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RE-DESCRIPTION AND NEOTYPIFICATION OF *ARCHAMPHIROA JURASSICA* STEINMANN 1930, A CALCAREOUS RED ALGA FROM THE JURASSIC OF ARGENTINA

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INTRODUCTION

ARCHAMPHIROA JURASSICA was described by Steinmann (1930) from carbonate deposits of the Cordillera de los Andes in Mendoza, central Argentina (Arroyo Negro, confluent of Malargüe River), assigned to the Callovian stage. Based on the general morphology and the internal structure of the identified fragments, Steinmann considered them to belong to the coralline algae. Comparisons made with some fossil and extant corallines species led him to the conclusion that *Archamphiroa jurassica* closely resembles some species of the extant genus *Amphiroa*.

The alga was subsequently mentioned by Johnson (1964) in his compilation on Jurassic algae, where some specimens illustrated by Steinmann were reproduced. *Archamphiroa* was also listed in Banks et al. (1967), Dragastan (1969), and Lemoine (1977), but these authors did not provide illustrations.

Many specimens of *Archamphiroa* were recently identified in samples collected by two of the present authors (W.K., R.A.S.) from the Tithonian Cotidiano Formation in the Lago Fontana region, southern Chubut (Patagonia, Argentina). These specimens fit well with the description given by Steinmann (1930), who gave a good and detailed description of the most important morphological characters and generally provided an adequate interpretation of the internal structure of this alga. However, he did not give a formal diagnosis of the genus and the type material appears to be lost. We therefore use the new material from the southern part of the Argentinean Cordillera for properly designating a neotype and giving a genus and a species diagnosis that correspond to essential features of the alga at the two taxonomic levels. We provide a description that corresponds to the modern terminology used in the study of recent and fossil corallines (Woelkerling, 1988; Braga et al., 1993). In addition we give an adequate illustration that constitutes good support for the new description and should facilitate an accurate identification of this alga in the future.

GEOLOGICAL SETTING

The algae were found in lagoonal limestone (wackestones and packstones) deposits of the Cotidiano Formation in the Lago Fontana region of southwestern Chubut (Patagonia, Argentina) (Fig. 1). The Cotidiano Formation (Ramos, 1976) is a limestone unit deposited on andesitic volcanoes assigned to the Lago La Plata Formation. Limestones of the Cotidiano Formation comprise mudstones, wackestones, packstones and boundstones of lagoonal to reefal facies (Ramos, 1978, 1981). According to this author, the formation has a quite limited exposure in just three small areas (Río Toqui, Arroyo Pedregoso and the type locality Arroyo Cotidiano). Our material comes from the type locality of the Cotidiano Formation (44°50′S, 71°39′W) where it overlies conformably andesitic breccias. Stromatoporoid-coral patch reefs are surrounded by lagoonal limestones, which consist mostly of bivalve packstones and algal wackestones and packstones. Corals, stromatoporoids, bivalves and crinoids are also common in the lagoonal sediments. *Archamphiroa* is the only floral element recognized in the limestones. Much of the micrite seems to stem from abraded algal thalli.

The Cotidiano Formation was previously broadly assigned to the Late Jurassic (Ramos, 1981), and its faunal association at the type locality suggests a Tithonian age (Olivero, 1987). A tuffitic sandstone bed conformably overlying the Cotidiano limestones bears large trigoniid bivalves, allowing for a more precise age assignment (Olivero, personal commun., 2002). Finding of *Steinmanella* (*Macrotrigonia*) sp. and *Megatrigonia* cf. *fontanaensis* and the close similarity to ammonite-dated faunas at Arroyo Pedregoso permits an assignment to the late Tithonian. The algal-bearing limestones of the Cotidiano Formation are thus assignable to the Tithonian, perhaps late Tithonian.

MATERIAL AND METHODS

Thirty-three samples were collected in total, six of which (LF1, LF3, LF4, LF5, LF6 and LF18) contain numerous algae. Eighty-one specimens of *Archamphiroa* were measured. Our observations are based on ten thin sections and one polished slab for SEM investigation. The thin sections were studied under a Zeiss petrographic microscope, and the polished slab was investigated by SEM.

RESULTS

The limestone is a bioclastic packstone made up mainly by fragments of *Archamphiroa jurassica* (Fig. 2.1–4, 7). Fragments of bivalves, rare echinoderms, and very rare corals also occur. The morphology of the algal fragments corresponds to the description given by Steinmann (1930) for *Archamphiroa jurassica*. This author gave a detailed description of the alga found in Mendoza, including the external form and the internal structure. The most important characteristics he emphasized are:

- sub-cylindrical, stick-shape of branches, sometimes bifurcating;
- differentiation into a "hypothallium" and "perithallium"; and
- absence of reproductive organs

Unfortunately, Steinmann did not designate a holotype and it appears that his original material was lost during World War II. Our efforts to find this material either in Argentina or in Germany were unsuccessful. Under these circumstances, the newly found material from Patagonia allows us to properly designate a type, to give a genus and a species diagnosis that corresponds to essential features of the alga at the two taxonomic levels, to give a description that corresponds to the modern terminology used in the study of recent and fossil coralline algae, and to provide an adequate illustration that constitutes good support for the new description.

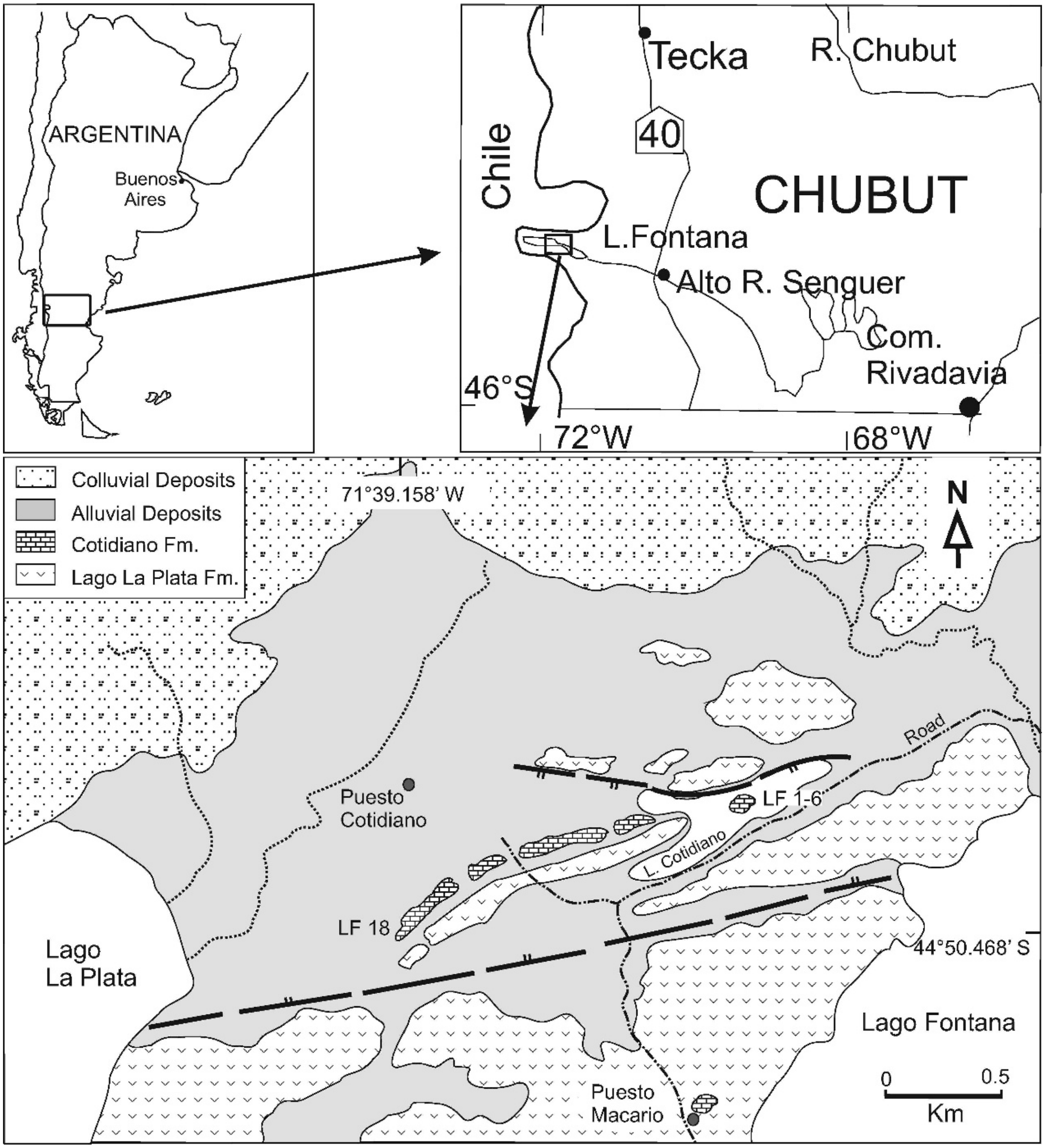


FIGURE 1—Location of the study area and outcrops of Cotidiano Formation. Positions of samples are indicated. Coordinates demarcate the position of sample LF 18 containing the neotype of *Archamphiroa jurassica* Steinmann (map after Ramos, 1978).

Class RHODOPHYCEAE Rabenhorst, 1863
Order ?CORALLINALES Silva and Johansen, 1986
Genus ARCHAMPHIROA Steinmann, 1930, emend.

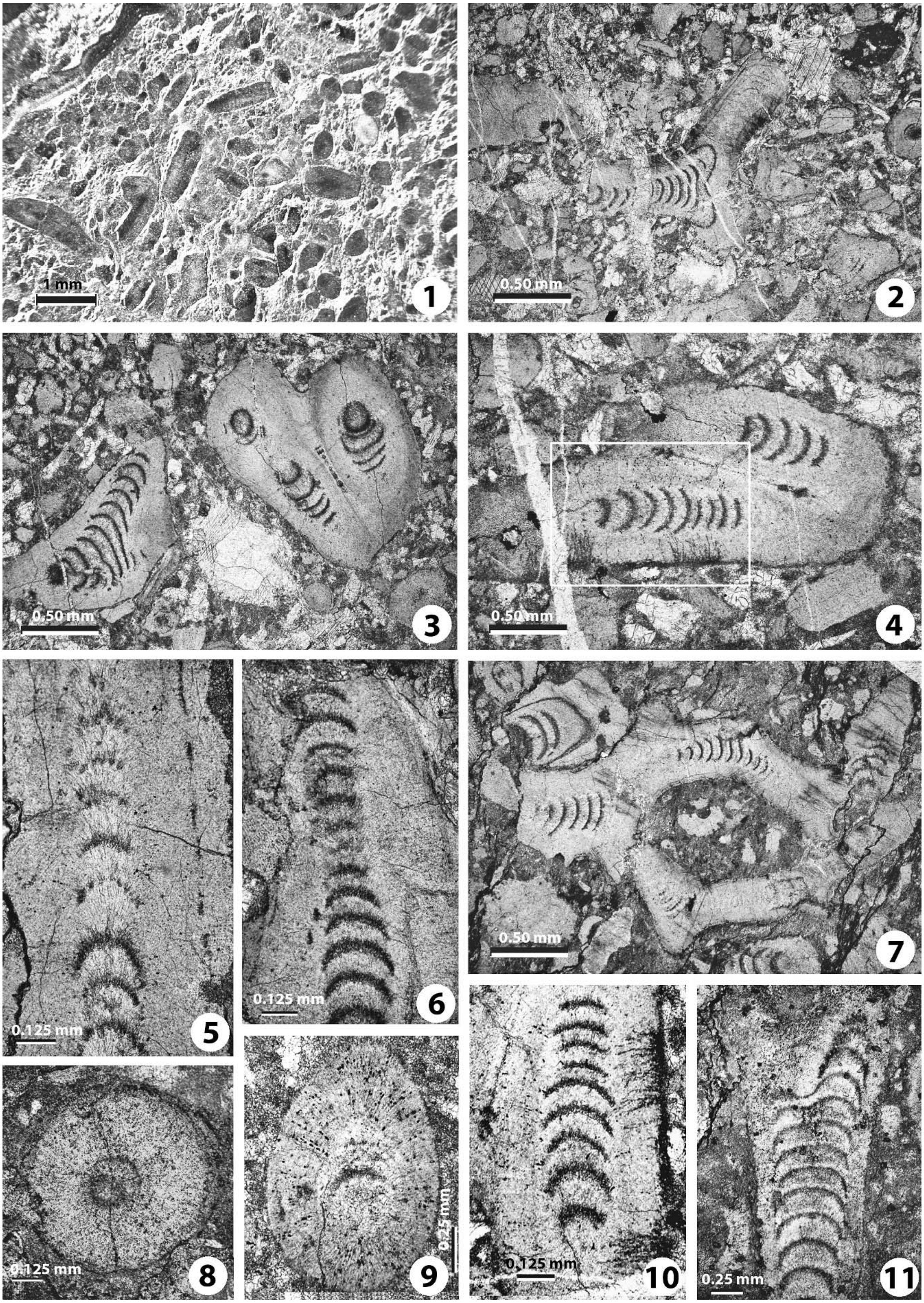
Archamphiroa – STEINMANN, 1930, p. 1; J. H. JOHNSON, 1964, p. 6; BANKS, CHESTERS, HUGHES, G. A. L. JOHNSON, H. M. JOHNSON, AND MOORE, 1967, p. 167; DRAGASTAN, 1969, p. 60; LEMOINE, 1977, p. 1321.

Diagnosis.—Steinmann (1930) gave no formal genus diagnosis of *Archamphiroa*. We propose here the following one: Non-geniculate monomerous thalli made up of cylindrical to subcylindrical branches, sometimes bifurcated. The branches are composed of a coaxial core with arched, alternating light-colored and dark-colored rows of cells, and a peripheral region. Cell filaments in the peripheral region are perpendicular to the core axis. Cell fusions are present in the peripheral region, and possibly also in the core.

ARCHAMPHIROA JURASSICA Steinmann, 1930
Figures 2–3

Archamphiroa jurassica – STEINMANN, 1930, p. 1–7, Pl. 1, figs. 1–9; JOHNSON, 1964, p. 6, Pl. II, figs. 1–9 (reproduced from Steinmann (1930, Pl.1, figs. 1–9); DRAGANSTAN, 1969, p. 60; LEMOINE, 1977, p. 1321.

Neotype.—Because Steinmann (1930) did not designate a holotype and the type material is lost, following the articles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9.6, 9.11 and 9.14 of the ICBN (McNeill et al., 2006), we designate here as neotype the specimen illustrated in Fig. 2.5 from the specimens found in the Cotidiano Formation. The neotype is stored in the Paleobotanical Collection of the Geological Sciences Department, Buenos Aires University under the number BAFC-Pb 17195.

Type locality.—Limestone ridge south of Puesto Cotidiano, Lago Fontana region of southern Chubut (Patagonia, Argentina).

Type horizon.—Algal packstones of the Cotidiano Formation, Tithonian (probably late Tithonian).

Material.—Several hundred thallus fragments in ten thin sections. Neotype, specimen in Fig. 2.5, thin section LF18/2.

Diagnosis.—As for the genus.

Description, external morphology.—Within the samples of the Cotidiano Formation, *Archamphiroa jurassica* is represented by branches of variable dimensions. Some thallus fragments show branching with a larger diameter at the point of branching (Fig. 2.2, 3, 4, 7, 11). Branch outline is round, with an elliptical form at some branching points. These characters are consistent with Steinman's original description.

Description, internal morphology.—Two distinct parts of the thallus could be observed in thin section: core and peripheral region (=hypothallium and perithallium respectively in Steinmann, 1930). The core is coaxial, made up of cells arranged in arching tiers. It is easily visible in longitudinal sections (Fig. 2.5, 6, 10, 11). A rhythmic alternation of growing rows, lighter and darker can be observed. It is likely that the darker bands reflect development stages of the thallus growth, i.e., a deceleration of growing, and not differences in calcification, as stated by Steinmann (1930. p. 3). Also, the coaxial cell filaments of the core seem to be made of small cells and not of a single long cell, as thought by Steinmann (1930, p. 4). At high magnification (Fig. 3.2, 3) it is possible to see that the lighter zones of the core are made up of small quadrangular cells, comparable in dimensions with the cells of the darker zones.

In the peripheral region the individual cells of the filaments are more easily distinguished than in the core (cell wall and cell lumen are more clearly delimited) (Fig. 2.8–10; Fig. 3.4). Cell fusions are present inside the peripheral region (Fig. 3.4, arrow). SEM images clearly show cell fusions between cells in adjacent filaments (Fig. 3.8–12, arrows).

Reproductive structures are absent in the studied material, as well as in Steinmann's (1930) material. Round voids observed in one specimen (Fig. 3.1) probably represent microborings.

Dimensions.—The dimensions of the most important parameters are given in Table 1.

Discussion.—Steinmann (1930) argued that *Archamphiroa jurassica* was most probably an articulated (i.e., geniculate) coralline. He therefore compared *A. jurassica* with species of the genus *Amphiroa* and considered *Archamphiroa* as an ancestor of an *Amphiroa* group containing *Amphiroa ephedraea* (Lamarck) Decaisne and *Amphiroa cretacea* (Postels and Ruprecht) Endlichter. However, there is no convincing evidence that genicula are present, especially at points of branching. There is no change in cellular structure between the light and dark bands shown in longitudinal sections; there are no breaks in the peripheral region in the area of possible genicula; the branch formation seen in some fragments is rather similar to branch formation in some nongeniculate corallines. Following these arguments we can conclude that *Archamphiroa jurassica* is not a geniculate coralline.

The vegetative characters of this alga, however, are quite similar to those of some corallines. The closest resemblance of *A. jurassica* is, in our opinion, with the Cretaceous coralline *Paraphyllum*, which belongs, according to Lemoine (1970) and Poignant (1979), to the Melobesioideae, but which is most probably a sporolithacean alga (taking into consideration the reproductive structures, e.g., Tomás et al., 2007). Both algae are ramified, have a coaxial core and a peripheral region made up of rows of small cells arranged around the core (Fig. 3.5–7). However, the lack of reproductive structure makes questionable the assignment of *Archamphiroa jurassica* to any family of extant corallines. This character calls for a comparison with the "Solenoporaceae," a group of red algae proliferating during the Paleozoic and Mesozoic (the uncertainity of the family name lies on the fact that the type genus of this family was recently assigned to chatetids by Riding, 2004). However, all described "solenoporaceans" have a different growth mode than does *Archamphiroa jurassica*. The "solenoporacean" thalli start from a basal encrustation of a substrate and develop hemispherical or columnar vegetative masses, which can be ramified. Following Moussavian (1989, translated from German): "The contention that the solenoporacean thalli are differentiated in a hypothallus, and a perithallus cannot be documented in any species. During their long evolution, the solenoporaceans could not develop any thallus differentiation corresponding to that of corallines." This is, in our opinion, the greatest difference between *Archamphiroa jurassica* (which has a branching thallus, differentiated into a core and a peripheral region) and the "solenoporaceans." Because the assignement to corallines is questionable due to the lack of reproductive structures, we prefer to keep *Archamphiroa* as an incertae sedis taxon inside the red algae.

Other reports of "coralline" algae in sediments older that Cretaceous.—Another species attributed to the genus *Archamphiroa* was described by Dragastan (1969) as *Archamphiroa carpiana*. The description of this species is based on small fragments from which it is impossible to see a real differentiation of a core (hypothallium) and peripheral region (perithallium). The illustrated specimens of Dragastan (1969) are more comparable with fragments of a peyssonneliacean alga (e.g., *Polystrata*).

Other reports of coralline algae in pre-Cretaceous sediments (e.g., Johnson, 1956; Wray, 1964; Imaizumi, 1965; Johnson and Kaska, 1965; Steiger and Wurm, 1980; Eliáš and Eliášová, 1986; Brooke and Riding, 1998; Riding et al., 1998; Senowbari-Daryan et al., 2002; Senowbari-Daryan and Velledits, 2007) are also doubtful. Some of these fossils (Steiger and Wurm, 1980; Eliáš and Eliášová, 1986) have been

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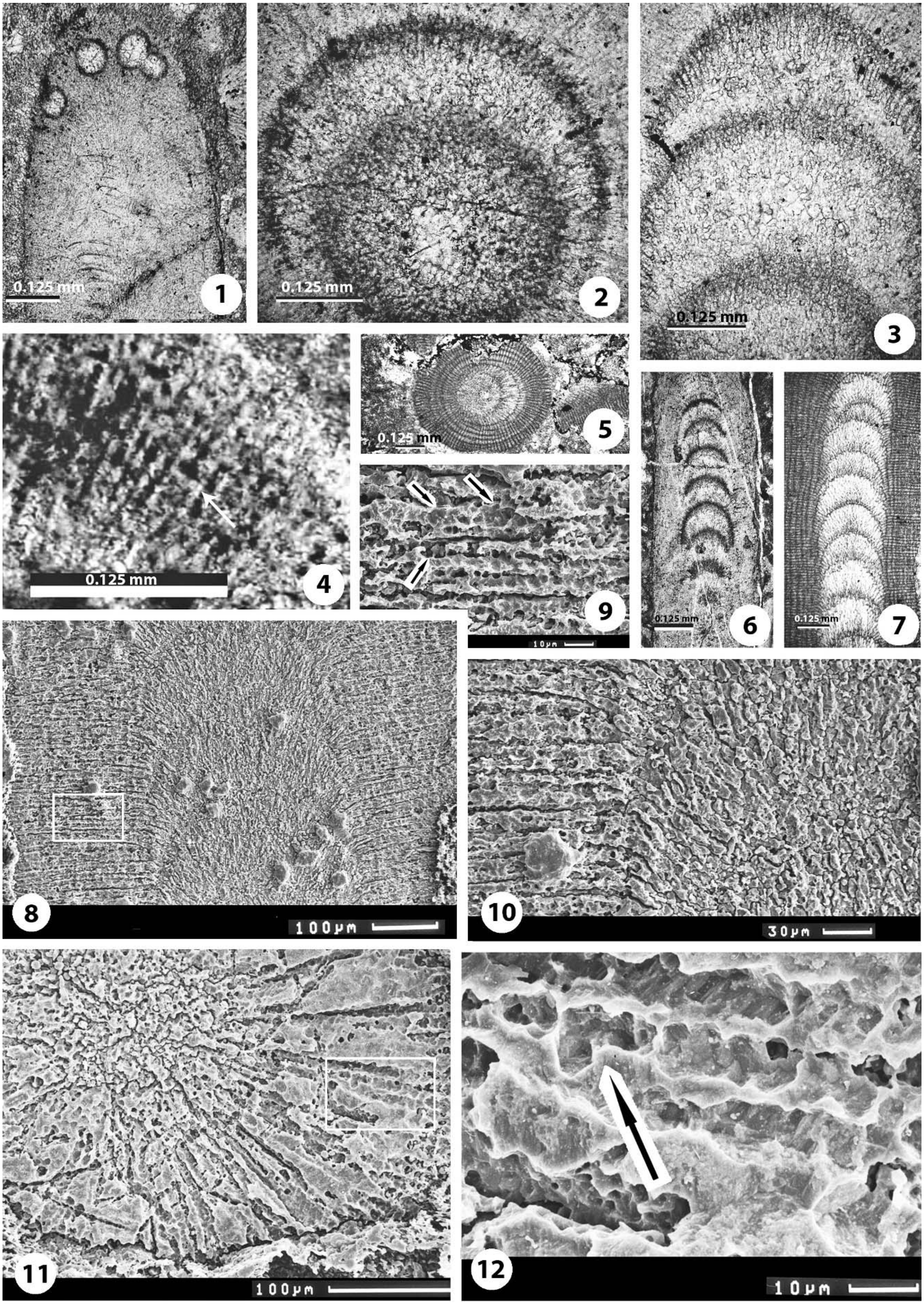
FIGURE 2—*1–8*, *Archamphiroa jurassica* Steinmann. *1*, polished slab showing the distribution of *Archamphiroa* thalli in the rock (darker in color); *2–4*, *7* thin section micrographs; different types of sections (from longitudinal to transverse) of *A. jurassica* surrounded by numerous fragments originating from thalli abrasion: *2–4*, thin section LF6/2; *7*, thin section LF18/2; *5–6*, *10–11*, longitudinal and oblique sections; the coaxial core is very well visible due to the arched darker thin zones; their lateral extension also delimitate the core from the peripheral region.: *5*, thin section LF 18/2 (neotype); *6*, thin section LF3/2; *10*, thin section LF6/2 (enlargement of the specimen in *4*-square); *11*, thin section LF 18. Note bifurcations of the thallus in *2–3*, *7* and *11*. Scale bar is 1 mm (*1*), 0.5 mm (2–4, 7), 0.25 mm (*9*, *11*), and 0.125 mm (*5–6*, *8*, *10*).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10
100μm
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TABLE *1*—Dimensional parameters of *Archamphiroa jurassica* Steinmann. In bold: dimensions of the neotype.

Specimen	Sample	ed	cd	prw	Specimen	Sample	ed	cd	prw
1	LF1	0.93	0.25	0.34	46	LF6	0.9	0.5	0.2
2	LF1	0.5	0.2	0.15	47	LF6	0.7	0.3	0.2
3	LF1	0.68	0.1	0.25	48	LF6	0.75	0.32	0.22
4	LF1	0.97	0.47	0.25	49	LF6	0.55	0.2	0.18
5	LF1	1.07	0.32	0.38	50	LF6	0.65	0.23	0.21
6	LF3	1.35	0.25	0.55	51	LF6	1.15	0.55	0.3
7	LF3	1.03	0.35	0.34	52	LF6	1	0.45	0.28
8	LF3	0.8	0.25	0.28	53	LF6	1.2	0.45	0.38
9	LF3	0.92	0.43	0.25	54	LF6	0.98	0.52	0.23
10	LF3	1.3	0.45	0.43	55	LF6	0.5	0.2	0.15
11	LF3	0.7	0.35	0.18	56	LF6	0.63	0.25	0.19
12	LF3	1.1	0.4	0.35	57	LF18	1.2	0.55	0.33
13	LF3	1.2	0.45	0.38	58	LF18	0.98	0.5	0.24
14	LF3	1.1	0.22	0.44	59	LF18	0.55	0.2	0.18
15	LF3	1	0.35	0.33	60	LF18	0.85	0.45	0.2
16	LF3	0.85	0.33	0.26	61	LF18	1.15	0.4	0.38
17	LF3	0.7	0.22	0.24	62	LF18	0.95	0.3	0.33
18	LF3	0.6	0.2	0.2	63	LF18	1.25	0.5	0.38
19	LF3	0.75	0.28	0.24	64	LF18	0.7	0.4	0.15
20	LF3	0.85	0.25	0.3	65	LF18	0.95	0.65	0.15
21	LF3	0.8	0.22	0.29	66	LF18	1.3	0.35	0.48
22	LF3	0.72	0.23	0.25	67	LF18	0.9	0.3	0.3
23	LF3	1.1	0.25	0.43	68	LF18	0.72	0.22	0.25
24	LF3	0.65	0.25	0.2	69	LF18	0.63	0.3	0.17
25	LF3	0.82	0.23	0.3	70	LF18	0.6	0.25	0.18
26	LF3	0.8	0.25	0.28	71	LF18	0.95	0.35	0.3
27	LF3	0.48	0.2	0.14	72	LF18	0.95	0.4	0.28
28	LF3	0.87	0.25	0.31	73	LF18	0.9	0.37	0.27
29	LF3	0.7	0.25	0.23	74	LF18	1.23	0.55	0.34
30	LF3	1.3	0.5	0.4	**75**	**LF18**	**0.76**	**0.23**	**0.27**
31	LF4	0.93	0.3	0.32	76	LF18	0.78	0.3	0.24
32	LF5	0.65	0.22	0.22	77	LF18	0.65	0.27	0.19
33	LF5	0.8	0.33	0.24	78	LF18	1	0.4	0.3
34	LF5	0.7	0.25	0.23	79	LF18	1	0.3	0.35
35	LF5	0.72	0.28	0.22	80	LF18	0.73	0.3	0.22
36	LF5	0.57	0.24	0.17	81	LF18	0.6	0.3	0.15
37	LF6	1.1	0.35	0.38	Total		81	81	81
38	LF6	0.96	0.35	0.31	Minimum		0.48	0.1	0.14
39	LF6	0.75	0.33	0.21	Maximum		1.35	0.65	0.56
40	LF6	1.1	0.35	0.38	Average		0.88	0.33	0.28
41	LF6	0.95	0.27	0.34	Standard deviation		0.22	0.109	0.085
42	LF6	0.55	0.2	0.18					
43	LF6	1	0.4	0.3	ed = external diameter				
44	LF6	0.97	0.47	0.25	cd = core diameter				
45	LF6	1.17	0.48	0.35	prw = width of the peripheral region				

included in the synonymy of the incertae sedis *Iberopora bodeuri* Granier (Schlagintweit, 2004), and others have a questionable systematic position. Following Aguirre et al. (2000) and Tomás et al. (2007), the attribution of all these specimens to corallines is doubtful: "Despite references to corallines in older sediments, the assignment of those reported to this algal order and their age attribution are questionable" (Tomás et al., 2007, p. 79). These authors consider *Sporolithon rude* (Lemoine), which first occurs in the Hauterivian, as the oldest true coralline alga. However, some of the taxa described in the mentioned papers (e.g., *Graticula gotlandica* Brook and Riding, 1998, 2000) may belong to the order Corallinales, even if they don't belong to the extant families of the order. The same could be true for *Archamphiroa jurassica*.

CONCLUSION

Many specimens of *Archamphiroa jurassica* Steinmann were found in the Tithonian Cotidiano Formation from Lago Fontana (Patagonia, Argentina). They gave us the opportunity to provide a new description of this alga that corresponds to modern terminology. The vegetative and anatomical features indicate that *Archamphiroa jurassica* is not a geniculate coralline alga, the thallus morphology suggesting rather a non-geniculate coralline.

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FIGURE *3*—*1–4*, 6, Thin section and SEM micrographs of *Archamphiroa jurassica* Steinmann. *1*, specimen showing round, well outlined spaces within the peripheral region, interpreted as borings; *2–4*, details of the internal structure of *Archamphiroa jurassica* Steinmann; *2*, *4*, details of transverse sections showing the internal structure of the core (*2*) and of the peripheral region (*4*). The small rectangular cells are well visible in areas with a dark material infilling the cell lumen (e.g., *4*); *3*, details of longitudinal section showing the structure of the core. It seems that the arched zones of the coaxial core are made up of several rows of small rectangular cells, and not of a single row of long cells; *6*, longitudinal section; *5*, *7*, transverse (*5*) and longitudinal (*7*) sections of the Cretaceous coralline *Paraphyllum amphiroaeforme* (Rothpletz) with a general thallus morphology similar to *Archamphiroa jurassica*); *8–12*, Scanning electron micrographs of *Archamphiroa jurassica* Steinmann. *8*, Fragment of a specimen in longitudinal section. The coaxial core (middle part) and the filaments of the peripheral region (lateral parts) are visible; *9*, Enlargement of the specimen in *8* (square) showing the cell fusion between cells in adjacent filaments (arrows); *10*, An enlargement of the same specimen, showing the passage between the core and the peripheral region; *11*, Specimen in transverse-oblique section. Cells within core are cut transversally; cells within peripheral region are set in rows arranged perpendicularly to the core; *12*, Enlargement of the specimen in *11* (square) showing the fusion between cells in adjacent filaments (arrow). *1*, *6*, thin section LF3; *2*, thin section LF1; *3*, thin section LF6; *4*, thin section LF18; *5*, *7*, thin section 1b (Hăşdate, Romania).

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