

RECOVERY OF SCLERACTINIAN MORPHOLOGIC DIVERSITY DURING THE EARLY JURASSIC IN MENDOZA PROVINCE, ARGENTINA

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Abstract. After a diversity peak during the Late Triassic, corals were severely affected by the end-Triassic extinction. The study of their recovery is fundamental for a better understanding of the ecological rearrangement undergone by Early Jurassic marine invertebrate faunas. In this contribution we analyze the morphologic recovery shown by scleractinians in southern Mendoza Province, which is the only place in the Neuquén Basin with marine outcrops spanning the Triassic/Jurassic boundary. A two-stage recovery pattern was recognized. During the first stage (Hettangian–Sinemurian) only solitary corals, most of them discoidal, could be found. After a hiatus encompassing the latest Early Sinemurian and the Late Sinemurian, the second stage (Pliensbachian) developed. A sharp increase in morphological diversity of solitary corals is then recorded, with discoidal, cupulate, patellate, turbinate, trochoid/turbinate, trochoid/ceratoid and maybe cylindrical morphologies. Additionally, colonial forms with low degree of corallite integration (phaceloid and cerioid colonies) appeared in the basin. The diversification trend hereby described provides useful insight regarding the scleractinian recovery after the end-Triassic mass extinction event within southern basins of South America. Furthermore, this recovery pattern is comparable with the one recognized for other regions (Chile, western North America, central Asia) yet it differs from that observed in some European basins. The trend outlined herein for Early Jurassic corals from the Neuquén Basin may reflect a large-scale phenomenon and/or the action of local adverse conditions (such as fluvial influence), which is open to further testing.

Key words. Scleractinia. Early Jurassic. Neuquén Basin. Diversity recovery.

Resumen. RECUPERACIÓN DE LA DIVERSIDAD MORFOLÓGICA DE LOS ESCLERACTINIOS DURANTE EL JURÁSICO TEMPRANO EN LA PROVINCIA DE MENDOZA, ARGENTINA. Después de un máximo de diversidad durante el Triásico Tardío, los corales se vieron severamente afectados por la extinción del final del Triásico. El estudio de su recuperación resulta fundamental para una adecuada comprensión del reacondicionamiento ecológico de las faunas de invertebrados marinos del Jurásico Temprano. Se analiza aquí la recuperación morfológica experimentada por los escleractinios en el sur de la Provincia de Mendoza, único lugar en la Cuenca Neuquina con afloramientos marinos del pasaje Triásico–Jurásico. Se reconoce un patrón de recuperación de dos fases. Durante la primera fase (Hettangiano–Sinemuriano) sólo se registran corales solitarios, en su mayoría discoidales. Después de un hiato que abarcó la última parte del Sinemuriano Temprano y todo el Sinemuriano Tardío se desarrolló la segunda fase (Pliensbachiano). Se registra entonces un incremento marcado en la diversidad morfológica de los corales solitarios, con formas discoidales, cupulares, pateladas, turbinadas, trocoides/turbinadas, trocoides/ceratoides y posiblemente cilíndricas. Además, aparecen en la cuenca formas coloniales con bajo grado de integración de sus corallitos (faceloides y cerioides). La diversificación reconocida aporta información útil acerca de la recuperación de los escleractinios tras la extinción masiva de finales del Triásico en cuencas australes de Sudamérica. Este patrón de recuperación es comparable al de otras regiones (Chile, oeste de Norteamérica, Asia central) aunque difiere del hallado en algunas cuencas europeas. La tendencia aquí esbozada para los corales del Jurásico Temprano de la Cuenca Neuquina podría estar reflejando un fenómeno de gran escala y/o condiciones locales adversas (como influencia fluvial), lo cual plantea la posibilidad de futuros estudios.

Palabras clave. Scleractinia. Jurásico Temprano. Cuenca Neuquina. Recuperación de la diversidad.

CORAL faunas were severely affected by the Triassic/Jurassic mass extinction event (Lathuilière and Marchal, 2009). This event, one of the ‘big five’ of Raup and Sepkoski (1982), affected many groups of marine and continental organisms (Sepkoski, 2002; Hallam, 2002; Kiessling *et al.*, 2007, and

references therein) and resulted in a restructuring of ecological communities (Sepkoski, 1984; further examples in Tomašových and Siblík, 2007; Ros and Echevarría, 2011). Environmental impoverishment has been invoked as the most likely cause of this mass extinction (McHone, 2003;

Pálffy, 2003; Schootbrugge *et al.*, 2008) as well as of the breakdown of reef environments (Flügel, 2002; Lathuilière and Marchal, 2009). This breakdown is one of the major ecological effects of the end-Triassic mass extinction event. Nevertheless, non-framework-building corals also suffered diversity reduction.

Hettangian–Sinemurian non-reefal benthonic assemblages containing scleractinian corals are well known and widespread (Duncan, 1867, 1868; Beauvais, 1976, 1986; Prinz, 1991; Melnikova and Roniewicz, 2012; Gretz *et al.*, 2013; Hodges and Stanley, 2015) although examples of scleractinian reefs are rare (Stanley and McRoberts, 1993; Stanley and Beauvais, 1994; Kiessling *et al.*, 2009; see also Lathuilière and Marchal, 2009, for a summary on the subject). Even though Early Jurassic corals are known from the Pacific regions of both North and South America (Gerth, 1925, 1928; Weaver, 1931; Wells, 1953; Pérez d'Angelo, 1982; Stanley and McRoberts, 1993; Senowbari-Daryan and Stanley, 1994; Stanley and Beauvais, 1994; Stanley and González-León, 2000; Morsch, 2001), only a few corals have been definitely confirmed as being Hettangian or Sinemurian in age (Prinz, 1991; Hodges and Stanley, 2015).

In South America, scleractinian corals from the Neuquén Basin have received little attention, compared to other benthonic faunas (molluscs, brachiopods, see synthesis and references in Riccardi *et al.*, 1993, 2011), probably due to their usually poor preservation, which hinders their detailed systematic assignment. Late Triassic scleractinians are known from the south central Andes (Prinz, 1991; Prinz-Grimm, 1995), but there is only a single reference from Rhaetian deposits of the Neuquén Basin (a colonial coral attached as an epizoan on a bivalve shell, Riccardi *et al.*, 1997, fig. 3.2). On the other hand, corals are occasionally frequent and even abundant in some localities and stratigraphic horizons within the Hettangian–Pliensbachian interval. Yet, they are not usually frame builders or, at most, they can form small patch reefs. Considering the ecological significance of the group, an adequate characterization of reliably dated specimens results in a fundamentally better understanding of the invertebrate communities with corals (Hodges and Stanley, 2015).

Previous knowledge of Early Jurassic corals from Argentina was limited to about a dozen Pliensbachian to Toarcian species (Jaworski, 1915; Gerth, 1926, 1928; Weaver, 1931;

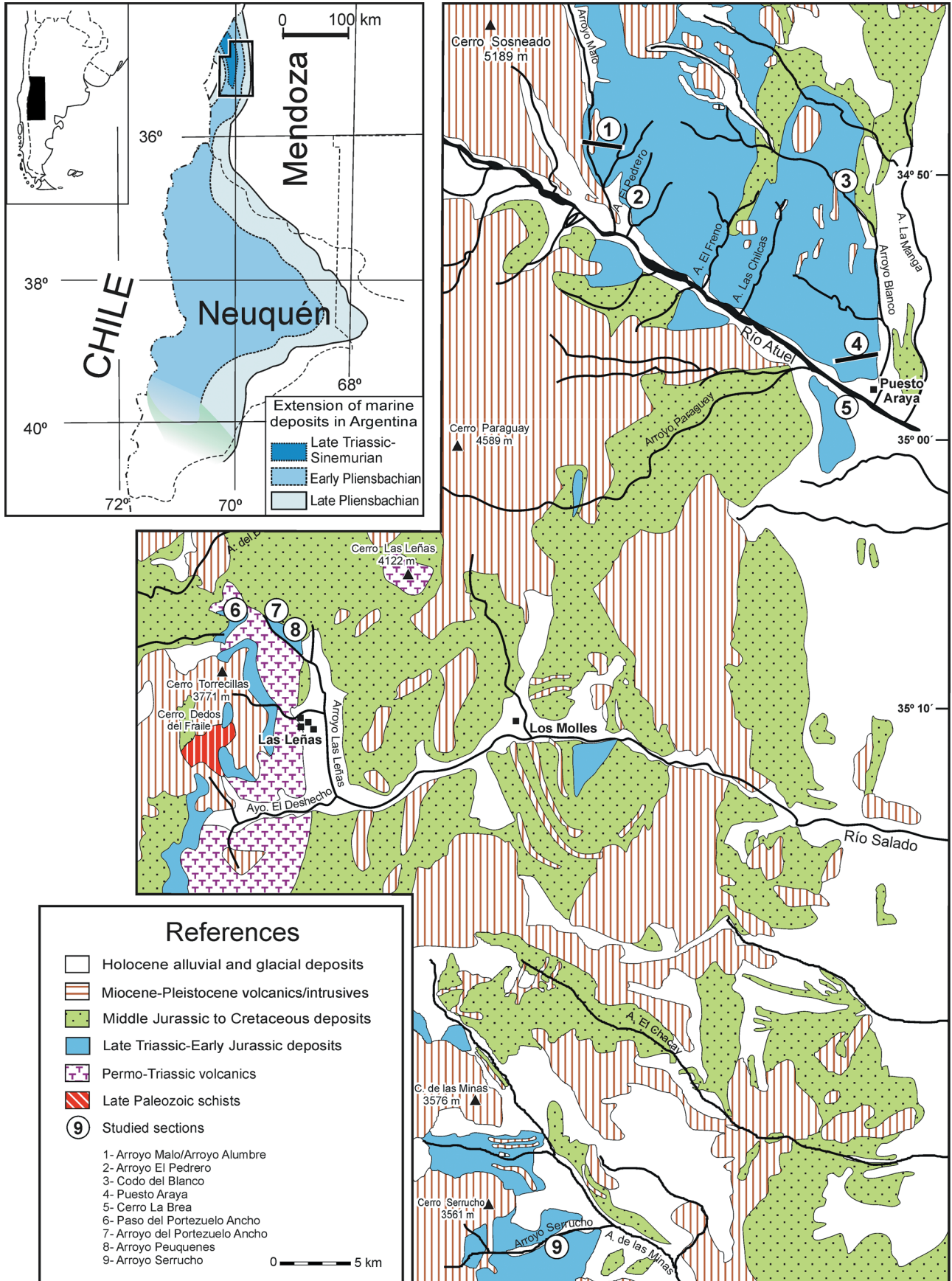
Carral Tolosa, 1942; Morsch, 2001; Massaferro, 2001). Although a series of Hettangian and Sinemurian biofacies based on bivalve and brachiopod distributions were distinguished and solitary corals were mentioned as occasional elements of benthonic assemblages (Damborenea and Manceñido, 2005: p. 169), there is no publication referring in detail to Jurassic corals of that age. Pending a formal systematic treatment, the Hettangian and Sinemurian material herein discussed and figured adds considerably to the understanding of early local recovery and diversification of scleractinians after the Triassic/Jurassic biotic crisis.

GEOLOGICAL SETTING

Latest Triassic and Early Jurassic sediments are known from several locations in western South America yet there are few well-exposed sections through marine sediments spanning the Triassic/Jurassic boundary. One continuous section from the Neuquén Basin exists in the Río Atuel area of southern Mendoza (Riccardi *et al.*, 1988, 1997, 2004; Damborenea and Manceñido, 2012, and references therein). During the Late Triassic–Early Jurassic, the western margin of the South American Plate was characterized by large transcurrent fault systems leading to the evolution of a series of narrow and isolated depocenters (Uliana and Biddle, 1988; Legarreta and Uliana, 1996). From the Early Jurassic to the Early Cretaceous, the development of an active subduction zone and a magmatic arc along the western margin of Gondwanaland led to back-arc subsidence within the Neuquén Basin (Uliana and Biddle, 1988; Legarreta and Uliana, 1996; Howell *et al.*, 2005).

The earliest Jurassic (Hettangian–Sinemurian) marine deposits in Argentina are confined, as shown in Figure 1, to the southern area of Mendoza Province, in the northern end of the Neuquén Basin. In this region, Lanés (2005) and Lanés *et al.* (2008) identified two stages of tectonic behavior: a first (synrift) stage, Rhaetian to late Early Sinemurian in age, during which accommodation was greater than sedimentary supply, thus leading to slope-type fan delta deposits; and a second (sag) stage, late Early Sinemurian to Toarcian, showing a varying accommodation rate (Fig. 2, inset). In the Early Pliensbachian the basin expanded towards the south, reaching its maximum extension in the Late Pliensbachian (Fig. 1, inset).

The marine synrift stage is well recorded towards the



west of the basin and was interpreted by Lanés (2005) as a delta front. Its lithology is dominated by shales and mudstones with subordinated sandstones (more frequent in Arroyo El Pedrero, Fig. 2) referred to the Arroyo Malo and the lower Puesto Araya formations. During the late Early Sinemurian, accommodation was outpaced by the sediment supply, thus allowing the progradation of the fan delta (Lanés, 2005; Lanés *et al.*, 2008). Bivalve/brachiopod associations indicate a normal marine environment, even though a brackish-water association developed in some localities (Damborenea and Manceñido, 2005; Damborenea and Lanés, 2007). Pre-Pliensbachian deposits recognized in eastern localities (like Puesto Araya, Fig. 2) are represented by the fluvial conglomerates of the El Freno Formation (Lanés *et al.*, 2008). The lowest part of the sag stage is well represented towards the east by the upper Puesto Araya Formation, with siliciclastic deposits indicating a storm-dominated shelf evolving from wave-dominated estuary to turbidity-current-influenced outer shelf (Lanés, 2005).

Paleomagnetic studies performed on the same sections which provided the material herein discussed indicate that during the Late Triassic and earliest Jurassic the area was located further south than it is nowadays and then it moved apparently northwards, reaching its northernmost position by the late Early Jurassic (Iglesia-Llanos *et al.*, 2006).

MATERIAL AND METHODS

Fossils were gathered from nine sections and other isolated localities along the Río Atuel, at the Arroyo Las Leñas and Arroyo Serrucho regions, in southern Mendoza (Fig. 1). Only the Arroyo Malo and Arroyo El Pedrero sections contain Hettangian–Sinemurian deposits. The stratigraphic positions of the coral specimens are shown in Figure 2 for four of those localities. Data about lithology, facies, associated fauna and detailed sample locations can be found in Damborenea (1987), Gulisano and Gutiérrez Pleimling (1995) and Lanés (2005). The stratigraphic provenance of the material is dated based on ammonites from the same sections,

using the local ammonite zonations shown in Figure 3 (Hillebrandt, 2006; Riccardi, 2008a, b). The specimens are deposited in the collections housed in the Museo de Ciencias Naturales La Plata (MLP) and the Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, Mendoza (IANIGLA-PI).

RESULTS

Hettangian–Sinemurian

Although corals are rare in Hettangian–Sinemurian beds of the Neuquén Basin, six specimens (all solitary forms) were recovered. These specimens ranged –in terms of local ammonite zonation– from the *D. reissi* (~ Liasicus) to the *Coroniceras-Arnioceras* (~ Bucklandi/Semicostatum) Zones. Most of the available specimens are preserved as moulds, so precise systematic assignments were not possible. However, the preserved morphologic characteristics show no major variation (Fig. 4). Calyx diameter ranges between 18 and 25 mm and shows four well developed septa cycles. S1 and S2 are both similarly developed while S3 and S4 are progressively shorter and thinner. An incipient fifth cycle appears in some samples (Fig. 4.7). Distal edges of the septa bear small beaded tubercles (Fig. 4.7) and there might be a columella. Dissepiments can be identified in one sample (Fig. 4.9). At least two forms of coralla can be recognized: one specimen displays a discoidal corallum type (Fig. 4.5–6) while one of the moulds seems to belong to a cylindrical or turbinate corallum (Fig. 4.1–3). Most of these specimens, as well as some of the Pliensbachian discoidal morphologies discussed below, strongly resemble the species *Haimeicyclus haimeii* (Chapuis and Dewalque, 1853), known from Hettangian–Sinemurian strata of Europe (Beauvais, 1976; Stolarski and Russo, 2002). Gerth (1926) already mentioned a *Stylophyllopsis cf. haimeii* from Pliensbachian beds at Portezuelo Ancho (locality 6 here). Unfortunately, he provided no illustration, although his description matches the materials examined in this study.

Figure 1. Location map for the Neuquén Basin (inset) and detail of Mendoza Early Jurassic outcrops with location of coral-bearing localities. (Simplified from Nullo *et al.*, 2005; Lanés *et al.*, 2008).

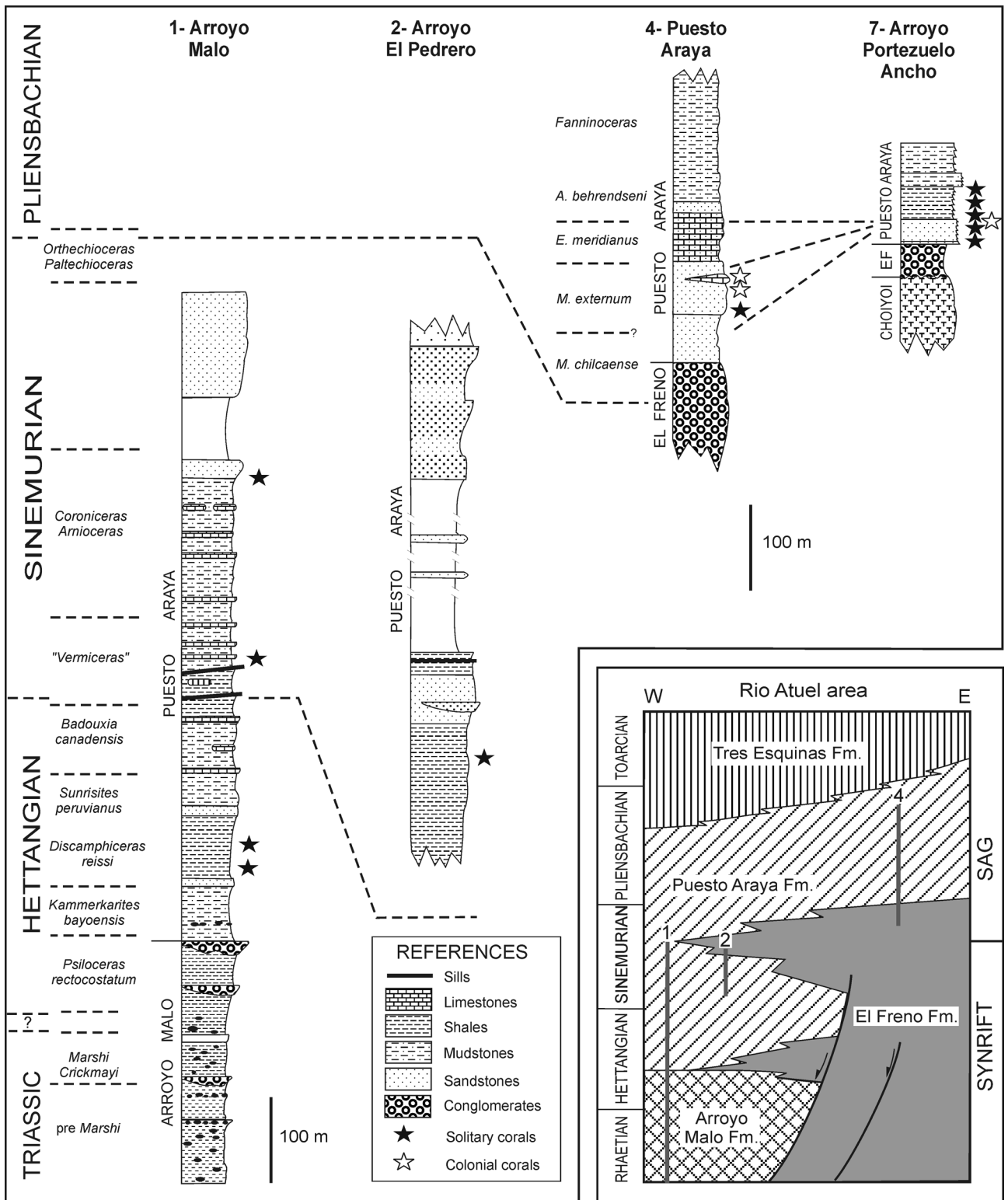


Figure 2. Sketch of four of the analyzed sections (including the two sections with pre-Pliensbachian outcrops), showing the provenance of samples with scleractinians. (Adapted from Damborenea, 1987; Damborenea and Manceñido, 2005). Inset: Schematic diagram showing overall tectono-stratigraphical relationships for the Atuel river area and approximate location and extension of sections 1, 2 and 4. (After Lanés *et al.*, 2008).

Pliensbachian

After a local coral gap in the record spanning roughly the Turneri to Raricostatum ammonite zones, corals reappear in the earliest Pliensbachian (Fig. 3) and co-occur with ammonites of the local *M. chilcaense* Zone (~ Jamesoni).

Solitary corals. Solitary corals show a high degree of diversification during the Pliensbachian, with at least seven different growth morphologies based on shape represented (Fig. 3). These are recognized mostly by coralla form, *i.e.*,

cupulate, discoidal, patellate, cylindrical, turbinate, trochoid/turbinate and trochoid/ceratoid (Fig. 5). All specimens can be assigned to one of these morphological categories, although there seems to be a morphological gradient between some of them.

Discoidal. Some of the discoidal morphologies (Fig. 5.1–2) are closely similar to those observed in the Hettangian–Sinemurian samples, although others seem to have more densely arranged septa (Fig. 5.4).

STAGE	STANDARD ZONES	ARGENTINA
PLIENSBACHIAN	S	SPINATUM
		14. <i>F. disciforme</i>
		MARGARITATUS
		13. <i>F. fannini</i>
	I	DAVOEI
		12. <i>A. behrendseni</i>
	IBEX	
	11. <i>E. meridianus</i>	
	JAMESONI	
	10. <i>M. externum</i>	
	9. <i>M. chilcaense</i>	
SINEMURIAN	S	RARICOSTATUM
		8. <i>Orthechioceras - Paltechioceras</i>
		OXYNOTUM
		OBTUSUM
	I	TURNERI
		?
	SEMICOSTATUM	
	7. <i>Coroniceras - Amioceras</i>	
	BUCKLANDI	
	6. " <i>Vermiceras</i> "	
HETTANGIAN	S	ANGULATA
		5. <i>B. canadensis</i>
	M	LIASICUS
		4. <i>S. peruvianus</i>
	3. <i>D. reissi</i>	
I	PLANORBIS	
	2. <i>K. bayoensis</i>	
	1. <i>P. rectocostatum</i>	
	?	



Figure 3. Local ammonite biozones compared to the standard zones (from Riccardi, 2008a, b) together with the stratigraphic distribution of the main coral morphologies. Black bars represent studied material while grey bars represent field observations.

Cupolate. Cupolate corals bear a high number of septa (~120) densely disposed, with beaded distal margin and maybe with synapticulae (Fig. 5.5–7). Columella is developed and individuals are relatively small (17–26 mm diameter). Gerth (1925, 1926) described the cupolate species *Anabacia andina* Gerth, 1926, from Early Jurassic beds at Arroyo El Deshecho (SW of Las Leñas, Mendoza, see Fig. 1), which according to his description and illustrations might be a

Cycloseris species. Nevertheless, the material described herein is shorter and lacks the depression seen on the oral surface of Gerth's species.

Patellate. Patellate corals (Fig. 5.8–10) are also small (12–23 mm diameter) and present between 80 and 160 septa, differently developed according to the number of cycles (Fig. 5.10). Distal margins are beaded. Columella is developed and the wall is thick (Fig. 5.9). There is an epitheca

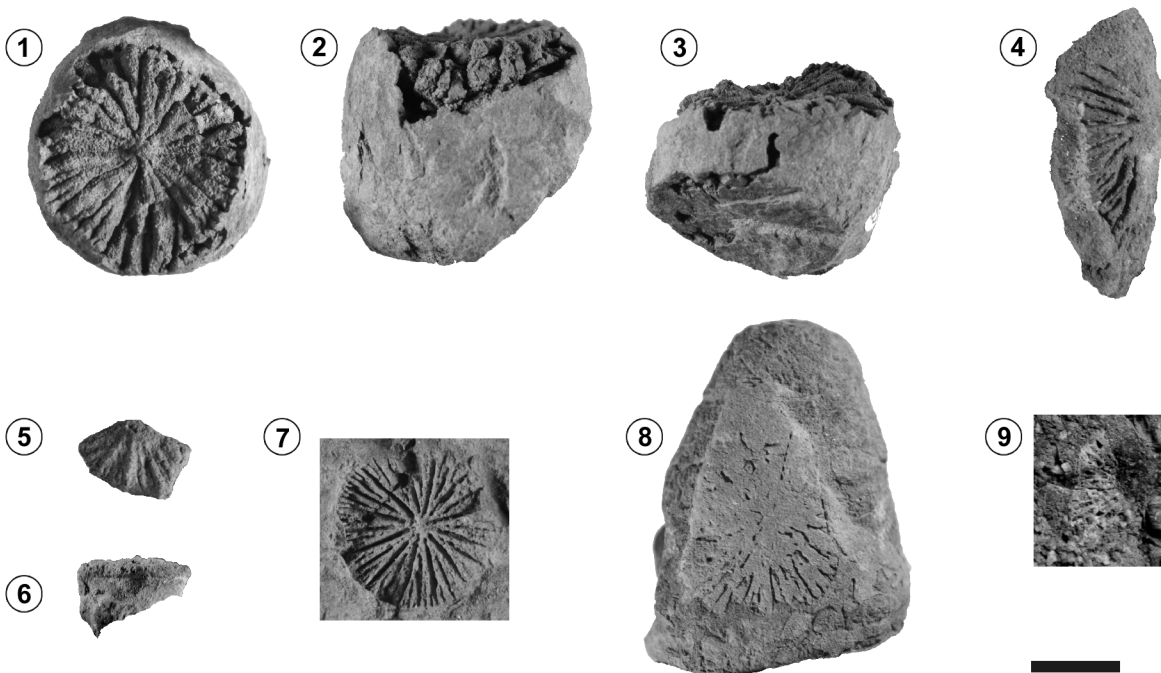
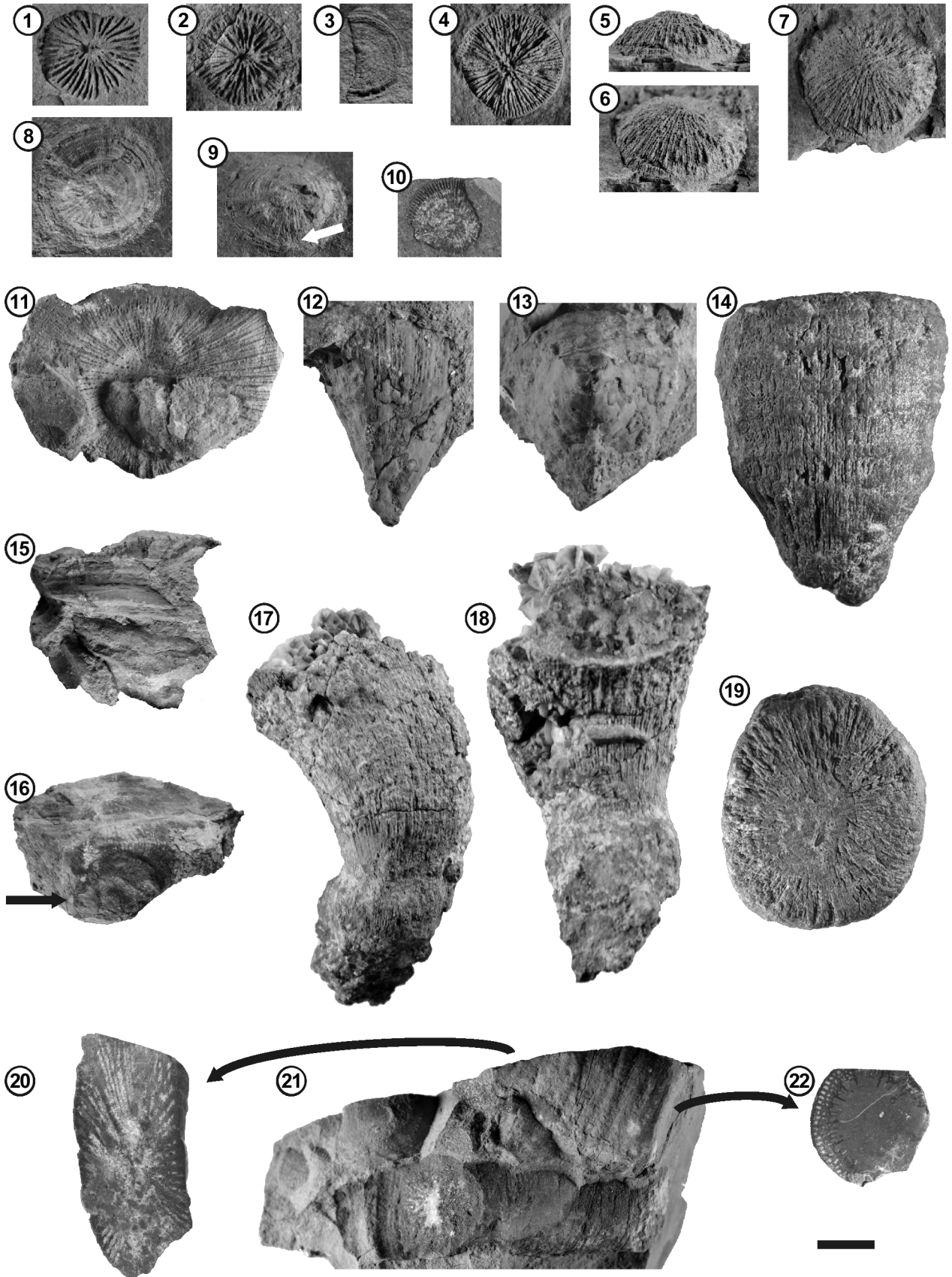


Figure 4. Hettangian–Sinemurian Scleractinia. 1–3, MLP 32755, from Ao. Alumbre, *D. reissi*? Zone, 1, oral mould, 2–3, lateral views; 4, MLP 35451, from Ao. Alumbre, *D. reissi*–*S. peruvianus* Zones, oral mould; 5–6, MLP 35449, from Ao. Alumbre–Ao. Malo, “*Vermiceras*” Zone, 5, oral view, 6, lateral view; 7, MLP 18427, from Ao. Alumbre–Ao. Malo, *Coroniceras*–*Arnioceras* Zone, oral mould; 8, MLP 18503, from Ao. El Pedrero, *Coroniceras*–*Arnioceras*? Zone, coral calyx preserved on a gastropod; 9, MLP 32818, from Ao. El Pedrero, *Coroniceras*–*Arnioceras*? Zone, oral view. Scale bar = 1 cm.

Figure 5. Pliensbachian solitary Scleractinia. 1–4, Discoidal coralla; 1–3, MLP 20652, from Paso del Portezuelo Ancho, late Early Pliensbachian; 1, MLP 20652/1, oral mould; 2, MLP 20652/3, oral mould; 3, MLP 20652/4, aboral mould; 4, MLP 31535, from Codo del Blanco, *A. behrendseni*–*F. disciforme* Zones. 5–7, Cupolate corallum, IANIGLA-PI 1655, from Ao. Serrucho, Early Pliensbachian; 5, lateral view; 6, oro-lateral view; 7, oral view. 8–10, patellate coralla; 8–9, MLP 27948, from Ao. Peuquenes, Early Pliensbachian; 8, aboral view; 9, aboro-lateral view (white arrow shows a section of the wall with septa included in it). 10, MLP 20658/1, from Ao. del Portezuelo Ancho, *A. behrendseni*–*F. disciforme* Zones, oral mould. 11, 15–16, turbinate coralla, MLP 20656 from Ao. del Portezuelo Ancho, *E. meridianus* Zone; 11, MLP 20656/1, oral view; 15, MLP-20656/1, lateral view; 16, MLP 20656/2, lateral view (black arrow shows the apex, pointing laterally). 12–14, 19, trochoid/turbinate coralla; 12–13, MLP-20655, from Ao. del Portezuelo Ancho, Early Pliensbachian, 12, lateral view, 13, aboral view; 14, 19, MLP 6671, from Co. de La Brea, Pliensbachian; 14, lateral view; 19, oral view. 17–18, trochoid/ceratoid coralla, IANIGLA-PI 1654, from Ao. Portezuelo Ancho, Early Pliensbachian, both in lateral view; 18, showing the recrystallized oral surface. 20–22, MLP 20671, from Ao. Serrucho, Early Pliensbachian; 20, longitudinal (right end) and oblique section; 21, lateral view; 22, oral view. Scale bar = 1 cm.



with slight transverse wrinkles and 24 radial folds (Fig. 5.8).

Turbinate. In this group (Fig. 5.11, 15–16) the apex of the corallite is curved (sometimes strongly, Fig. 5.16) and seems to adhere onto solid substrates (sometimes even other corallites). Usually, calyx diameter expands at a high rate, therefore resulting in concave walls. Corallites are medium-sized (24–47 mm diameter, 22–28 mm height). Septa are numerous (~120) and with beaded distal margins bending down towards the center (Fig. 5.11), resulting in a concave calycular surface. The wall is well developed and there is an epitheca usually transversely wrinkled (Fig. 5.15).

Trochoid/turbinate. Trochoid/turbinate morphologies (Fig. 5.12–14, 19) include one of the specimens (Fig. 5.14, 19) identified by Morsch (2001, p. 323) as *Stylophyllopsis?* cf. *victoriae* (Duncan, 1868). They are medium sized (20–40 mm diameter, 20–60 mm height) with numerous (~140–180) and densely disposed septa. There are dissepiments and the wall is poorly developed, most likely epithecal. Although the trochoid/ceratoid morphologies (Fig. 5.17–18) could belong to this same taxon, they both have some differences (see below).

Trochoid/ceratoid. This corallite is gently curved (Fig. 5.17), with an elongated calyx (Fig. 5.18). It is medium sized with oval calyces (30 mm x 40 mm diameter, 72 mm height). Unfortunately, most of it was recrystallized (Fig. 5.18) and preserved with moldic porosity, remaining only features of the external surface. It lacks any epitheca but bears numerous costae with small tubercles on them. Also, some dissepiments can be observed.

Cylindrical. Cylindrical corallites (Fig. 5.20–22) are 15–45 mm in diameter, and are all broken, the highest (Fig. 5.21) being about 60 mm tall (19 mm in diameter). They bear five cycles of septa, with S1 and S2 similarly developed (Fig. 5.22), and S3 to S5 progressively reduced in development, although the number of septa in S5 seems to be reduced to half. Distal margins of the septa bend down towards the center, somewhat resembling turbinate morphologies (Fig. 5.20, 22). The wall is thick and parathecal (Fig. 5.22) and the epitheca bears transverse wrinkles (Fig. 5.21). Considering that these cylindrical corallites are all broken, it is even possible that they may actually be branches of a phaceloid colony.

Colonial corals. Early Jurassic colonial corals are first recorded in the northern Neuquén Basin in the Early Pliens-

bachian (*M. chilcaense* Zone), and they show low level of corallite integration, low morphologic diversity and low abundance. Two main morphologies are easily recognized: phaceloid and cerioid.

Phaceloid colonies. The phaceloid colonies (Fig. 6.1–4) are represented by fragmented branches, 25 to 60 mm long, usually showing budding (Fig. 6.1, 4). Calyces are subcircular with diameters ranging from 9 to 20 mm. The epitheca is thin and bears transverse wrinkles while septa are numerous (about 60), well developed and present dissepiments.

Cerioid colonies. Cerioid colonies are usually complete and well preserved (mostly they show superficial corrosion). Coralla are massive and hemispheric (Fig. 6.5), relatively small (between 50 and 100 mm diameter and 55 to 90 mm high) and present a basal epitheca with faint transverse wrinkles. Calycular diameter (Fig. 6.6–7) is between 5 and 9 mm, and there are up to 44 septa; S1, S2 and S3 cycles are characterized by long septa while S4 cycle is characterized by short ones (Fig. 6.6). Walls between corallites are developed, although at some points they seem to disappear (Fig. 6.7) likely due to recrystallization. This taxon resembles *Isastrea jaworskii* Gerth, 1926 (p. 142 [= 383], pl. 4, fig. 24 [= pl. 12, fig. 4], from Cerro Puchenque, Mendoza) = *Meandrostylis? jaworskii* according to Morsch 2001 (p. 325, fig. 3.3, from Puesto Araya, Mendoza).

DISCUSSION

Although formal systematic determinations are still underway, it is clear that corals of the Neuquén Basin displayed morphologic differentiation during the Pliensbachian. In contrast, Hettangian and Sinemurian corals are morphologically more uniform and low in diversity, likely representing only one or two taxa. On the other hand, by the Early Pliensbachian at least three new solitary corals with different morphologies are recognized (Fig. 3). *Stylophyllopsis?* sp. cf. *S. victoriae*, with its turbinate coralla, was recorded from the Pliensbachian of Mendoza and Neuquén Provinces (Lanés and Morsch, 1998; Morsch, 2001) and northwestern Chubut Province (Massaferro *et al.*, 1998; Massaferro, 2001). Cupolate and patellate forms, plus the discoidal *Haimeicyclus? haimeii* discussed here, represent further taxa occurring in the Lower Pliensbachian strata. Interestingly, the two solitary coral morphologies –discoidal/cupolate and trochoid/turbinate morphologies– have ecological im-

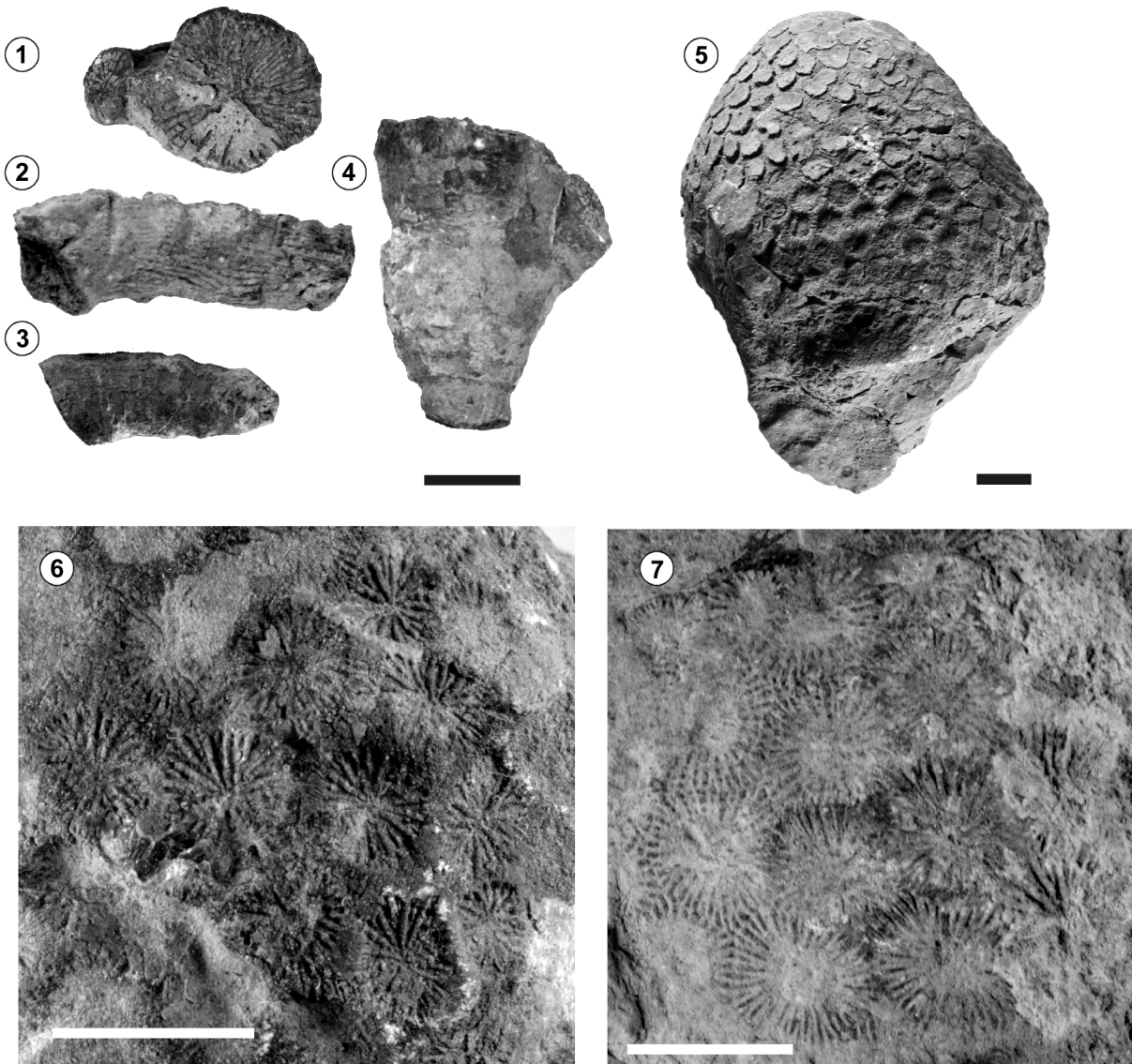


Figure 6. Pliensbachian colonial Scleractinia, all from Puesto Araya, *M. externum* Zone. 1–4, phaceloid colonies; 1, MLP 35452, oral view; 2, MLP 35447, lateral view; 3, MLP 35448, lateral view; 4, MLP 35452, lateral view. 5–7, cerioid colonies; 5, MLP 35454, lateral view of the colony; 6, MLP 35453, oral view of the corallites; 7, MLP 35450, oral view of the corallites. Scale bar = 1 cm.

plications. The discoidal/cupulate morphologies are usually associated with lower energy environments and paleoecologically related to mobile polyps, whereas tall morphologies of trochoid/turbinate corals are associated with somewhat higher-energy environments and a semi-infaunal sedentary mode of life (Filkorn, 1994; Lanés and Morsch, 1998). The analysis of these two gross morphologies in the Arroyo Serrucho section showed that tall solitary forms are absent below the storm wave-base, and above it, they are

usually linked to sandy sediments; while low morphologies are generally associated with mudstones (Echevarría *et al.*, 2016).

During Early Pliensbachian time in the study area, the first colonial corals appear locally after the Triassic/Jurassic mass extinction, but less frequently than the solitary forms. Only simpler, lower integrated phaceloid and cerioid colonies are recognized in Mendoza, and these occasionally form patch reefs (as in Puesto Araya area), and most likely

belong to the taxa already identified by Morsch (2001). Ecologically, the presence of these forms would imply euhaline, clear water conditions with low sedimentation rates (Beauvais, 1985) and low-energy regime (Morsch, 1986).

By latest Early Pliensbachian to Late Pliensbachian times towards the south part of the basin, colonial forms appear locally with higher frequency and greater morphological diversity. These include higher integrated corals (*i.e.*, thamnasterioid, meandroid types along with phaceloid), and they occur only in the southernmost Neuquén Province (see Damborenea *et al.*, 1975; Morsch, 2001). This suggests different ecological conditions for that locality, although its fauna may be slightly younger than the coral fauna discussed here. It seems that more favourable environmental conditions for scleractinians were established during the Late Pliensbachian, when they even reached the relatively high paleolatitudes of west-central Chubut Province (Carral Tolosa, 1942).

A biocalcification crisis was inferred for Late Triassic phytoplankton (Schootbrugge *et al.*, 2007) and a similar crisis accounts for the scarcity of corals and reefs in the Early Jurassic (Martindale *et al.*, 2012). The diversification trend here described thus coincides with a global phenomenon and provides useful insight into the scleractinian recovery after the end-Triassic mass extinction event within southern basins of South America. Comparable patterns can be found in the literature. In Northern Chile, a trend of increasing coloniality since Hettangian times was summarized by Schäfer and Hillebrandt (1984). In western North America, the earliest Jurassic corals (Early Sinemurian) were solitary (Hodges and Stanley, 2015). In the Pamir Mountains of Central Asia, during the Hettangian, solitary corals predominated too (Melnikova and Roniewicz, 2012).

Our data also agree with a global diversity peak within solitary corals during the Pliensbachian (Lathuilière and Marchal, 2009). Nevertheless, caution must be taken when analyzing the data presented here. Firstly, this pattern of increasing coloniality is not evident in some European basins. In France, colonial corals with low levels of corallite integration appeared in Hettangian reef limestones soon after the end-Triassic mass extinction (Kiessling *et al.*, 2009). Similarly, Hettangian corals from Scotland contributed to small levels of reef development (Gretz *et al.*,

2013). According to Lanés (2005), most Hettangian–Sinemurian rocks in the studied area were deposited on a fluvio-dominated slope-type fan delta, despite their clear marine nature (mainly supported by the occurrence of stenohaline fossil fauna). The lack of colonial corals and the low diversity of solitary forms in those deposits may reflect some adverse local environmental conditions (Morsch, 1986) such as a response to fluvial influences. Rather than general global trends, these examples might represent merely local basin conditions instead. This may be further tested through more detailed stratigraphic comparison with other South American basins.

CONCLUSIONS

A two-stage scleractinian coral recovery pattern is recognized in the Early Jurassic of southern Mendoza (Neuquén Basin, Argentina). During the Hettangian–Sinemurian time interval, morphologic diversity was low, with only few solitary corals recorded. During the early Pliensbachian, diversity increased sharply, as a great variety of solitary coralla developed and also during this interval colonial forms appeared in the basin.

Further understanding of this recovery pattern for corals will require detailed systematic studies of fossils within the basin coordinated with stratigraphic field explorations. As corals from other basins, especially those from South America, are documented, detailed stratigraphic comparisons will shed more light on the diversification of scleractinians after the Triassic/Jurassic biotic crisis.

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