colonies with columnar pro-

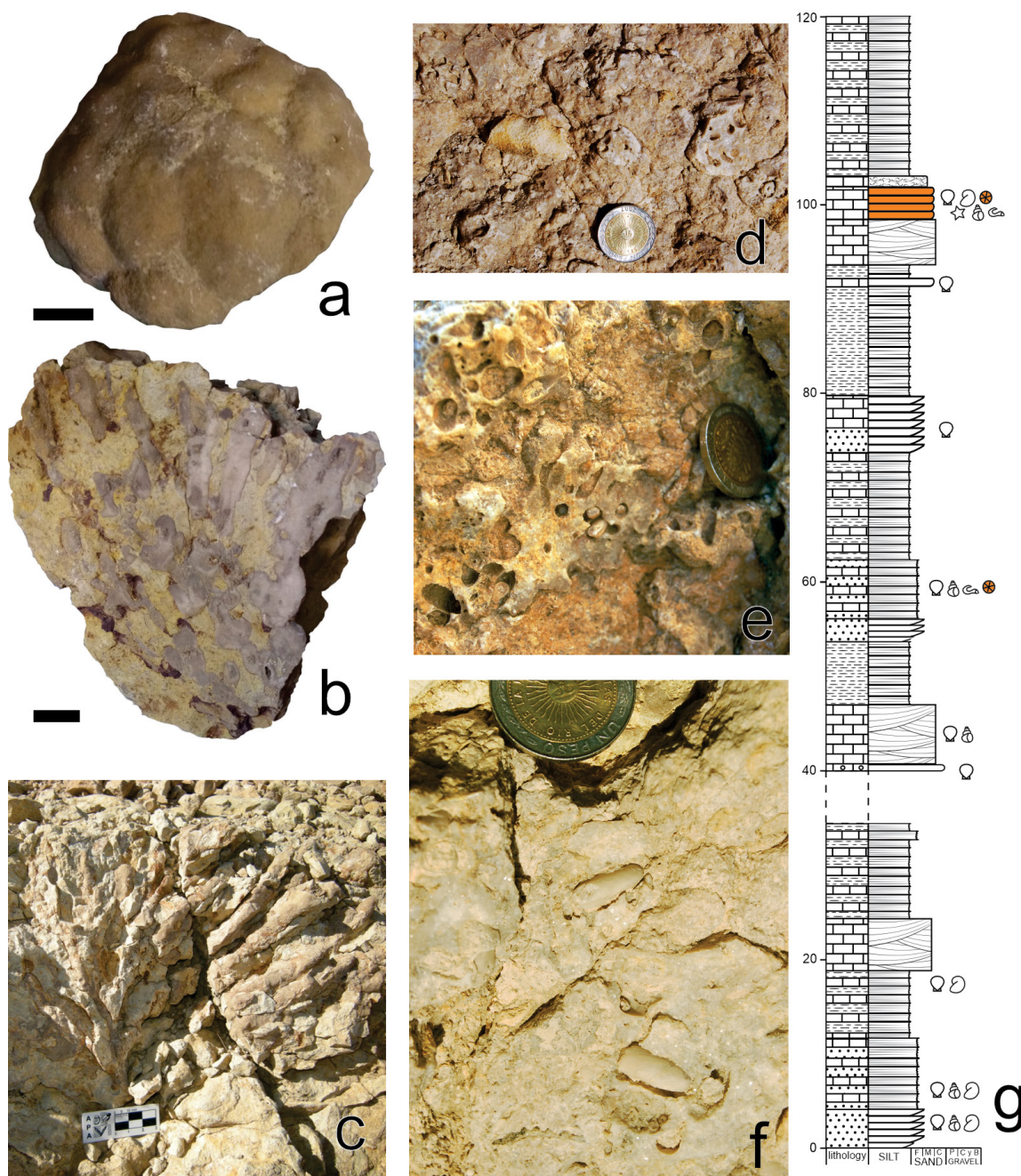


Figure 12. a-b. *Stelidioseris* sp. coralla from the Tithonian of the Picún Leufú Formation. a. Massive colony (CPBA 23453-29). b. Ramose colony (CPBA 23453-23). c. Field photograph of ramose colony. d-f. Field photographs of ramose colonies bored by bivalves (detail in f), coin diameter 23 mm. g. Simplified log of section of the lower third of Picún Leufú Formation; fossil content as in Fig. 3.

jections are cemented, and in present-day environments they are usually found in wave-break zones (Hubmann et al. 2002, Denis et al. 2017).

At all mentioned localities the accompanying fauna includes a variety of crevice dwellers, reclining and cementing bivalves, spines and plates of regular echinoids such as *Balanocidaris* sp., thecideid brachiopods, bryozoans, polychaetes, high-spined gastropods, miliolid and agglutinated foraminifers, and reproductive organs of Dasycladales (*Terquemella* spp.) (Bucur et al. 2008, 2014) (Fig. 11.h). Microbialitic crusts with both stromatolitic and thrombolitic fabrics are also common.

Tithonian - *Corongoceras alternans* Zone

Within the Neuquén Basin, Tithonian corals were reported from the Picún Leufú Formation (Fig. 12.g) in central Neuquén Province (Leanza 1973, Leanza et al. 1997, Cucchi et al. 2005, Armella et al. 2007); these authors mentioned the corals as palaeoecological indicators, but none of them undertook systematic studies. Tithonian corals have also been mentioned in the regions of Chile adjacent to the Neuquén Basin, some of them belonging to the genus *Stelidioseris* (Salazar and Stinnesbeck 2015, Vidal et al. 2016), but their studies are still preliminary. Recently, the genera *Eocolumastrea* and *Stelidioseris* were recognized in the type locality of the Picún Leufú Formation (Fig. 8.d) in Neuquén Province (Garberoglio et al. 2023). Ongoing studies indicate that there would be only one species of each genus: *Stelidioseris columbaris* (Scott and Aleman 1984) (Fig. 12.a-b, at Picún Leufú, Cerrito Caracoles and Cerro Bayo Chico localities, Fig. 8.c-d) and *Eocolumastrea octaviae* (Prever 1909) at Picún Leufú (Fig. 8.d). Both genera are the most abundant in the coral fauna of the Agrio Formation (Valanginian-Hauterivian) of the Neuquén Basin (Garberoglio et al. 2020, 2021), indicating a closer relationship of Tithonian corals with these faunas than with Oxfordian ones. Both have plocoid corallites of less than 2 mm in diameter, and their colonies could be massive or ramose; *Stelidioseris*, the most abundant, in Picún Leufú presents ramose colonies (Fig. 12.c) with delicate branching at low angles growing subparallel and reaching more than 20 cm in height, suggesting constratal growth in an environment with moderate sediment supply, thus resembling phaceloid colonies. Sometimes the coral colonies may be heavily bioeroded by *Gastrochaenolites* borings, often containing snugly-fitting, conjoined shells of the bivalve producers in life position (Fig. 12.d-f). At Cerrito Caracoles, corals grew in an inner shelf margin environment, developing coralgal patch reefs (Armella et al. 2007).

In southwestern Chubut Province (Austral Basin), small, massive corals of the genus *Stelidioseris* were mentioned in the Cotidiano Formation (Mallín Cotidiano, Fig. 8.a). This

formation comprises limestones alternating with volcanites accumulated in small and disconnected depocentres, which hinders dating and correlation. Later studies assigned this formation to the Tithonian (Aguirre-Urreta et al. 2022). The small, massive coral colonies are associated with small bioherms constituted mostly by 'stromatoporoids', though corals can dominate at some points, generating coral-stromatoporoid patch reefs (Ramos 1978, 1993). Among the associated fauna crinoids are very frequent, as well as thick-shelled bivalves (Ramos 1978).

GLOBAL PATTERNS AND THE ARGENTINIAN RECORD

The general trends found in coral-dominated communities from Argentina show close correspondence with those recognized in the Northern Hemisphere, supporting the idea that most of them may represent global patterns. The Pliensbachian peak in solitary coral diversity recognized by Lathuilière and Marchal (2009) matches the variety of solitary forms identified by Echevarría et al. (2017).

The Puesto Araya reef was built by Triassic holdovers, at least at the genus level (Morsch 2001), with an important contribution from phaceloid morphologies, as observed in many Hettangian-Sinemurian examples (Terquem and Piette 1865, Elmi 1990, Simms et al. 2002, Kiessling et al. 2009), particularly from the Pacific margin of America (Wells 1953, Stanley and McRoberts 1993, Stanley and Beauvais 1994). Nonetheless, the presence of massive and platy cerioid colonies as more typical constructors, replacing phaceloid morphologies during ecological succession and generating relatively thick deposits, stands out as a peculiarity of this South American example.

The Puesto Araya reef also shows several features indicative of high sedimentation rates, typical of Early Jurassic environments (Leinfelder et al. 2002). Phaceloid morphotypes seem to cope with higher sedimentation rates (Leinfelder et al. 1994), but even cerioid colonies show frequent episodes of partial burial followed by recovery by overgrowth. The scarcity of bioerosion and encrustation also suggests a short residence time for coral skeletons. In contrast, the Piedra Pintada coral meadows show evidence of longer residence time, with intense encrustation and bioerosion.

The difference in coral composition between both localities could be in part due to these environmental variations. The higher corallite integration found in the Piedra Pintada meadows may indicate a higher dependence on zooxanthellae, hence requiring oligotrophic environments with little or no

siliciclastic input. On the other hand, corallite integration has been interpreted as an adaptation to sediment clearance, with plocoid, meandroid and thamnasterioid arrangements being more efficient than cerioid ones (Ricci et al. 2018).

Some major palaeobiogeographical events from the Early Jurassic may offer an alternative explanation. The different systematic composition between both Early Jurassic localities was highlighted by Morsch (2001), suggesting a lack of direct connection between both parts of the basin, or else, separate depositional events for each coral community. Considering the different times of deposition, the second option seems more plausible. The genus *Phacelostylophyllum*, one of the main components of the Puesto Araya reef, is frequently mentioned in the few reefs from the Early Jurassic East Pacific realm (Stanley and McRoberts 1993, Stanley and Beauvais 1994). *Meandrostylis* is also frequently mentioned from the American Pacific coast, but during the Triassic (e.g., Prinz-Grimm 1995, Stanley and González-León 1997, Caruthers and Stanley 2008), yet, according to Morsch (2001) *M.?* *jaworskii* may actually belong to a new genus. Contemporary reefs from Morocco reveal the presence of Triassic holdovers but with a significant contribution of newly evolved genera as well (Stone et al. 2022). On the other hand, the records of some of the genera from the Piedra Pintada meadows with Tethyan affinities (like *Myriophyllum* and *Goldfussastraea*) are the earliest in the South Pacific (Morsch 2001). Considering that the opening of the Hispanic Corridor probably began during the Pliensbachian (Damborenea et al. 2013), the main systematic differences between the Puesto Araya and Piedra Pintada areas may have been the result of the arrival of Tethyan coral faunas during the late Early Pliensbachian. Nonetheless, due to the unsatisfactory preservation of the Argentinian material (without preserved microstructural characters), no detailed palaeobiogeographical interpretation can be sustained (Morsch 2001).

The end-Pliensbachian and early Toarcian crises seem to have affected the coral communities of the west central basins of Argentina since neither bioconstructions nor coral-dominated communities have been identified so far after the local expression of the Early Toarcian Oceanic Anoxic Event (T-OAE). A similar situation occurs in Chile, where only one locality (Cerro Moctezuma) yielded thin and loosely scattered coral lawns of almost exclusively cerioid colonies and solitary forms during the Toarcian (Prinz 1991).

It is noteworthy how phaceloid coralla are not recorded from Argentinian basins in the Middle Jurassic, but branching colonies of higher corallite integration seem to develop a similar ecological role, coping with relatively high sedimentation rates, as observed for the Late Jurassic examples. The Bajocian increase in coral diversity documented in the Tethys is

well reflected in the Argentinian coral faunas as attested by the richness of taxa described thus far (Morsch 1996; Table 1).

The marked coral retraction from high latitudes between the Bathonian and the Early Oxfordian might be recognized in the scarce Callovian records in Argentina. In contrast, during the Middle Oxfordian optimum the largest Jurassic coral reef developed within the region, with outcrops at several localities encompassing a wide geographical range, and even developing a 13 km long reef. Surprisingly, coral generic diversity is low in these environments. This marks an important difference with other Oxfordian, mainly Tethyan and low-latitude, reefs, where alpha diversity is on average, 24 genera for final reef developmental stages (Martin-Garin et al. 2012).

At the same time, the Oxfordian assemblages recognized in the Neuquén Basin are represented by genera which are also recorded in the (northern) Tethys and in the incipient North Atlantic, except for *Australoseris*, an endemic genus (Hoqui 2022). This could indicate that their origin was Tethyan and that after the opening of the Hispanic Corridor during the Early Jurassic (Stanley and Beauvais 1994, Damborenea et al. 2013, Abdelhady and Fürsich 2015) they dispersed to the Pacific Realm (Leinfelder et al. 2002).

Platy colonies were frequently identified in the early stages of these communities as colonizers. Though these morphologies are usually interpreted as a response of the colony to low-light environments (Chappell 1980, Insalaco et al. 1997, Martindale et al. 2012, Olivier et al. 2012), they have also been related to low sedimentation and relatively high hydrodynamic stress (Chappell 1980). Interestingly, this last interpretation has been favoured for the platy colonies colonizing mobile substrates in La Manga Formation (Hoqui 2022), but also for the platy colonies of the Puesto Araya reef (Echevarría et al. 2024).

During the Kimmeridgian, a distinct global reduction of coral reef occurrences has been recognized (Leinfelder et al. 2002). The lack of coral communities in Argentina for this stage, nonetheless, responds to the temporary lack of open-marine sedimentation within the Neuquén Basin (see Fig. 1).

Despite the fact that the Tithonian (and Early Cretaceous) was marked by an extreme shallowing owing to a general drop in sea level (Leinfelder et al. 2002), that was not the case for Argentina where a new marine sedimentary cycle started in the Neuquén Basin and the Austral Basin opened to marine sedimentation. In both cases, coral-dominated communities developed reaching relatively high latitudes in Mallín Cotidiano (Fig. 8).

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