

1	Coral-dominated communities from the Jurassic of Argentina:
2	an overview
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17 Abstract

This paper is a synthesis of the knowledge on the Jurassic coral-dominated 18 19 communities of Argentina, providing novel information for some of them. Scleractinian 20 corals were scarce during the Hettangian-Sinemurian but were frequent and diverse 21 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 22 23 Late Pliensbachian Piedra Pintada coral meadow (Neuquén Province), and the Late 24 Pliensbachian to earliest Toarcian patches from Chubut Basin. After the end-Pliensbachian and Early Toarcian biotic crises, scleractinian corals reappeared in the 25 26 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 27

28 Callovian coral records spread throughout the Neuquén Basin. During the Oxfordian, 29 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 30 31 Blancas (Mendoza Province), recognizing different zones within it. Coral meadows were described at Coihue Co and Covunco, while small patches developed at Las 32 Lajas (Neuguén Province). Finally, during the Tithonian, coral meadows developed at 33 Picún Leufú (Neuguén Province), and some corals were recorded in Mallín Cotidiano 34 35 (Chubut Province, Austral Basin). The general trends observed for corals in Argentina (diversity peaks during the Pliensbachian and Bajocian, severe reduction during the 36 37 Toarcian, the Oxfordian bioconstruction optimum) match the 'global' trends based mostly on the records from the Northern Hemisphere. These communities also bear 38 great relevance in palaeoenvironmental interpretations, indicating shallow and well-lit 39 40 marine environments.

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

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43 Resumen

Comunidades dominadas por corales del Jurásico de Argentina: una 44 45 revisión general - Este trabajo procura sintetizar el conocimiento de las comunidades 46 dominadas por corales del Jurásico de Argentina, aportando información inédita para algunas de ellas. Los corales escleractinios fueron escasos durante el Hettangiano-47 48 Sinemuriano, pero se volvieron frecuentes y variados durante el Pliensbachiano. Tres 49 comunidades principales fueron reconocidas durante esta edad: el arrecife de Puesto 50 Araya (Mendoza) del Pliensbachiano Temprano más temprano, la pradera coralina de Piedra Pintada (Neuquén), del Pliensbachiano Temprano tardío al Pliensbachiano 51 52 Tardío más temprano, y parches del Pliensbachiano Tardío al Toarciano más 53 temprano de la Cuenca de Chubut. Después de las crisis bióticas de fines del

54 Pliensbachiano y del Toarciano más temprano, los corales escleractinios 55 reaparecieron en las cuencas jurásicas de la Argentina en el Aaleniano más tardío a Bajociano Temprano. Durante esta última edad muestran una gran diversidad, 56 57 probablemente generando praderas coralinas. Hay también registros callovianos dispersos en la Cuenca Neuquina. Durante el Oxfordiano las comunidades coralinas 58 alcanzaron su máximo desarrollo para el Jurásico de Argentina. Un arrecife de 13 km 59 de extensión fue descripto para Bardas Blancas (Mendoza), reconociéndose en ella 60 61 diferentes zonas. En Coihue Co y Covunco se describieron praderas coralinas, mientras que en Las Lajas (Neuquén) se desarrollaron pequeños parches. Finalmente, 62 durante el Tithoniano se desarrollaron praderas coralinas en Picún Leufú (Neuquén), y 63 se registraron algunos corales en Mallín Cotidiano (Chubut, Cuenca Austral). Las 64 tendencias generales observadas para los corales de Argentina (los picos de 65 diversidad durante el Pliensbachiano y el Bajociano, la drástica reducción durante el 66 Toarciano, el óptimo de desarrollo de las bioconstrucciones durante el Oxfordiano) 67 68 coinciden con las tendencias «globales» definidas mayormente sobre registros del 69 hemisferio norte. Estas comunidades presentan también una gran importancia en la 70 interpretación paleoambiental, indicando ambientes marinos someros y bien iluminados. 71

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

75 INTRODUCTION

76 Scleractinian corals appeared in the fossil record during the Anisian, but from 77 then to the early Norian they represented minor components of reef environments. After 78 a burst of taxonomic turnover in the Norian (Roniewicz 2011) both corals and sphinctozoid sponges began to dominate these environments (Stanley 2003). The Late 79 Triassic sponge- and coral-dominated reefs were severely affected by the 80 Triassic/Jurassic biological crisis (Stanley 2001, Flügel 2002, Lathuilière and Marchal 81 82 2009). The disruption of these environments was caused by a first-order extinction event that selectively affected reef communities more intensely than other benthonic 83 communities (Kiessling et al. 2007). 84

Much of the Early Jurassic is marked by an eclipse interval of 5 to 8 million years 85 with a global reduction in carbonate deposition and a virtual absence of reef-building 86 (Stanley 2001, 2003, Pandolfi and Kiessling 2014). The few coral taxa surviving from the 87 Triassic generated the scarce Hettangian-Sinemurian coral reefs (Leinfelder et al. 2002), 88 some of them reaching relatively high palaeolatitudes (see Stanley and McRoberts 1993, 89 90 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 91 diversity increase was interrupted by a new extinction at the end of the stage (considered 92 as a first-order crisis for Scleractinia) and a significant reef collapse (Lathuilière and 93 94 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 95 new genera and species that became dominant in later Jurassic times (Stanley 2003, 96 97 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

102 genera became more numerous and cosmopolitan, though species distribution allows 103 for the recognition of several distinct basins (Beauvais 1984). From the Bathonian to the 104 early Oxfordian a cooling trend developed, marked by the disappearance of coral reefs 105 from relatively high latitudes in North America and Europe, and a slight reduction in the 106 number of genera (Beauvais 1984), though coral-dominated communities were still 107 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 117 118 modern ones (Leinfelder 2001), probably encompassing two adaptive strategies: 1) the 119 adaptation to terrigenous settings, triggering partial adaptation towards turbidity and 120 siltation stress; and 2) the adaptation to truly oligotrophic tropical intra-ocean settings 121 (Leinfelder et al. 2002). The first strategy, nonetheless, was largely wiped out by the 122 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 123 oligotrophic environments, leading to the modern reefs (Leinfelder et al. 2002). This view 124 125 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 126 siliciclastic settings, even larger than the proportion of Jurassic reefs in this kind of 127 settings (Kiessling 2002, Dimitrijević et al. 2024). In any case, these variations highlight 128

the need for caution when comparing reefs in the geological record with their moderncounterparts (Leinfelder 2001).

131 This global picture is focused mostly on the Northern Hemisphere, particularly on 132 the Tethys and North America, with scarce examples of coral-dominated communities 133 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 134 previously less known coral-dominated communities from southern hemisphere mid-135 136 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 137 138 ages. А comprehensive synthesis, including palaeoecological and 139 palaeobiogeographical implications, is also provided.

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141 *Descriptive terminology.* It follows the usage among fossil Scleractinia 142 researchers as established in the Treatise on Invertebrate Paleontology (Wells 1956) 143 and still currently applied (e.g., Budd and Stolarski 2009, Löser 2024).

Both corallite arrangement and general shape of the corallum were considered 144 when characterizing coral associations, as they provide different palaeoecological 145 146 information. Corallite arrangement (or corallite integration) has been usually related to the inference of zooxanthellae symbiosis, with higher levels of integration considered as 147 148 one of the indications of the presence of zooxanthellae (Nose and Leinfelder 1997, Gill 149 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 150 provides systematic information, as it is crucial for the determination of the genera (Löser 151 152 2024).

153 Corallum shape, on the other hand, is usually related to environmental variables 154 such as hydrodynamic energy, sedimentation rates and sunlight incidence (Chappell 155 1980, Insalaco et al. 1997, Stanley and Lipps 2011, Ricci et al. 2018), being variable 156 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; 157 foliaceous, if they form thin, expanding, overlapping sheets with a small basal 158 159 attachment; and platy, if they have a thin, flattened, sheet-like form. Within the branching morphologies, three main types can be differentiated: caespitose, represented by small 160 colonies (up to 25 cm high and 40 cm basal diameter) with fine branches (0.5 cm to 1.5 161 cm diameter) of variable packing, without a main axis and with domical outline; 162 163 corymbose, represented by large colonies (up to 1.8 m high and 2 m basal diameter) 164 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 165 1.8 m high and 2 m basal diameter) with a main axis (up to 15 cm wide) and loosely 166 arranged branches (up to 5 cm at their base) decreasing in diameter towards the apex 167 (for more detailed description and measures see Hoqui 2022). 168

Also, the descriptive terminology of Insalaco (1998) for coral bearing beds was 169 applied, recognizing six styles of growth fabric development depending on the growth 170 171 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; 172 platestones are dominated by platy corals; sheetstones are generated by very thin and 173 174 laterally expanded colonies; domestones are constituted mostly by massive 175 morphologies; and mixstones are related to varied morphologies, none of them representing more than 60% of coral skeletons. 176

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 Burque 1992, Wood 2001). This structure is laterally constrained by
surrounding sediments that are linked to it in its genesis.

186 Also, and particularly to describe the reef facies in the Bardas Blancas area, 187 arbitrary categories were generated according to the size of the structures that make up 188 the reef complex. The reef is divided into zones or components; these are, in increasing order of size: colonies, patches and pseudobarriers (Hogui 2022). The minimum 189 component of this classification is the individual colony (never larger than 2.5 m in 190 191 diameter). This is followed by patches that originate because more than one colony 192 grows at a distance of less than 2.5 m. Each patch can be singled out and measured 193 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 194 195 can reach up to 100 m in horizontal extent and exceed ten metres in height.

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Repositories and institutional abbreviations. Specimens examined are housed in 197 the following repositories: IANIGLA-PI = Instituto Argentino de Nivología, Glaciología y 198 Ciencias Ambientales, Mendoza, Argentina; MCF-PIPH = Museo Municipal Carmen 199 Funes, Plaza Huincul, Argentina; MLP = División Paleontología Invertebrados, Museo 200 201 de Ciencias Naturales de La Plata, La Plata, Argentina; MOZ-PI = Museo Provincial de 202 Ciencias Naturales "Dr. Prof. Juan A. Olsacher", Zapala, Argentina; and MPEF-PI, Museo Paleontológico Egidio Feruglio, Chubut, Argentina. Further specimens examined 203 204 are housed in: CPBA = Geology Department, Universidad de Buenos Aires, Buenos 205 Aires, Argentina; SIRAME-SEGEMAR and DNGM= Dirección Nacional de Geología y Minería, Buenos Aires, Argentina. 206

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208 **GEOLOGICAL SETTING**

209 Marine Jurassic in Argentina developed in three main basins: Neuquén, Chubut 210 and Austral basins; coral-dominated communities were reported in all of them, though it 211 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 212 (Howell et al. 2005) and it encompasses most of the Jurassic stages in marine facies 213 214 (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 215 evolution of a series of narrow and isolated depocentres (Uliana and Biddle 1988, 216 217 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 218 Sinemurian to Toarcian) developed, causing the coalescence during the late 219 220 Sinemurian-Pliensbachian of the initial depocentres and the enlargement of the area under marine influence (Legarreta and Gulisano 1989, Legarreta and Uliana 1996, see 221 Fig. 2). From this time on, until the Early Cretaceous, it developed as a back-arc basin 222 related to circum-Pacific convergence (Legarreta and Uliana 1996, Howell et al. 2005). 223 According to Groeber (1946) a major sedimentary cycle (his 'ciclo Jurásico') developed 224 until Oxfordian-Kimmeridgian, with the closure to marine sedimentation; as a 225 226 consequence, no marine sediments were deposited during the Kimmeridgian (Fig. 1). During the Tithonian marine sedimentation resumed, marking the beginning of a new 227 sedimentary cycle ('ciclo Ándico'). Tithonian sediments are currently included in the 228 229 Mendoza Group (Groeber 1946, Digregorio and Uliana 1980, Riccardi 1988).

230 The Chubut Basin is a NNW-SSE elongated depocentre, lying unconformably 231 over late Palaeozoic rocks, with marine beds deposited during a short time interval from 232 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 233 western region of the Chubut Province, central-northern Santa Cruz Province, and 234 235 southwestern Río Negro Province (from 41º00'S to 44º30'S, Fig. 2) (Suárez and Márquez 2007). The sedimentary succession of the Chubut Basin accumulated under an 236 extensional tectonic regime (Lizuain 1999, Uliana and Legarreta 1999), starting with 237 continental deposits overlain by shallow marine and continental successions. These 238

marine beds normally interfinger with continental facies, mainly pyroclastic, to the east(Franchi et al. 1989).

241 The Austral Basin was a retro-arc marine basin developing between the Late 242 Jurassic and the Early Cenozoic, in southwestern Patagonia and Tierra del Fuego Island; 243 in Argentina it encompasses western Tierra del Fuego and Santa Cruz provinces, and 244 southwestern Chubut Province (Suárez et al. 2009, Cuitiño et al. 2019). The Jurassic 245 outcrops belong to the rift stage of sedimentation, with the marine transgression 246 developing over grabens and half-grabens on a Middle-Upper Jurassic volcanic 247 basement (Suárez et al. 2009, Cuitiño et al. 2019). Towards the north of the basin (southwestern Chubut Province) marine sedimentation began in small inner retroarc and 248 intra-arc depocentres, developed in a volcanic context (Folguera and lannizzotto 2004), 249 250 most likely during the Tithonian (Olivero 1987, Bucur et al. 2009, Aguirre-Urreta et al. 251 2022, Fig. 1).

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253 JURASSIC CORAL COMMUNITIES FROM ARGENTINA

The published information on Jurassic corals from this part of the world is limited 254 255 and scattered; the oldest references for Argentina date from late in the 19th century: 256 Behrendsen (1891) mentioned Montlivaltia? from Portezuelo Ancho, Mendoza. Later 257 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 258 259 deal with diverse aspects of the coral communities, their evolution and palaeoenvironment (Damborenea et al. 1975, Morsch 1986, Matheos and Morsch 1990, 260 Lanés and Morsch 1998, Massaferro et al. 1998, Palma et al. 2007, 2009, Echevarría et 261 262 al. 2017, in press, Hoqui et al. 2019). Unfortunately, despite their increasing records, taxonomic studies are few (Gerth 1926, 1928, Weaver 1931, Morsch 1990, 1991, 1996, 263 2001, Hoqui et al. 2019), in part due to the deficient preservation of the available 264 265 specimens. A list of the systematic identifications compiled from the literature is provided 266 (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.

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271 Early Jurassic

272 Hettangian-Sinemurian

273 As elsewhere in the world, scleractinians were scarce in Hettangian and 274 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 275 biofacies dominated by diverse pectinoid and limoid bivalves (Damborenea and 276 Manceñido 2005). The specimens were discussed and figured by Echevarría et al. (2017, 277 278 p. 73, fig. 4). Most of the materials so far available are preserved as moulds; hence, 279 precise systematic assignments are not possible, but these Hettangian and Sinemurian corals are morphologically rather uniform (simple discoidal coralla) and low in diversity, 280 281 likely representing only one or two taxa. As discussed by Echevarría et al. (2017), some of them strongly resemble the species Haimeicyclus haimei (Chapuis and Dewalque 282 1853), known from Hettangian–Sinemurian strata of Europe. 283

284

285 *Pliensbachian*

286 The impoverished picture described for Hettangian and Sinemurian drastically 287 changed by Early Pliensbachian times, when coral records became more common throughout the Neuguén Basin (Fig. 2.a). Solitary corallum shapes were more diverse 288 and colonial scleractinians were first recorded for the Jurassic in the basin (Echevarría 289 290 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 291 communities, in localities spanning a wide palaeolatitudinal range. We will focus on three 292 293 different time points, each of them developing a particular coral-dominated community: 294 (a) Early Pliensbachian Meridiceras 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

305 palaeomagnetic studies (Iglesia-Llanos et al. 2006).

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(a) Meridiceras externum Zone - The marine transgression was restricted to the 307 south of Mendoza Province during the Early Pliensbachian (Fig. 2.a). In the Atuel River 308 309 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 310 turbidity-current-influenced outer shelf (Lanés 2005). Close to the locality of Puesto 311 312 Araya (Fig. 2.b), on the slope of a hill just north of the road (Fig. 3.a) some beds corresponding to a small coral reef (Puesto Araya reef) were recognized in the 313 314 Meridiceras externum Zone. These beds were already mentioned by previous authors 315 (Lanés and Morsch 1998, Morsch 2001) and described in detail by Echevarría et al. (in press). The general logged section in which these beds are included (Fig. 3.b) shows 316 tidal-dominated deposits towards the base, followed by storm and fairweather deposits 317 318 fining and thinning upwards (Lanés 2005).

To better understand the development of Puesto Araya reef, Echevarría et al. (in press) logged five sections distributed 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 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 successions, as highlighted by some authors (see Mewis and Kiessling 2013).

At least two, but most likely three, phases could be recognized. The first phase 333 334 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 335 associated with this stage, as well as bivalves of varied life habits (epibyssate, 336 337 endobyssate, even occasionally burrowers); echinoid spines were recovered from micropalaeontological samples. In vertical succession, these beds are followed by a 338 339 rudstone to floatstone of resedimented phaceloid colonies with a similar taxonomic 340 composition, suggesting an increase in hydrodynamic energy. In turn, this structure is 341 covered by siliciclastic sediments, indicating the demise of an initial community (Fig. 3.c).

342 The second phase begins with similar beds (Fig. 3.c), though a stabilization stage 343 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 344 colonization one, marked by a platestone of platy to tabular cerioid colonies in life 345 346 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 347 were interpreted as a response to low siliciclastic sedimentation and relatively high 348 hydrodynamic stress (Echevarría et al. in press): a shell debris matrix alternates with 349 platy and laterally extended cerioid colonies, revealing the fast growth of the 350

351 scleractinians and of the whole structure. The flat colonies were better adapted to the352 increasing environmental energy, being resedimented only on rare occasions.

353 The following beds suggest an environmental change, and hence a third phase, 354 with lower hydrodynamic energy. A widely developed mixstone, with low-domal cerioid 355 as well as phaceloid colonies in life position, can be found with a very diverse associated fauna (byssate, crevice dweller and cementing bivalves, serpulids, echinoids, 356 357 holothuroids). The morphology of cerioid colonies, together with the phaceloid colonies 358 in life position, may imply a decrease in hydrodynamic energy and an increase in siliciclastic sedimentation (Echevarría et al. in press). At this point, the relatively loose 359 arrangement of coralla suggests that this extensive structure was more like a meadow 360 than a true framework. However, towards the north, a low-diversity domestone of 361 362 densely-packed hemispherical cerioid colonies suggests a small reef front, exposed to high hydrodynamic energy, hinting to an allogenic domination stage (Walker and 363 364 Alberstadt 1975).

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. in press).

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377 (b) *Austromorphites behrendseni* Zone - By this moment the Neuquén Basin 378 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.

384 It is towards the south of the basin (southern Neuquén Province, Fig. 2.a) that 385 coral-dominated communities reached a major development, generating an extensive 386 coral meadow. The Early Jurassic beds of the Piedra Pintada Formation bear a great 387 diversity of invertebrate faunas, known since the beginning of the 20th century (Roth 1902, Burckhardt 1902). Damborenea et al. (1975) recognized and characterized several 388 biofacies in these shallow marine deposits, and the coral beds (their sub-biofacies A2) 389 390 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 391 arrangement disparity are higher than in the Puesto Araya reef previously described, 392 393 with solitary [Styllophyllopsis? cf. victoriae (Duncan 1868), Myriophyllum sp.], phaceloid (Retiophyllia? sp.), cerioid [Distichomeandra cf. austriaca (Frech 1890), Microphyllia cf. 394 395 flemingi (Milne-Edward and Haime 1851)] and cerio-meandroid (Goldfussastraea? cf. 396 toarciensis Beauvais 1986) corallite arrangements. Nevertheless, the poor preservation 397 of these scleractinians hinders accurate systematic identifications, and further taxa may 398 be present, including forms with thamnasterioid corallite arrangements (Damborenea et 399 al. 1975). Regarding corallum shape, phaceloid coralla represent the branching forms, 400 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 407 occur at several levels, together with diverse bivalves, gastropods, brachiopods and
408 crinoid ossicles, but at about 100 m from the base of the measured section, there is an
409 extensive coral-dominated bed which can be tracked laterally for at least 1 km. The coral
410 bed thickness varies between 0.80 and 1.30 m.

411 Below this bed, a limestone of remobilised bivalve shells was recognized, 412 probably acting as a stabilization stage for the later development of corals. Towards the 413 south, (Fig. 5.b, d), the bed shows a growth fabric mainly built by calcareous skeletons 414 of a variety of solitary (Fig. 6.e) and especially colonial scleractinians, with most of the 415 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 416 followed by isolated, or groups of, tabular, fungiform, and hemispherical massive cerioid 417 and thamnasterioid colonies, also found in life position (locally domestone, Fig. 6.a-b). 418 This phaceloid to massive corals succession can occupy the whole bed thickness, or this 419 sequence of growing fabric styles may be repeated vertically within the bed (Fig. 6.b). 420 421 Laterally the growth fabric style continuity is not uniform, the coral bed may also show 422 just one of these growth fabric styles or a mixture of them.

423 The non-caliciferous epithecas of tabular and fungiform corals of this bed are 424 heavily encrusted by a variety of cementing organisms: bivalves, serpulids, bryozoans 425 and brachiopods, in addition to bearing diverse etchings and borings (Fig. 6.d). Less 426 frequently, some of these organisms may encrust solitary (turbinate to subcylindrical 427 corallites) caliciferous surfaces (Fig. 6.c) or shells. Encrusting bivalves include ostreids and Atreta sp. The distribution and orientation of the Atreta shells indicate that the 428 substrates were living organisms (Damborenea 2002, p. 98-99, text-fig. 47, pl. 11, figs. 429 430 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 431 (1991) recorded a couple of generations of thecideid brachiopods (Ancorellina ageri 432 433 Manceñido and Damborenea 1991) encrusting the same under surfaces (see Fig. 6.d), stressing that these sciaphilous, rugophilic cemented epibionts were most probably 434

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

444 On the other hand, towards the northern part of the bed, colonial corals become 445 very rare, although solitary corals are still present, and occasionally bear encrusters and 446 bioerosion. There, the accompanying fauna includes a large variety of shallow burrower 447 bivalves and even occasional deep burrowers.

448 Microfossil samples were taken at the main log trace (point "E", Fig. 5.b) and were 449 studied by Ballent (1987), who described Nodosariata foraminifers (vaginulinids and 450 polymorphinids) and ostracods (cypridoids, pontocypridoids, and cytherelloids).

In the nearby locality of Salitral Carrán Curá (Fig. 2.c), two successive coral-451 452 dominated beds were recorded (see section in Damborenea 1987, p. 49, t-fig. 5), with 453 comparable features and faunal content as the Cerro Roth beds. A similar coral fauna 454 was described by Morsch (2001) from Estancia Santa Isabel (Fig. 2.a), about 12 km NW 455 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 456 palaeoenvironmental conditions of probably low energy, shallow water depth and well-457 458 illuminated substrates.

459

(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 Cuche (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), 470 outcrops are better exposed, and small coral patches were recognized by the authors in 471 the lower part of the Mulanguiñeo Formation (Fanninoceras disciforme-Tenuicostatum 472 Zones), about 25 m above the local base of the unit (Fig. 7.a-b). These patches are 473 474 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 475 (Fig. 7.c-d). The growth fabric style appears to be a domestone. The coral epithecas are 476 477 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. 7c-d).

483

485

484 Middle Jurassic

486 some cerioid-thamnasterioid colonial corals associated with ammonites of late Aalenian 487 to earliest Bajocian age. Yet, the Bajocian diversification of scleractinians is better 488 reflected in the lower coral association (early Bajocian) of the Lajas Formation (or even 489 its transition to Los Molles Fm) from central Neuquén Province, showing the highest

In San Juan Province (Cordón de la Ramada, Fig. 8.a), Álvarez (1997) mentioned

alpha diversity of coral communities from the Jurassic of Argentina described so far 490 (Table 1). From lower Bajocian deposits at south of Barda Negra (=Paso del Carro 491 492 Quebrado, Fig. 8.d), Morsch (1996) described ten species distributed in nine genera, 493 with varied corallite arrangements, such as: plocoid [Pseudocoeniopsis cf. wintoni (Wells 494 1933)], cerioid (Araucanastrea minuscula Morsch 1996, A. majuscula Morsch 1996, Garateastrea bardanegrensis Morsch 1996, Mapucheastrea andina Morsch 1996), 495 496 thamnasterioid (Kobyastraea louisae Morsch 1996, Astraraea cf. fungiformis Beauvais 497 in Negus and Beauvais 1979) and meandroid (Complexastreopsis sp.), as well as 498 different solitary morphologies [Cyathophylliopsis delabechei (Milne-Edwards and Haime 499 1851), Neuquinosmilia gerthi Morsch 1996]. Massive morphologies were identified for most of the colonial coralla, with scarce laminar morphologies in A. cf. fungiformis, while 500 501 the solitary forms were mostly of low height (discoidal, cupolate or short cylindrical). 502 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 503 504 (Volkheimer 1973). Despite their diversity, none of these localities shows unmistakable 505 reefal structures, perhaps attaining patchy thickets very locally (scarce coralline 506 biostromes, according to Volkheimer 1973). Associated fauna shows great diversity, with 507 bivalves, gastropods and some brachiopods, bryozoans, echinoderms and serpulids. 508 This variety of morphologies and diversity of species and genera suggests that a coral meadow may have developed in the area. 509

510 On the other hand, another set of coral occurrences has been reported from a couple of areas in central Neuguén Province (the vicinities of Los Molles-Chacaico and 511 of Los Pozones, Weaver 1931, see Fig. 8.d), and northern Neuguén Province (Vega de 512 513 la Veranada, Groeber et al. 1953, Stipanicic 1965, Fig. 8.a). The coral assemblage from brown bioclastic sandstones of variable grain size, in central Neuguén Province, appears 514 characterized by fewer genera/species, including conspicuous solitary Montlivaltia aff. 515 kobyi Beauvais 1966, plus cerioid "Convexastrea" weaveri Gerth 1928 and meandroid 516 517 Complexastreopsis caracolensis (Steinmann 1881). Notice that members of this

association have been usually regarded as Callovian (Weaver 1931, Stipanicic, 1965,
Volkheimer 1973), though allegedly early Bajocian by Morsch (1996). The arcosic 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.).

530 From this general background, it seems clear that the Middle Jurassic of 531 Argentina still requires a thorough assessment of its coral-dominated communities,

532 being a promising field for future studies.

533

534 Late Jurassic

535 During this lapse of time, two main intervals with well-developed coral-dominated 536 communities were recognized in western Argentina: the late Middle Oxfordian, with the 537 coral bioconstructions of La Manga Formation; and the Tithonian, with the well-538 developed coral communities of the Picún Leufú and Cotidiano formations (Fig. 1).

539

540 Late Middle Oxfordian - Perisphinctes-Araucanites Zone

541 Coral-dominated beds and reefs can be recognized within deposits of La Manga 542 Formation at several localities in the Neuquén Basin. In this paper, coral communities 543 from Bardas Blancas, Coihue Co (both in southern Mendoza Province, Fig. 8.b), Cuchillo 544 Curá and Covunco (both in Neuquén Province, Fig. 8.c) will be described. Although 545 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 546 547 genera (Stelidioseris, Australoseris, Etallonasteria and Stephanastrea) were recognized 548 (Morsch 1990, Beresi et al. 2017, Hoqui et al. 2019); however, estimates of diversity 549 based on a taxonomic list may be seriously biased because most of the fossil samples 550 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 551 552 necessary for systematic assignments (Hoqui et al. 2019). Corallum growth forms can 553 be branched (caespitose, corymbose and arborescent), platy and domal. The corallite arrangement is usually plocoid to ceriod with very small calices in the branched colonies 554 and thamnastero-meandroid with calices up to 1 cm in diameter in the platy and domal 555 556 forms.

Three main types of coral-dominated communities were identified in La Manga 557 Formation for the Late Middle Oxfordian (Fig.10): (a) coral meadows of platy corals with 558 559 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 560 extension can be tens of metres (tabular strata); (b) small reef patches of domal section, 561 562 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 563 564 and arborescent forms can also be recognized; c) large patches that can amalgamate 565 and generate pseudo-barriers; in this case, all the associated growth types may be 566 recognized in the same biocenosis or they can replace each other in the same beds (ecological succession). 567

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 along 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).

574 This reef can be divided into a core reef zone, a back reef zone and a frontal reef 575 zone (Hoqui 2022). Each of these zones is characterized by morphofunctional coral 576 associations. The back reef has densely packed corymbose colonies associated with 577 platy and caespitose colonies. The reef core shows a progression from associations with 578 small platy and branching corals to associations dominated by large globose colonies 579 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 580 that may sometimes be surrounded by caespitose forms (Hogui 2022). Below the reef 581 deposits, tabular beds dominated by platy colonies can be recognized; these layers 582 583 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 584 particular ecological dynamics where a mobile substrate (above the storm surge line) 585 586 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. 587 588 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).

595 Similar associations developed in Covunco (Neuquén Province), in the first 596 metres of the logged section. Nonetheless, dome-shaped patches up to ten metres in 597 lateral extension and two metres in thickness developed above such beds. These 598 patches are characterized by two morphologies, almost equally abundant (Hoqui 2022): 599 either platy colonies similar to those represented in the underlying beds, or else,

600 branching colonies with very loosely packed, corymbose forms (Fig 11). The corymbose 601 forms recognized mainly in Covunco show a large vertical development and a much 602 wider spacing or separation among branches than in specimens with this type of growth 603 from other localities. Based on the inferences of Beresi et al. (2017) about the 604 sedimentation rate at this locality, it can be assumed that the corymbose forms, with 605 plocoid corallite arrangement (Stelidioseris) played the same environmental role as the 606 phaceloid forms in Early Jurassic examples. They developed in slightly agitated but 607 somewhat turbid waters (either due to sedimentary input or resuspension of sediments), 608 being able to cope with relatively high sedimentation rates.

In the Cuchillo Curá provincial protected area (south of Las Lajas, central 609 Neuguén Province, Fig. 8.c) the bioconstructions are very different from those mentioned 610 above. In this case, they are small clusters (1 m high and 80 cm in diameter) of small 611 discoidal Stelidioseris sp. colonies with columnar projections and a plocoid corallite 612 arrangement though with very narrow coenosteum and hence appearing cerioid. The 613 614 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 615 occurred in environments where the oolitic fabric was optimal, indicating that the 616 617 environmental energy was high to very high. As a result, the bioconstructions are made 618 up of this single morphological type. These discoidal colonies with columnar projections 619 are cemented, and in present-day environments they are usually found in wave-break 620 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, long-spired gastropods, miliolid and agglutinated foraminifers, and calcareous algae of the *Acicularia/Terchemella* group (Bucur et al. 2008, 2014) (Fig.11.h). Microbialitic crusts with both stromatolitic and thrombolitic fabrics are also common.

628 Tithonian - Corongoceras alternans Zone

629 Within the Neuquén Basin, Tithonian corals were reported from the Picún Leufú 630 Formation (Fig. 12.g) in central Neuquén Province (Leanza 1973, Leanza et al. 1997, 631 Cucchi et al. 2005, Armella et al. 2007); these authors mentioned the corals as palaeoecological indicators, but none of them undertook systematic studies. Tithonian 632 633 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 634 635 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. 636 8.d) in Neuguén Province (Garberoglio et al. 2023). Ongoing studies indicate that there 637 would be only one species of each genus: Stelidioseris columbaris (Scott and Aleman 638 639 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 640 genera are the most abundant in the coral fauna of the Agrio Formation (Valanginian-641 642 Hauterivian) of the Neuquén Basin (Garberoglio et al. 2020, 2021), indicating a closer 643 relationship of Tithonian corals with these faunas than with Oxfordian ones. Both have 644 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. 645 12.c) with delicate branching at low angles growing subparallel and reaching more than 646 647 20 cm in height, suggesting constratal growth in an environment with moderate sediment supply, thus resembling phaceloid colonies. Sometimes the coral colonies may be 648 649 heavily bioeroded by Gastrochaenolites borings, often containing snugly-fitting, 650 conjoined shells of the bivalve producers in life position (Fig. 12.d-f). At Cerrito Caracoles, 651 corals grew in an inner shelf margin environment, developing coralgal patch reefs 652 (Armella et al. 2007).

653 In southwestern Chubut Province (Austral Basin), small, massive corals of the 654 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. Latest 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 coralstromatoporoid patch reefs (Ramos 1978, 1993). Among the associated fauna crinoids are very frequent, as well as thick-shelled bivalves (Ramos 1978).

662

663 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).

669 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 670 671 in many Hettangian-Sinemurian examples (Terguem and Piette 1865, Elmi 1990, Simms 672 et al. 2002, Kiessling et al. 2009), particularly from the Pacific margin of America (Wells 673 1953, Stanley and McRoberts 1993, Stanley and Beauvais 1994). Nonetheless, the 674 presence of massive and platy cerioid colonies as more typical constructors, replacing 675 phaceloid morphologies during ecological succession and generating relatively thick 676 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 meadowsshow 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 ceroid ones (Ricci et al. 2018).

Some major palaeobiogeographical events from the Early Jurassic may offer an 691 692 alternative explanation. The different systematic composition between both Early 693 Jurassic localities was highlighted by Morsch (2001), suggesting a lack of direct 694 connection between both parts of the basin, or else, separate depositional events for 695 each coral community. Considering the different times of deposition, the second option 696 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 697 East Pacific realm (Stanley and McRoberts 1993, Stanley and Beauvais 1994). 698 Meandrostylis is also frequently mentioned from the American Pacific coast, but during 699 700 the Triassic (e.g., Prinz-Grimm 1995, Stanley and González-León 1997; Caruthers and 701 Stanley 2008), yet, according to Morsch (2001) M.? jaworskii may actually belong to a 702 new genus. Contemporary reefs from Morocco reveal the presence of Triassic holdovers, 703 but with a significant contribution of newly evolved genera as well (Stone et al. 2022). 704 On the other hand, the records of some of the genera from the Piedra Pintada meadows 705 with Tethyan affinities (like Myriophyllum and Goldfussastraea) are the earliest in the 706 South Pacific (Morsch 2001). Considering that the opening of the Hispanic Corridor 707 probably began during the Pliensbachian (Damborenea et al. 2013), the main systematic 708 differences between the Puesto Araya and Piedra Pintada areas may have been the 709 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).

713 The end-Pliensbachian and early Toarcian crises seem to have affected the coral 714 communities of the west central basins of Argentina since neither bio-constructions nor coral-dominated communities have been identified so far after the local expression of 715 716 the Early Toarcian Oceanic Anoxic Event (T-OAE). A similar situation occurs in Chile, 717 where only one locality (Cerro Moctezuma) yielded thin and loosely scattered coral lawns 718 of almost exclusively cerioid colonies and solitary forms during the Toarcian (Prinz 1991). 719 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 720 develop a similar ecological role, coping with relatively high sedimentation rates, as 721 722 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 723 724 the richness of taxa described thus far (Morsch 1996; Table 1).

The marked coral retraction from high latitudes between the Bathonian and the 725 Early Oxfordian might be recognized in the scarce Callovian records in Argentina. In 726 727 contrast, during the Middle Oxfordian optimum the largest Jurassic coral reef developed 728 within the region, with outcrops at several localities encompassing a wide geographical 729 range, and even developing a 13 km long reef. Surprisingly, coral generic diversity is low 730 in these environments. This marks an important difference with other Oxfordian, mainly 731 Tethyan and low-latitude, reefs, where alpha diversity is on average, 24 genera for final 732 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, 737 Abdelhady and Fürsich 2015) they dispersed to the Pacific Realm (Leinfelder et al. 2002). 738 739 Platy colonies were frequently identified in the early stages of these communities 740 as colonizers. Though these morphologies are usually interpreted as a response of the 741 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 742 743 high hydrodynamic stress (Chappell 1980). Interestingly, this last interpretation has been 744 favoured for the platy colonies colonizing mobile substrates in La Manga Formation (Hogui 2022), but also for the platy colonies of the Puesto Araya reef (Echevarría et al. 745 746 in press).

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 Neuguen 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 Mallin Cotidiano (Fig. 8).

757

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1205

1206 FIGURE CAPTIONS

1207 Figure 1: General development of the Jurassic basins in Argentina and stratigraphic

1208 position of the coral-dominated communities discussed in the text. Light blue stripes

1209 indicate the temporal ranges of marine sedimentation.

Figure 2: Early Jurassic location maps. a. Map of western Argentina showing the 1210 maximum extension of the sea during the Early Jurassic at different times (modified from 1211 1212 Legarreta and Uliana 1996, and Vicente 2005), and the location of Early Jurassic 1213 scleractinian records (based on data from previously known records and new ones from 1214 the authors). The localities with known coral-dominated communities are in red, those 1215 described in the text are underlined. b-d. Location sketch maps of the examples 1216 discussed in the text. **b.** Puesto Araya in the upper Atuel river region, Mendoza Province. 1217 c. Cerro Roth and Salitral Grande de Carrán Curá in the Piedra Pintada region, Neuquén 1218 Province. d. La Trampa and Nueva Lubecka in the Genoa river region, Chubut Province.

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. in press).

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.

Figure 5: Coral-dominated bed at Cerro Roth, Piedra Pintada area, Neuquén Province. 1235 a. General view of the outcrops at Cerro Roth and Cerro Roth South, taken from west to 1236 1237 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)-1238 S (to the right) extension of the outcrops of the coral bed (white dashes) and the 1239 observation points along it (red dots, A to M from South to North). c. Simplified measured 1240 1241 section (logged at yellow line in a and b, including point "E" in b), showing the location of 1242 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 1243 outcrops of the coral bed at the observation points indicated in b (see discussion in text). 1244

Figure 6: Field photographs showing some features of the coral-dominated bed at Cerro 1245 Roth and its fauna. a. General view of the bed near point "C", showing the density of the 1246 1247 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 1248 1249 of mixstone bed at point "H", sowing a repetition of the coral growing sequence (p-m, p-1250 m), rock hammer length 28 cm. c. Massive colony in life position at point "A", with the 1251 thamnasterioid calical surface encrusted by cemented bivalves. d. A fungiform colony showing the encrusted epitheca (non calical surface), small thecideid brachiopod shells 1252 1253 and oysters (MLP 24470). e. Cylindrical-throchoid solitary corallites from point "E" (MCF 1254 653a). f. Detail of the surface of a massive cerio-meandroid colony from point "F" (MLP 1255 36580). g. Detail of the surface of a massive colony from point "E" (MCF 653b), scale 10 mm. See relative location of observation points in Fig. 5. 1256

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.

1264 Figure 8: Middle and Late Jurassic location maps. a. Map of western Argentina showing 1265 the maximum extension of the sea during the Jurassic at different times (modified from Legarreta and Uliana 1996, and Suárez et al. 2019), and the location of Middle and Late 1266 Jurassic scleractinian records (based on data from previously known records and new 1267 1268 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 1269 1270 examples discussed in the text. b. Late Jurassic localities Coihue Co and Bardas 1271 Blancas in southern Mendoza Province. c. Late Jurassic localities Cerrito Caracoles, 1272 Covunco and Cuchillo Curá, central Neuquén Province. d. Middle Jurassic localities in central Neuquén Province (Los Pozones, South of Barda Negra, Los Molles, Cerro 1273 Chacaico) and Picún Leufú (Late Jurassic). 1274

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.

Figure 10: Middle Oxfordian coral-dominated communities from La Manga Formation. **ab**. 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.

1291 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 1292 24.5 mm. d. Branch of arborescent colony, coin diameter 24.5 mm. e. Platy colony, rock 1293 hammer 28 cm long. f. Platy colony with knobs or overgrowth (Sob). g. Bioclastic 1294 1295 wackestone/packstone with large articulated bivalves, marker length 16.8 cm. h. Microphotograph of bioclastic wackestone/packstone in g: Ds dasycladacean algae 1296 (Acicularia/Terchemella group); Cf calcispheres; Fr foraminifers; Onc oncoids; Ac 1297 Acicularia, scale 0.5 mm. 1298

Figure 12. a-b. *Stelidoseris* 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.

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

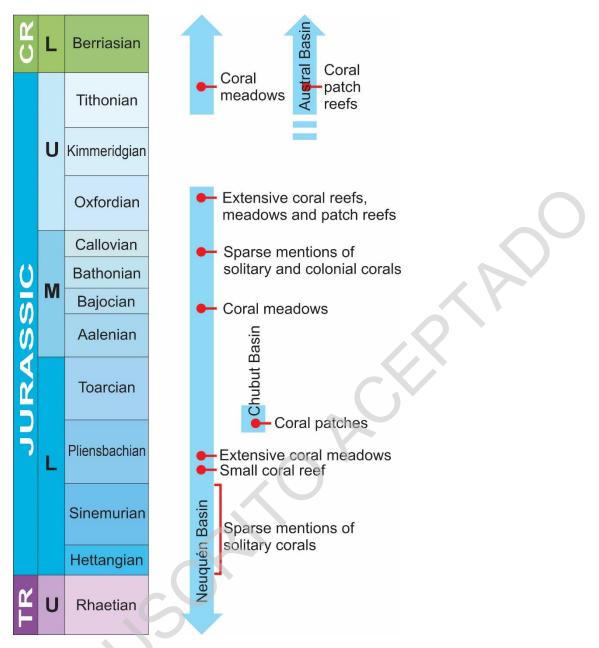


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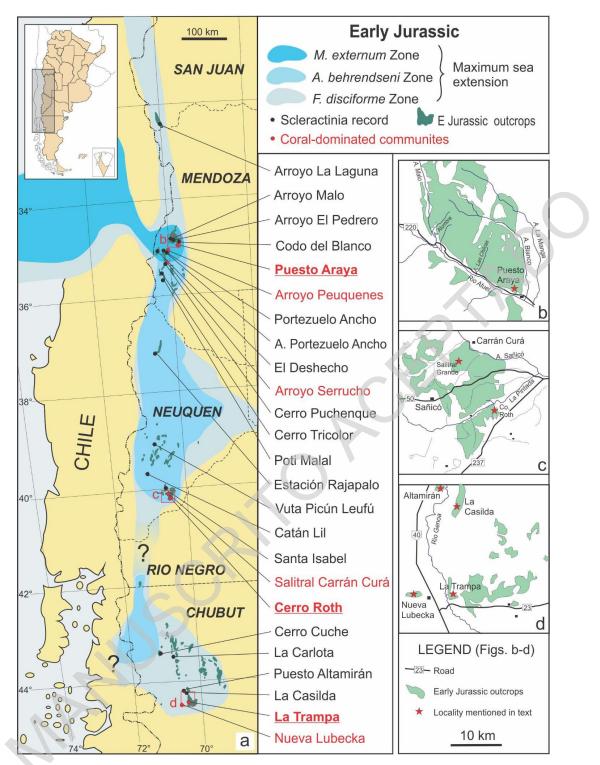


Figure 2: Early Jurassic location maps. **a**. Map of western Argentina showing the maximum extension of the sea during the Early Jurassic at different times (modified from Legarreta and Uliana 1996, and Vicente 2005), and the location of Early Jurassic scleractinian records (based on data from previously 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.

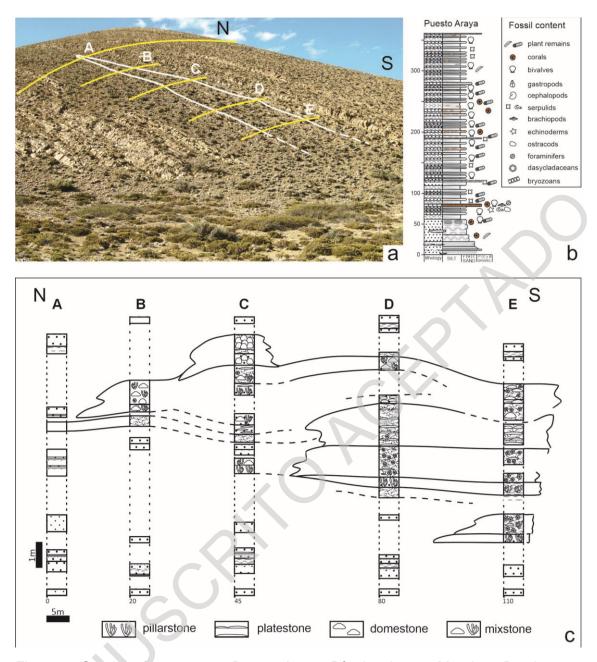


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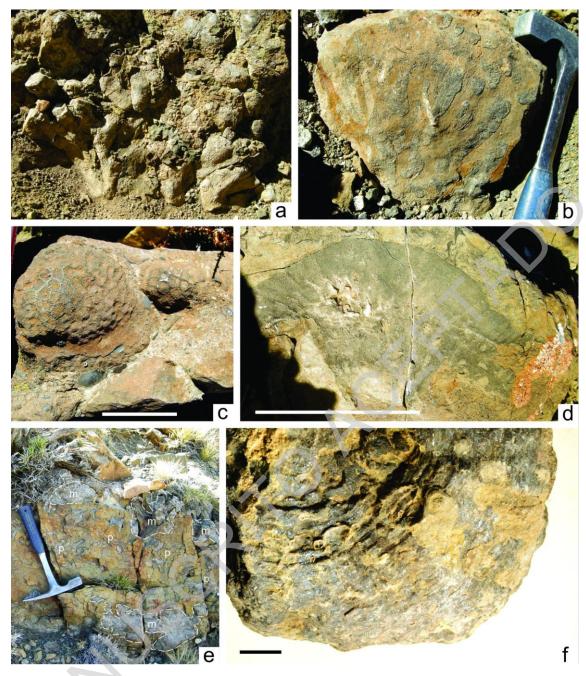


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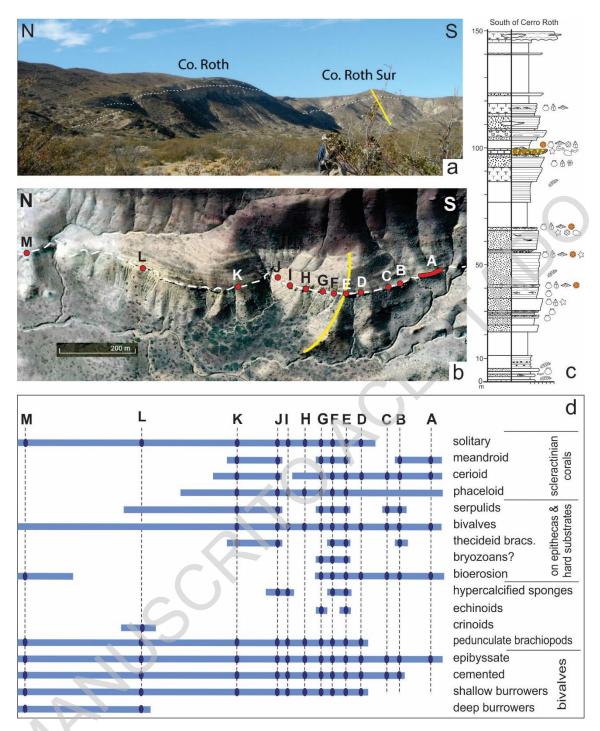


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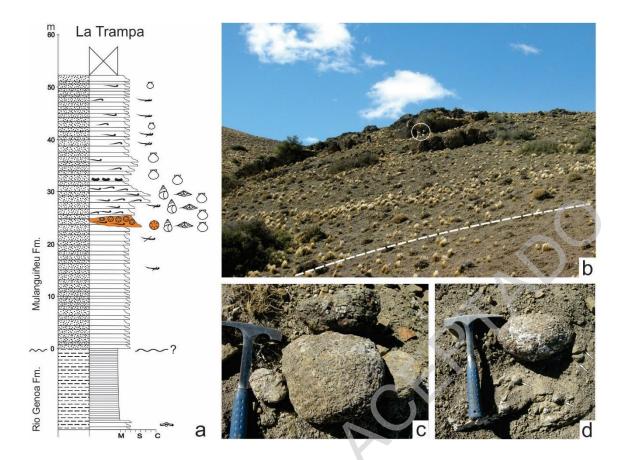


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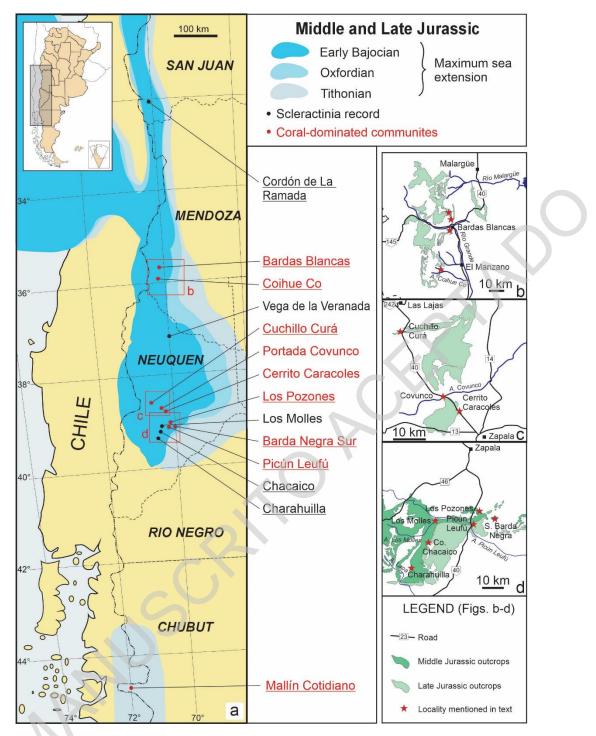


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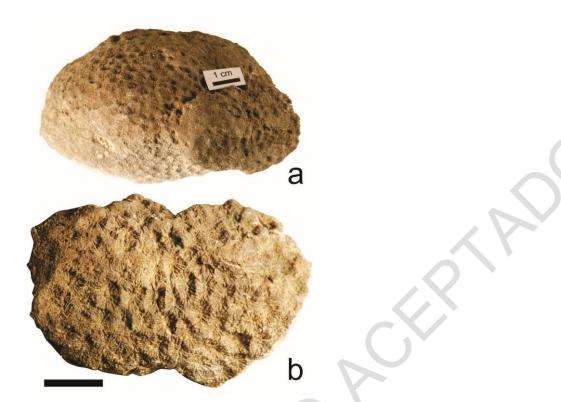


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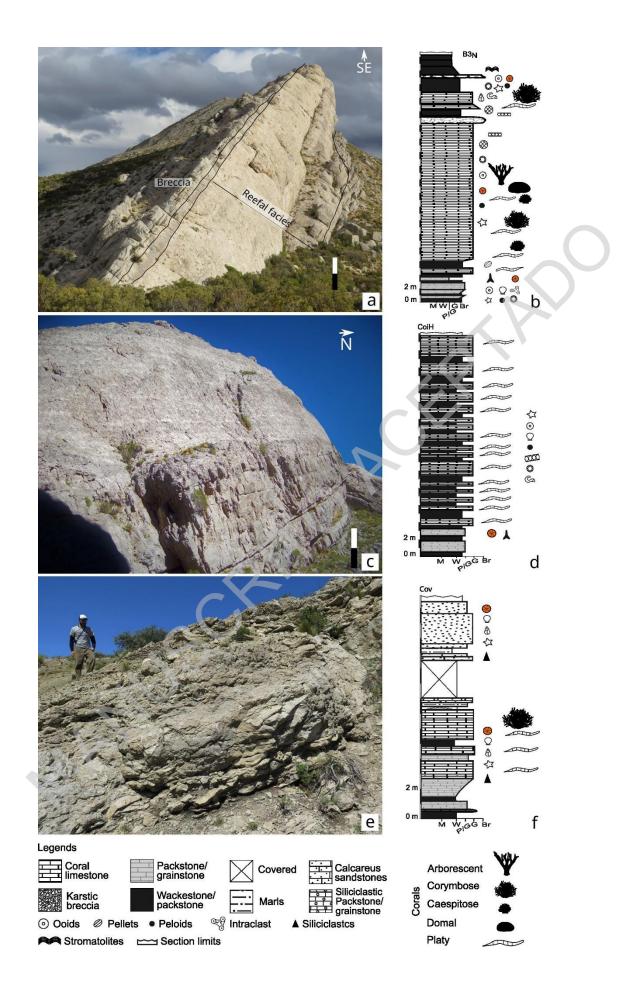


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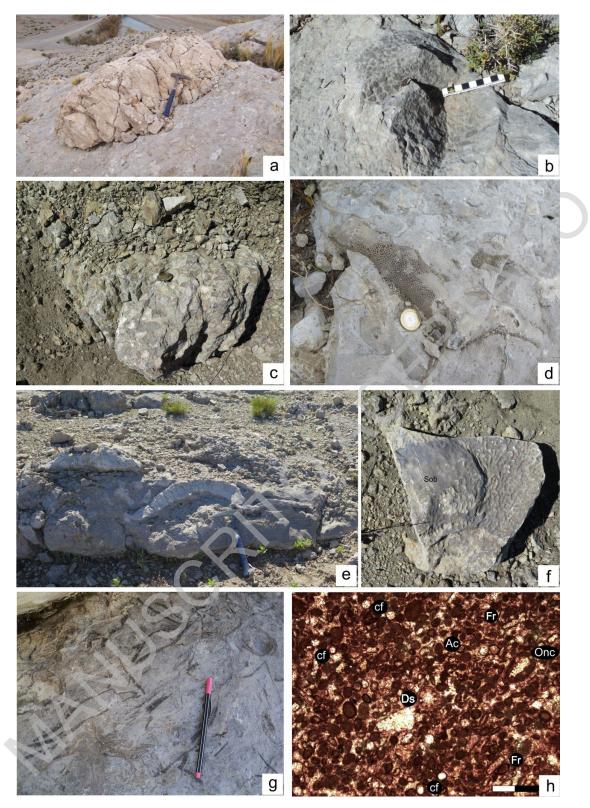


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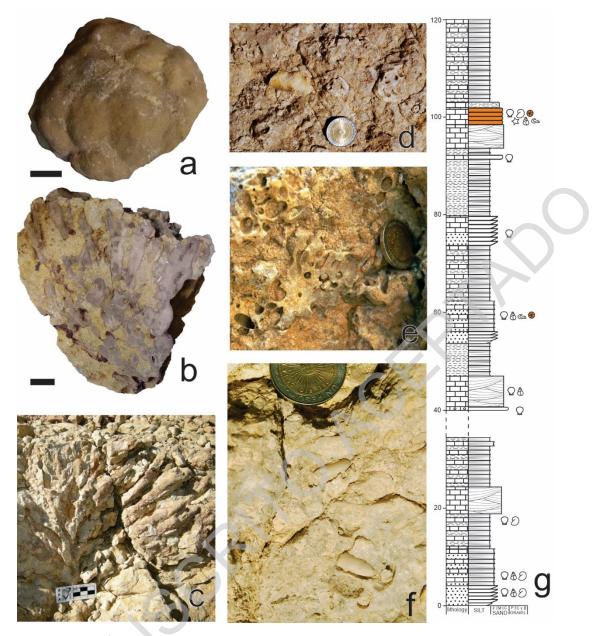


Figure 12. **a-b**. *Stelidoseris* sp. coralla from the Tithonian of the Picún Leufú Formation. **a**. Massive colony (CPBA 23453-29). **b**. Ramose colony (CPBA 23453-23). **c**. Field photograph of ramose colony. **d-f**. Field photographs of ramose colonies bored by bivalves (detail in f), coin diameter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

Time slice	Таха	References	Localities (maps in Figs. 2, 8)	Age
	Eocolumastrea octaviae (Prever 1909)	Garberoglio et al. 2023	Picún Leufú (Neuquén)	Late Tithonian
Late Jurassic	Stelidioseris columbaris (Scott & Aleman 1984)	Garberoglio et al. 2023	Picún Leufú (Neuquén)	Late Tithonian
	Stelidioseris sp.	Aguirre-Urreta et al. 2022, fig. 9.a-b	Mallín Cotidiano (Chubut)	Tithonian
	Stephanastrea sp.	Beresi et al. 2017, fig. 8e-f	Covunco (Neuquén)	Oxfordian
	<i>Etallonasteria</i> cf. <i>minima</i> (Étallon in Thurmann & Étallon1864)	Palma et al. 2009: fig. 7c; Hoqui et al. 2019: fig. 8	Bardas Blancas (Mendoza); Covunco (Neuquén)	Oxfordian
	Stelidioseris 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
	Australoseris radialis 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
	<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
	"Convexastrea" weaveri 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
	Convexastraea sp.	Weaver 1931, pl. 11, fig. 12	Ayo Los Molles (Neuquén)	Callovian
	Neuquinosmilia lospozonensis Morsch 1991	Morsch 1991b: 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?
ssic	?S <i>tephanastrea ramulifera</i> Étallon (in Thurmann & Étallon) 1864	Morsch 1996: pl. 83, fig. 1a-e	Los Pozones (Neuquén)	Bajocian? Callovian?
Middle Jurassic	Mapucheastrea andina Morsch 1996	Morsch 1996: pl. 89, fig. 1a-d. t-fig. 11	Barda Negra S, Los Pozones (Neuquén)	Bajocian - Callovian?
lidd	Araucanastrea minuscula Morsch 1996	Morsch 1996: pl. 84, fig. 1a-e; t-fig. 2	Barda Negra S (Neuquén)	Early Bajocian
Σ	Araucanastrea majuscula Morsch 1996	Morsch 1996: pl. 84, fig. 2a-c	Barda Negra S (Neuquén)	Early Bajocian
	Garateastrea bardanegrensis Morsch 1996	Morsch 1996: pl. 85, fig. 1a-f, t-fig. 4-7	Barda Negra S (Neuquén)	Early Bajocian
	Kobyastraea louisae Morsch 1996	Morsch 1996: pl. 86, fig. 1a-e, t-fig. 8-9	Barda Negra S (Neuquén)	Early Bajocian
	Astraraea cf. fungiformis Beauvais (in Negus & Beauvais) 1979	Morsch 1996: pl. 89, fig. 2a-c	Barda Negra S (Neuquén)	Early Bajocian
	Pseudocoeniopsis cf. wintoni (Wells 1933)	Morsch 1996: pl. 86, fig. 2a-c	Barda Negra S (Neuquén)	Early Bajocian
	Convexastreopsis sp.	Morsch 1996: pl. 88, fig. 2a-b	Barda Negra S (Neuquén)	Early Bajocian
	Cyathophylliopsis delabechei (Milne Edwards & Haime 1851)	Morsch 1996: pl. 87, fig. 3a-c	Barda Negra S (Neuquén)	Early Bajocian
	Neuquinosmilia gerthi 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
	Cyathophora decamera Gerth 1928	Gerth 1928: pl. 2, fig. 4; Weaver 1931: pl. 11, fig. 8	N Catán Lil (Neuquén)	Pliensbachian?
Early Jurassic	Stylophyllopsis? cf. victoriae (Duncan 1868)	Gerth 1928; Weaver 1931: Carral Tolosa 1942: pl. 1, fig. 1; Morsch 2001: fig. 2.1; Ferrari & 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
	Phacelostylophyllum cf. peruvianum (Wells 1953)	Morsch 2001: fig. 2.2	Puesto Araya (Mendoza)	Early Pliensbachian
	Meandrostylis? jaworskii (Gerth 1926)	Gerth 1926: pl. 4, fig. 24; Morsch 2001: fig. 3.3	Cerro Puchenque, Puesto Araya (Mendoza)	Pliensbachian
	Collignonastrea? sp.	Damborenea 2002, pl. 11, fig. 13	Cerro Roth (Neuquén)	Pliensbachian

Distichomeandra cf. austriaca (Frech 1890)	Morsch 2001: fig. 4.2	Santa Isabel, Cerro Roth (Neuquén)	Pliensbachian			
Retiophyllia? sp.	Morsch 2001: fig. 2.3	Cerro Roth (Neuquén)	Pliensbachian			
Microphyllia cf. flemimgi (Milne-Edwards & Haime 1851)	Morsch 2001: fig. 4.1	Santa Isabel, Cerro Roth (Neuquén)	Pliensbachian			
Myriophyllum sp.	Morsch 2001: fig. 3.1	Santa Isabel, Cerro Roth (Neuquén)	Pliensbachian			
Goldfussastraea? cf. toarciensis Beauvais 1986	Morsch 2001: fig. 3.2	Santa Isabel (Neuquén)	Pliensbachian?			
Anabacia andina Gerth 1926	Gerth 1926: pl. 4, fig.25	El Deshecho (Mendoza)	Pliensbachian			
Cnidaria gen. et sp. indet.	Ferrari & Bessone 2015: fig. 3.Z	La Casilda (Chubut)	Pliensbachian			
Stylophyllopsis sp.	Massaferro 2001, fig. 3	Cerro Cuche (Chubut)	Early Pliensbachian?			
Scleractinia indet. (solitary, cupolate)	Echevarría et al. 2017: fig. 5.5-7	Arroyo Serrucho (Mendoza)	Early Pliensbachian			
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			
Stylophyllopsis? cf. victoriae (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. Meandrostylus? jaworskii (Gerth 1926)	Echevarría et al. 2017: fig. 6.5-7	Puesto Araya (Mendoza)	Early Pliensbachian			
cf. <i>Haimeicyclus haimei</i> (Chapuis & Dewalque 1853)	Echevarría et al. 2017: fig. 4	Arroyo Malo (Mendoza)	Hettangian- Sinemurian			
Table 1. Coral taxa from Argentina recognized by the different authors at different moments during the Jurassic.						