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REMARKS ON THE CORTICAL STRUCTURE OF LATE PALEOZOIC "PHYLLOID ALGAE"

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ABSTRACT—The cortical structure of the green anchicodiacean alga *Anchicodium* in the Pennsylvanian Dueñas Formation of the Cantabrian Zone (northwestern Spain) is described and illustrated. *Anchicodium* is characterized by a broad phylloid or leaflike calcified thallus, consisting of a bilateral cortex and a poorly calcified central medulla. The organization and morphology of the cortical system have been revealed with great detail using cathodoluminescence microscopy. *Anchicodium* cortex is composed of up to three (four?) orders of dichotomized branched cortical siphons that are usually swollen at the center; primary siphons are bulbous and are followed by elongate cylindrical siphons. Cortical siphons are preserved as dull-bright luminescent molds filled with micrite or microsparite, and contrast sharply with the surrounding non-luminescent calcite infilling the intersiphonal spaces, originally occupied by aragonite. *Anchicodium* in the Dueñas Formation exhibits a variety of preservational stages. Through a compilation of the taxonomic nomenclature and morphologic re-interpretations, it is concluded that some late Paleozoic anchicodiacean algae might represent diagenetic stages of *Anchicodium* or *Eugonophyllum* without any taxonomic significance. This conclusion is suggested particularly for the taphotaxon *Ivanovia*.

INTRODUCTION

"PHYLLOID ALGAL" remains were important and abundant constituents of tropical and subtropical carbonate platforms during the Carboniferous–Permian, particularly in shallow open shelf or shelf-margin environments where they constituted bioherms, build-ups or bioaccumulations, many of which became important hydrocarbon reservoirs (Wray, 1977; West, 1988; Toomey, 1991a; Wahlman, 2002). "Phylloid algae" are known from the Devonian (Maslov, 1956; Mamet and Préat, 1983) but they were not highly successful carbonate producers until the late Carboniferous to early Permian (e.g., Wray, 1977; West, 1988; Toomey, 1991a; Wahlman, 2002; Kiessling et al., 2003). Atypical early Mesozoic representatives of "phylloid algae" have been described from Triassic rocks of the Yukon Stikine Terrane in Canada (Reid, 1986; Torres, 2003) and from the Late Cretaceous of the Northern Calcareous Alps (Schlagintweit, 2010). The term "phylloid algae" was created by Pray and Wray (1963) to group some late Paleozoic calcified algae without any consideration of their taxonomic status, sharing similar leaflike forms, but lacking sufficient internal morphologic features for generic identification. Therefore, this term is descriptive rather than taxonomic, and is most useful for field and rock texture descriptions. Nevertheless, because the term "phylloid" does not imply either a particular growth form or taxonomic affinity, some authors have suggested that this artificial group of algae is a "waste-paper basket" (Schlagintweit, 2010) and others have even considered it as unnecessary due to several paleobotanical inconsistencies (Granier, 2012; Vachard et al., 2012; Parvizi et al., 2013).

On the basis of the internal structure and thallus organization, "phylloid algae" can be subdivided into two major groups: 1) rhodophycean "phylloid algae," including *Archaeolithophyllum*, its junior synonym *Kasimophyllum*, and the problematic paleoaplysinaceans (Vachard and Kabanov, 2007; Anderson and Beauchamp, 2010); and 2) "phylloid algae" with green algal affinities, including anchicodiacean algae. The latter have a thallus composed of a thick and recrystallized central medulla surrounded by a cortical region, and are morphologically similar to modern, calcified (e.g., *Halimeda*, *Udotea*), or non-calcified (*Codium*) Bryopsidales. This medulla is formed of several relatively broad, rectilinear to twisted, and interweaved siphons that are arranged more or less parallel to the surface of the blades, whereas the cortical zones are formed by utricular molds (sensu Torres and Baars, 1992b) mainly disposed perpendicularly to the surface of the thallus. Anchicodiacean algae include *Anchicodium* Johnson, 1946, which is the object of this study, *Ivanovia* Khvorova, 1946, *Eugonophyllum* Konishi and Wray, 1961, *Neoanchicodium* Endo and Kanuma, 1954, and the poorly known genera *Kansaphyllum* Baars, 1992, *Calcipatera* Torres et al., 1992, and *Iranicodium* Senowbari-Daryan and Rashidi, 2010. It is worth mentioning that during the re-evaluation of *Anchicodium* topotypes, and contrary to Laporte (1962), Torres et al. (1992) erected *Calcipatera* as a membranous cyathiform algal genus that they considered to be distinct from *Anchicodium*. Despite the usual interpretation as monostromatic "phylloid algae" (Wray, 1977), the genus *Calcifolium* Maslov, 1956, was recently re-described as an algospongia (Cózar and Vachard, 2004; Vachard and Cózar, 2010).

Johnson (1946) originally described *Anchicodium* as "a crustose mass from which straight or nearly straight cylindrical thalli develop" (p. 1098). Endo (1951), Baars and Torres (1991), and Torres and Baars (1992a) also suggested that the thallus of *Anchicodium* is cylindrical and branching and hence, the organism is not etymologically a "phylloid alga." However, the current consensus suggests that *Anchicodium* is a "phylloid alga" (bladed or membranous shaped) with protuberances or tubercules (e.g., Konishi and Wray, 1961; Laporte, 1962; Pray and Wray, 1963; Wray, 1977; Mamet, 1991; Schlagintweit, 2010; Senowbari-Daryan and Rashidi, 2010). In fact, circular sections of *Anchicodium*, such as those reported by Torres and Baars (1992a), might correspond to transverse sections of cylindrical protuberances developed from the phylloid thallus. A similar feature can be observed in the red alga *Archaeolithophyllum* (having a typical phylloid thallus), which shows

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sporadic circular sections corresponding to ventral protuberances developed from the bladed thallus (e.g., Forsythe, 2003). In the present paper, the leaf-shape of *Anchicodium* has been confirmed with 3-D core fragments and axial sections of the thallus.

Although the internal structure of *Anchicodium* differs from that of many Paleozoic siphonous algae (e.g., *Dimorphosiphon*, *Succodium*, *Aphroditicodium*, *Tauridium*, and *Thaiporella*), *Anchicodium* is usually assigned to the Codiaceae or allied families. The morphology of the cortical system (e.g., shape and number of cortical siphons) is crucial for species and genus identifications of modern siphonous algae (e.g., Hillis-Colinvaux, 1984; Littler and Littler, 1990; Dragastan et al., 2002). Nevertheless, late Paleozoic green "phylloid algae" are usually highly neomorphosed due to their originally aragonitic composition and hence, most descriptions of the cortical structure are incomplete and only a few examples tentatively reconstruct the cortical organization of anchicodiacean "phylloid algae" (e.g., Torres 1995, 2003; Senowbari-Daryan and Rashidi, 2010). In fact, most of *Anchicodium* species are poorly described and illustrated (see review in Senowbari-Daryan and Rashidi, 2010), and many of them are probably synonymous. Furthermore, many of the examples reported in the literature are too poorly preserved to allow satisfactory species or generic identifications. Detailed descriptions of the cortical system (e.g., number, length, diameter, and shape of the cortical siphons) are crucial for consistent taxonomic identifications of late Paleozoic anchicodiacean algae.

Among "phylloid algae," skeletal microstructures can hardly be observed under plane polarized light microscopy; hence, most of taxonomic affinities of neomorphosed "phylloid algae" are uncertain, and some details of the algal structures are not recognizable. On the other hand, cathodoluminescence (CL) and epifluorescence microscopy have been successfully used to identify the skeletal structure and nature of these algae (Dawson, 1992; Moshier and Kirkland, 1993; Kirkland et al., 1993; Corrochano et al., 2013). Using CL microscopy on exceptionally preserved material, this paper describes and discusses: the cortical structure of well-preserved specimens of *Anchicodium*; their siphonous organization and cortical structure; the different appearances of the cortical system seen in transmitted versus CL microscopy; the different modes of preservation and calcification of these algae; and their comparison with some other late Paleozoic anchicodiacean algae. Finally, this paper constitutes a first integrated approach of the most significant group of the "phylloid algae."

MATERIAL AND METHODS

The specimens of *Anchicodium* reported herein were collected from the Dueñas Formation of the Lena Group, late Moscovian (Myachkovian), in the Lois-Ciguera sector, Central Asturian Coalfield, Cantabrian Zone, León (northwestern Spain) (Fig. 1). *Anchicodium* was collected from several recovered subsurface drill core fragments (cores SS-14 and SS-16) of the Salamón Gold District (just east of the village of Salamón, UTM coord. 30T 326530/4757012).

All samples were collected during the logging of stratigraphic sections, and are marked with the abbreviation of the name of the section followed by a dash followed by an additional number (e.g., SS-14–13); polished and uncovered thin sections have the suffix "CT." Thin sections and polished slabs containing the specimens illustrated here are housed at the Department of Geology, University of Salamanca, Spain, Lois-Ciguera collection.

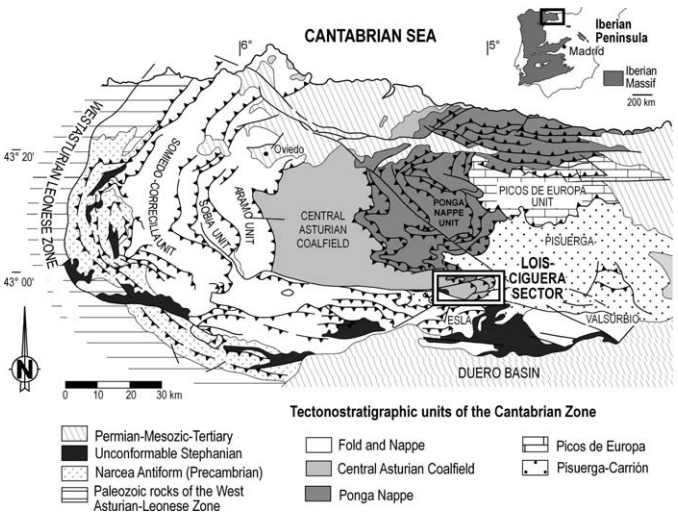


FIGURE 1—Geological map of the Cantabrian Zone showing the location of the Lois-Ciguera sector, modified from Julivert (1971) and Pérez-Estaún et al. (1988).

Samples were examined under a petrographic microscope with transmitted and polarized light, and were stained with combined Alizarin red S and potassium ferricyanide for revealing the skeletal microstructure of the algae (e.g., Moshier and Kirkland, 1993), and for distinguishing between carbonate minerals (Dickson, 1966). Selected thin sections were polished and observed uncovered under a cold cathodoluminescence unit, model CCL 8200 mkIII, with a vacuum chamber coupled to an optical microscope (Nikon Labophot 2-Pol), operating under standard analytical conditions of 12–20 kV accelerating voltage, 200–400 mA beam current and vacuum of 0.2–0.1 torr. Measurements of the cortical system were made on cathodoluminescence images.

GEOLOGICAL SETTING

The Cantabrian Zone is the foreland fold- and thrust-belt in the north of the Iberian Variscan Massif (Fig. 1), which formed during the collision between Gondwana, Laurentia and several microplates in Late Devonian–Carboniferous times (e.g., Martínez-Catalán et al., 1999). At least during the Carboniferous, the Cantabrian Zone comprised a marine and asymmetric foreland basin, developed on the continental (passive) margin of Gondwana and located on the eastern coast of Pangea at paleoequatorial latitudes. The basin originally had a linear SW-NE trend, and later acquired its present-day arcuate shape due to the closure of the Ibero-Armorican Arc (e.g., Weil et al., 2013). The Cantabrian Zone is characterized by thin-skinned tectonics, low or absent metamorphism and scarce cleavage (Julivert, 1971; Pérez-Estaún et al., 1988). Its deformation began in the Late Mississippian (Dallmeyer et al., 1997) and the basin was progressively narrowed during the forward advance of the Variscan orogenic front up to its final consumption at the Carboniferous–Permian boundary (e.g., Pérez-Estaún et al., 1988). Stratigraphic and structural characters have been used to subdivide the Cantabrian Zone into several major geological units (Fig. 1). The most complete Carboniferous successions are located in the eastern units (Central Asturian Coalfield, Ponga Unit, Picos de Europa and Pisuerga-Carrión), and as the result of the eastern-western progression of deformation, the top of the Pennsylvanian successions becomes younger toward the east. Due to the synorogenic context, these deposits exhibit remarkable thickness and lateral facies changes.

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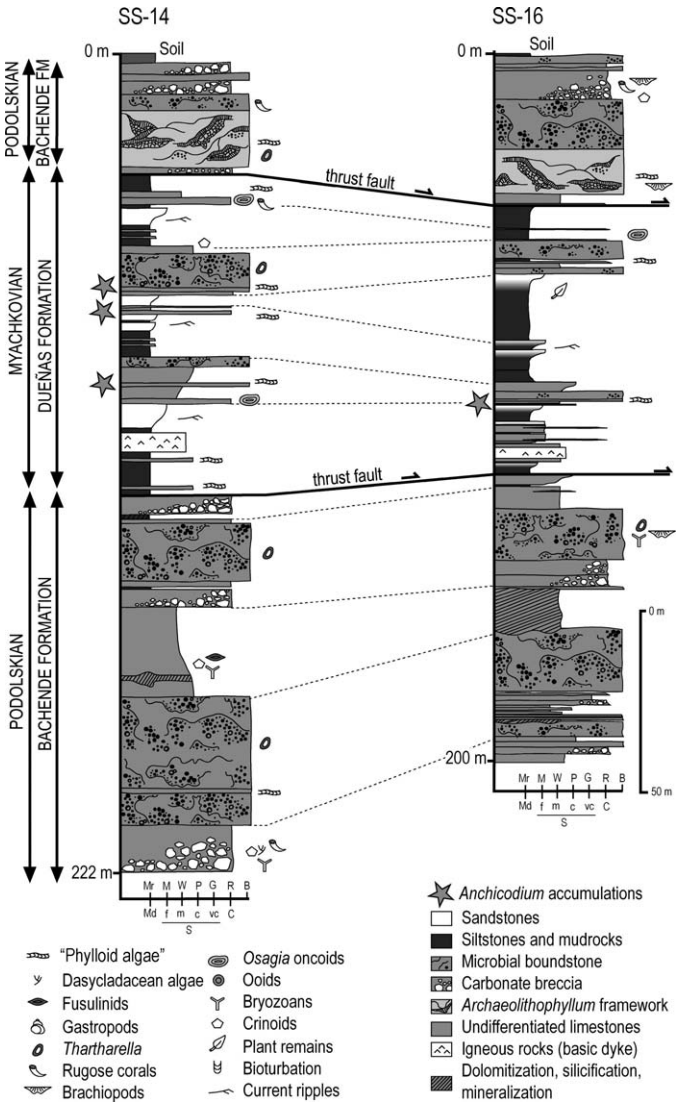


FIGURE 2—Stratigraphy of the Lena Group at the Salamón Gold District showing the stratigraphic correlation of the subsurface drill cores SS-14 and SS-16, and the location of the *Anchicodium* Johnson, 1946, accumulations. Abbreviations: Mr=marl; M=mudstone; W=wackestone; P=packstone; G=grainstone; R=rudstone/floatstone; B=boundstone; Md=mudrock; f, m, c, vc=fine, medium, coarse, and very coarse grained sandstone, respectively; C=conglomerate. Modified from Corrochano et al. (2013).

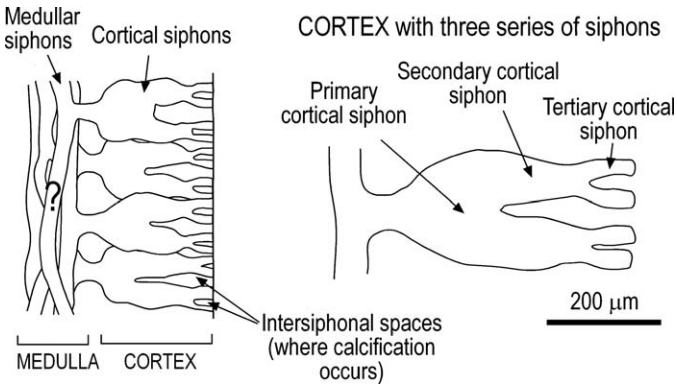


FIGURE 3—Reconstruction of the internal microstructure of the thallus of *Anchicodium* and enlarged cortical structure.

The foreland basin was mostly filled with thick, paralic, siliciclastic wedges that pass laterally into shallow-water and open marine limestones. The Dueñas Formation (up to 300 m thick) is a dominantly deltaic unit of mudrocks with interbedded siltstone and fine- to coarse-grained litharenites, which was deposited in shelf lobes and delta-front environments in distal shelf areas of the basin (Corrochano et al., 2012) (Lois-Ciguera sector, Fig. 1). This unit changes laterally to several shallowing-upward mixed cycles (cyclothems) that are meter-to-decameter thick and consist of subtidal carbonates at the base and coarsening-upward deltaic siliciclastics at the top (Fig. 2). Landward (to the west), the Lois-Ciguera succession alternates and interfingers with deltaic sandstones and shallow marine mudrocks (Lena and Sama groups). Distally (to the east), the Lois-Ciguera deposits overthrust the siliciclastic succession of the Pisuerga-Carrión Unit (Fig. 1), which mostly consists of deep water and submarine slope deposits (olistostromes, breccias, turbidites, etc.) and sporadic intercalations of deltaic deposits and shallow-water carbonates. Further stratigraphic information about the Dueñas Formation is given in Ginkel (1965), Barba et al. (1991), and Corrochano and Barba (2007). Pennsylvanian calcareous algae from the Lois-Ciguera sector have been documented in Rácz (1966), Meijer (1971), and Corrochano et al. (2013).

TERMINOLOGY

Morphologic terms employed here are those commonly used for fossil siphonous green algae (Fig. 3). The overall thallus of the alga is differentiated into two zones: inner (medulla) and outer (cortex). The medulla contains longitudinal tubes (medullar siphons) that give rise to lateral cortical siphons. The latter typically branch one or more times and become more or less perpendicular to the surface of the thallus. It is worth mentioning that the term "filament," used by previous workers to describe the medullar siphons (e.g., Konishi and Wray, 1961; Torres et al., 1992; Baars, 1992; Torres and Baars, 1992a; Torres, 2003; Baars and Torres, 1991) is not used here. Littler and Littler (1990) emphasized that filament is generally defined as a "chain of cells attached end to end" and is incorrectly applied to siphonaceous algae. Various terms have been employed to describe the cortical siphons in late Paleozoic anchicodiacean algae. The most extended term is "utricle" (e.g., Konishi and Wray, 1961; Baars and Torres, 1991; Baars, 1992; Torres and Baars, 1992a; Torres et al., 1992, 2003; Kirkland et al., 1993; Torres, 1995, 1997, 2003; Mamet and Villa, 2004), although other expressions, such as "cylindrical cells" (Khvorova, 1946), "utricular casts" (Torres and Baars, 1992b), or "secondary threads" (Senowbari-Daryan and Rashidi, 2010) have been employed. In the present paper, the different cortical siphon orders or series will be termed "primary cortical siphons," "secondary cortical siphons," "tertiary cortical siphons," and "quaternary cortical siphons" (Fig. 3).

TAXONOMIC OVERVIEW

Taxonomic classification of fossil siphonous algae ("halimediform udoteaceans" sensu Flügel, 2004) is difficult and controversial (Schlagintweit, 2010). Johnson (1946) erected the genus *Anchicodium* and assigned it to the Codiaceae, based on the similarities between its siphonal structure and that of the Recent and non-calcified green calcareous alga *Codium*, and hence the name *Anchi* (near) *Codium*. Later authors, such as Endo (1951), Wray (1977), Baars and Torres (1991), and Torres and Baars (1992), among others, also placed *Anchicodium* in the family Codiaceae, or alternatively in the Anchicodiaceae

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(Shuysky *in* Chuvashov et al., 1987; Mamet, 1991; Senowbari-Daryan and Rashidi, 2010). The family Codiaceae includes the Udoteaceae (represented by *Halimeda* and *Udotea*) and the non-calcified Codiaceae (represented by *Codium*). Because Udoteaceae is often given as a synonym of Codiaceae (e.g., Papenfuss, 1955), and as Codiaceae is an accepted conserved family name (Silva, 1980), some authors still include *Anchicodium* in the Codiaceae. In addition, other workers suggest that another family name, Halimedaceae, should have priority over Udoteaceae (Hillis-Colinvaux, 1984). Following the criteria of Schlagintweit (2010), *Anchicodium* should be placed in Udoteaceae, since Halimedaceae only includes the genus *Halimeda*. The Cretaceous "phylloid alga" *Gosavisiphon* was compared with *Anchicodium* and placed within Udoteaceae (Schlagintweit, 2010). Other "bladed udoteaceans" (Flügel, 2004, p. 423), such as *Eugonophyllum*, have been placed either in Udoteaceae (Kirkland et al., 1993) or in Halimedaceae (Forsythe, 2003).

The family Anchicodiaceae appeared in the Moscovian (older taxa like *Anchicodium magnum* sensu Lemosquet and Poncet, 1977, are considered here as being part of another genus) and some of its genera range to the top of the Permian. However, fossil algae from Canada identified as *Ivanovia* by Reid (1986) suggest that this family might range into the Late Triassic (Norian). The Anchicodiaceae were originally subdivided into three tribes: 1) Ivanoviae Shuysky *in* Chuvashov et al. (1987), which includes *Anchicodium*, *Eugonophyllum*, *Ivanovia*, the relatively atypical *Neoanchicodium*, and poorly known genera, such as *Kansaphyllum*, *Calcipatera*, and *Iranicodium*; 2) Paradelleae Maslov 1956, with *Paradella*; and 3) Calcifoliae Shuysky *in* Chuvashov et al. (1987), represented by *Calcifolium*. However, other studies have evidenced that: 1) *Paradella* is a dasycladacean alga (Maslov, 1956; Vachard et al., 1989); 2) *Calcifolium* is an algospongia (Cózar and Vachard, 2004), a group of incertae sedis algae recently revised by Vachard and Cózar (2010); and 3) several *Ivanovia* specimens reported in literature might actually represent diagenetic stages of *Anchicodium* or *Eugonophyllum*.

Contrary to traditional classifications, Vachard et al. (1989, 2001, 2012) included *Anchicodium* and related "phylloid algae" in the family Archaeolithophyllaceae. These authors suggested that those "phylloid algae" might correspond to the red alga *Archaeolithophyllum* that underwent a series of recrystallization stages and microborings by cyanobacteria. It means that the observed morphological variability in the "phylloid algae" is due to diagenetic processes, and hence, "phylloid algal remains are not botanical but sedimentological objects" (Vachard et al., 2012). During the present study, in the well-preserved material from the Dueñas Formation, the complex and symmetrical cortical structure of *Anchicodium* appeared perfectly similar to that reported in modern siphonous calcareous algae, suggesting that the degradatory origin of *Anchicodium* from a red alga is very improbable. The diagenetic hypothesis of Vachard et al. (1989) remains only suitable for some specimens of *Eugonophyllum*, as they exhibit superficial conceptacles the same as those of *Archaeolithophyllum*.

SYSTEMATIC PALEONTOLOGY

Family ANCHICODIACEAE Shuysky *in* Chuvashov et al., 1987
Genus ANCHICODIUM Johnson, 1946 emend

Type species.—*Anchicodium funile* Johnson, 1946.

Diagnosis.—Thallus calcified in wide phylloid blades; thallus siphonous, differentiated into bilateral outer cortex and poorly calcified central medulla; in some species, thallus surface exhibits swellings or buds; on apical extremity of blades, cortices fuse forming a rounded termination; medullar siphons relatively small, disposed more or less parallel to surface of thallus, interwoven, giving rise to cortical siphons; number of central siphons remains undeterminable; cortex consists of multi-seried cortical siphons (2–4 series), semiparallel, arranged perpendicularly or slightly inclined to surface of thallus; primary cortical siphons bulbous, followed by elongate, cylindrical, dichotomously branched siphons, usually swollen at center; after branching, diameter of cortical siphons become successively thinner (emended from Johnson, 1946).

Occurrence.—*Anchicodium* is a cosmopolitan genus. It is known from the Pennsylvanian (Podolskian) up to the Permian (Kungurian), and possibly to the Triassic.

Remarks.—All the specimens examined in this study match the original illustrations and descriptions of *Anchicodium* Johnson (1946) and are similar to many specimens of *Anchicodium* reported in the literature. Currently, there are fifteen species of *Anchicodium*, although most of them are poorly described and illustrated and some may be synonymous (see critical review in Senowbari-Daryan and Rashidi, 2010). On the basis of biometric data available in the literature, the overall shape of the thallus and the organization of the cortical system, the specimens described here might tentatively be assigned to *A. gracile* and *A. magnum*. Nevertheless, 1) some morphologic and biometric differences exist; 2) the original descriptions of these species are very short and poorly illustrated; and 3) most of the previously reported biometric data of the cortical siphons are imprecise and without any detailed description or location.

ANCHICODIUM GRACILE Johnson, 1946
Figures 4, 5

1946 *Anchicodium gracile* JOHNSON, p. 1098, pl. 3, figs. 1, 2.
1981 *Anchicodium gracile*; RAUZER-CHERNOUSOVA AND KOROLYUK, p. 161, pl. 1, figs. 5, 6, pl. 2, figs. 1, 2.

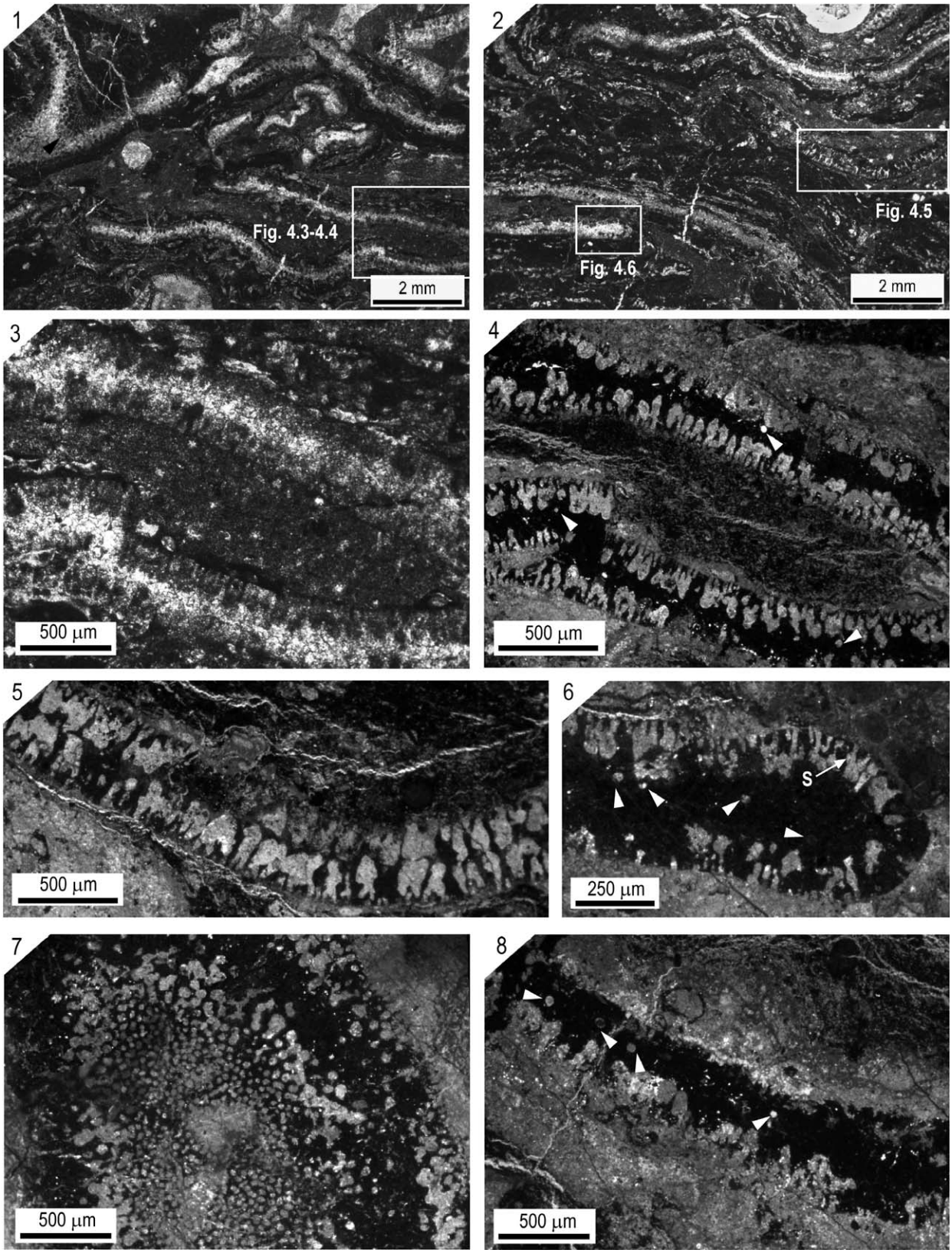
Description.—Phylloid thallus several centimeters in length, 360 to 680 μm thick (average 525 μm), which pinches and swells slightly at termination of blades; one specimen reaches thallus length of 1.81 cm; central medulla with variable thickness, up to 210 μm; in general, this medulla is weakly calcified and composed of siphons with average diameter of 43 μm; in one specimen (Fig. 4.2, 4.5) medulla is inconspicuous or poorly developed; cortex well-calcified and shows two layers of cortical siphons; primary bulbous dichotomously branched siphons have diameter of 62–93 μm (average of 81.5 μm) and length of 102–148 μm (average 125 μm); they support cylindrical and long secondary siphons, which have diameter 25–50 μm (average 36 μm) and length of 36–77 μm (average 65 μm); no reproductive organs found. Biometric data of thallus elements given in Table 1.

Occurrence.—*Anchicodium gracile* occurs in Middle and Upper Pennsylvanian strata of the Midcontinent and southwestern

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FIGURE 4—Photomicrographs of *Anchicodium gracile* Johnson, 1964, from the Dueñas Formation, Myachkovian, NW Spain. *1–3*, plane polarized light images; *4–8*, cathodoluminescence (CL) images. *1–8*, sample SS–14–13CT: *1*, typical aspect of fragmented and undulating algal thalli in the Dueñas Formation; black arrow points to an apparent thallus bifurcation, probably as the result of the cut through an undulating blade; for magnification of encased zone, see *3*, *4*; *2*, "phylloid algal" plates acting as nuclei for microbially coated *Ottonosia* oncoids, consisting of alternating homogeneous micritic and sparitic laminae, *Claracrusta* and foraminifers; note the specimen enlarged in *5* with a medulla almost absent or poorly developed; *3*, *4*, plane polarized light and CL photomicrographs of the same curved specimen, showing the cortical structure of *Anchicodium gracile* composed of two series of cortical siphons; *3*, note the

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micrite-filled siphons; *4*, cortical siphons are preserved as dull-bright luminescent molds (light gray) whereas the intersiphonal spaces, originally occupied by aragonite, are filled by non-luminescent (dark lines and spaces) calcite; note the presence of primary bulbous cortical siphons and their dichotomous divisions; white arrows point to small circles interpreted as transverse sections of medullar siphons; *5*, CL detail view of a specimen exhibiting a thallus composed of a bilateral cortex and a central medulla almost absent or poorly developed; *6*, CL magnification of quadrangle in *2* showing the flared termination of a "phylloid" thallus; white arrows point to transverse sections of medullar siphons; note the swollen (S) cortical siphons after branching; *7*, *8*, SS–14–15CT: *7*, CL section cut parallel to a plate; *8*, CL photomicrograph of another specimen showing the transverse sections of medullar siphons (arrowed).

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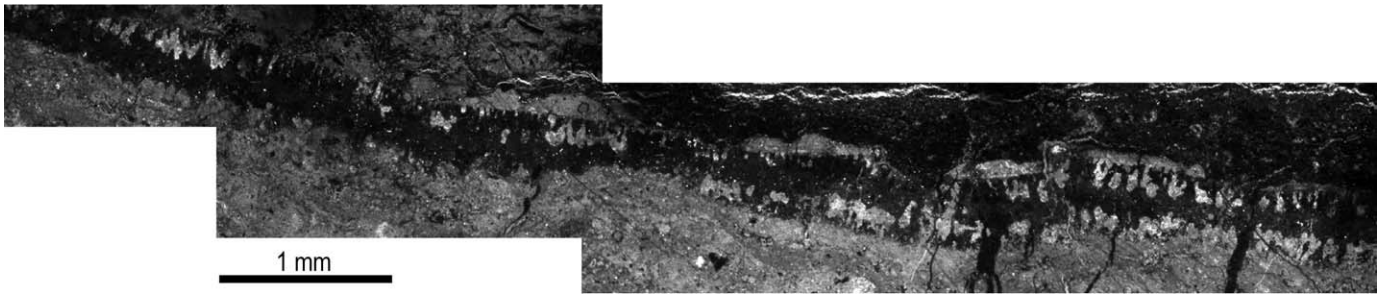


FIGURE 5—Cathodoluminescence photomosaic of *Anchicodium gracile* Johnson, 1946, from the Dueñas Formation, Myachkovian, NW Spain. Sample SS–14–15CT; diagenetic preservation varies throughout a single "phylloid algal" plate; siphonous structure is preserved at the right side of the image, whereas at the left side, the "lower" cortex has been obliterated during neomorphism.

regions of the United States, the southern Urals (Russia), and northern Spain.

Remarks.—Among the half-dozen species originally described by Johnson (1946), a platy growth was only mentioned in *A. gracile*. In the studied area of northern Spain, other "phylloid algae" with strong thickness variation of the medulla have been reported; for instance, *Eugonophyllum mulderi*, a species erected by Rácz (1966) in the Lois-Ciguera sector. However, *E. mulderi* differs from *A. gracile* by: 1) a thicker thallus and a thinner cortical layer; and 2) a "sub-cortex" thinner than the secondary cortical siphons reported here.

In the studied material, *A. gracile* appears to form the nucleus of *Ottonosia*-type oncoids, with coatings of *Claracrusta catenoides* and encrustations of small foraminifers (*Palaeonubecularia* and *Tuberitina*). Also occurring in the microfacies are crinoids, brachiopods, gastropods, fusulinids, sphinctozoan sponges and chaetetid demosponges.

ANCHICODIUM MAGNUM Endo, 1951
Figures 6, 7

1951 *Anchicodium magnum* ENDO, p. 125, pl. 11, figs. 3–5.
1952 *Anchicodium magnum*; ENDO, pl. 23, figs. 6, 7.
1972 *Anchicodium magnum*; HOMANN, p. 175, pl. 2, fig. 13 (with synonymy).

Description.—Phylloid thallus 550–810 μm in thickness (average 715 μm) and exhibits sporadic swellings; specimens reach lengths of at least 1.22 cm; central medulla 270–300 μm thick, and medullar siphons average 57 μm in diameter (65–53 μm); three (four?) series of cortical siphons distinguished; primary siphons bulbous (up to 140 μm wide, 145 μm long), and followed by secondary, long (up to 195 μm) and cylindrical (diameter up to 82 μm), dichotomized siphons; third layer composed of relatively short (45–31 μm), cylindrical siphons, also dichotomous and arranged perpendicular to surface, diameter of 32–21 μm (average 26 μm); secondary and tertiary siphons often slightly swollen at center; when present, fourth layer composed of hair-like cortical siphons (diameter 7 μm). Biometric data of thallus elements given in Table 1.

Occurrence.—*Anchicodium magnum* ranges from the late Moscovian (Myachkovian) up to the early Permian. It occurs in Japan, the Carnic Alps and Karavanken (Austria, Italy, Slovenia), southern Turkey, Spain, and probably in the Midcontinent and southwestern regions of the United States.

Remarks.—*Anchicodium magnum* appears as disoriented thalli floating in a silty micritic matrix of packstones/floatstones with abundant fusulinids. Crinoids, echinoids, gastropods and beresellid algae also occur.

CALCIFICATION AND PRESERVATION

In modern seas, calcareous siphonous algae are major bioherm-builders and producers of the carbonate factory worldwide, in subtropical and tropical shallow-water areas (e.g., Granier, 2012 and references therein). The dominant ecological and sedimentological role of these algae is permitted by a seawater Mg/Ca ratio which favors the nucleation of aragonite over calcite (molar Mg/Ca >2) (Stanley and Hardie, 1998; Stanley, 1999). In fact, during the beginning of the "aragonite interval" of the late Paleozoic and early Mesozoic (Sandberg, 1983, 1985; Stanley, 2006), "phylloid algae" flourished and became important contributors to the worldwide development of carbonate platforms and ramps (Kiessling et al., 2003).

"Phylloid algae" are usually too strongly neomorphosed to allow satisfactory generic identifications (Wray, 1977). The susceptibility of these algae to replacement, dissolution and recrystallization is a function of their original metastable mineralogy (aragonite or high-Mg calcite) and the highly porous nature of their original skeletal microstructure (e.g., Dawson and Carozzi, 1993; Corrochano et al., 2013). For generic identification of "phylloid algae," Baars and Torres (1991) noted that the different modes and degree of calcification are as important as the general shape of the algae. It has been suggested that the red alga *Archaeolithophyllum* was originally composed of aragonite (James et al., 1988; Moshier and Kirkland, 1993) or high-Mg calcite (Corrochano et al., 2013), as would be expected given the high Mg/Ca ratio of ambient

TABLE 1—Variability in morphometric parameters (in microns) of *Anchicodium* from the Dueñas Formation, Myachkovian, northwest Spain. For a complete biometrical compilation of *Anchicodium* species see Senowbari-Daryan and Rashidi (2010). Abbreviations: TT=thallus thickness (mean value); mT=medullar thickness; dms=diameter medullar siphons; n=cortical siphons layers; $dc_{1,2,3,4}$=diameter of the primary, secondary, tertiary and quaternary cortical siphons; $lc_{1,2,3,4}$=length of the primary, secondary, tertiary and quaternary cortical siphons.

				Cortical system								
Species	TT	mT	dms	n	dc_1	dc_2	dc_3	dc_4	lc_1	lc_2	lc_3	lc_4
Anchicodium gracile	680–360 (525)	Variable (up to 210)	53–34 (43)	2	93–62 (81)	50–25 (36)	–	–	148–102 (125)	77–36 (65)	–	–
Anchicodium magnum	810–550 (715)	270–300	65–53 (57)	3–4	140–100 (120)	82–35 (56)	32–21 (26)	7	145–140 (142)	195–75 (109)	45–31 (38)	15

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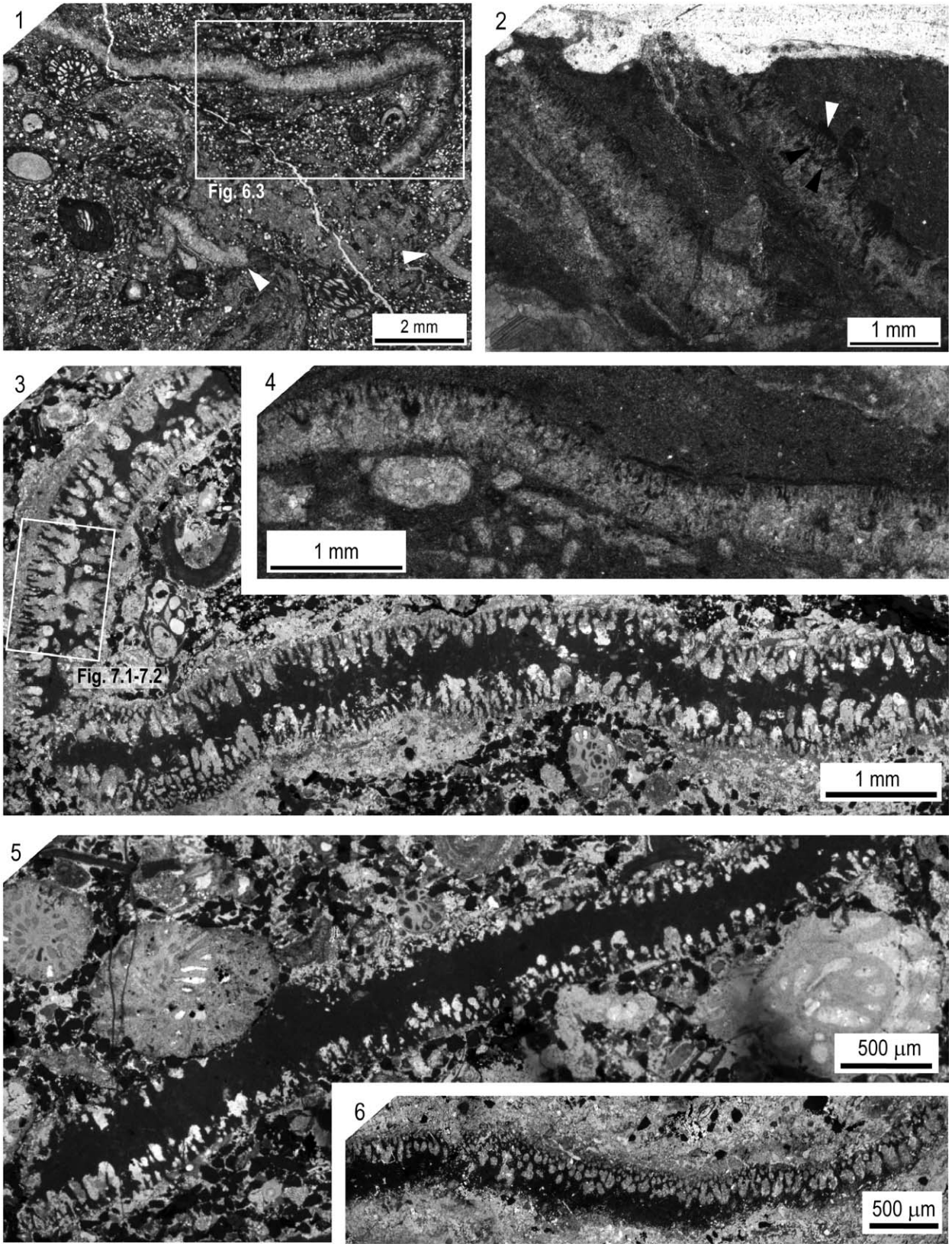


FIGURE 6—Photomicrographs of *Anchicodium magnum* Endo, 1951, from the Dueñas Formation, Myachkovian, NW Spain. *1*, *2*, *4*, plane polarized light images; *3*, *5*, *6*, cathodoluminescence (CL) images. *1*, sample SS–16–99,8CT; section through three specimens of curved and fragmented thalli; the large specimen, which shows micrite-filled cortical siphons, is enlarged in *3*; note that the two small and fragmented specimens are completely neomorphosed to calcite spar and the relic siphonous structure is almost imperceptible in plane polarized light although visible under CL; *2*, sample SS–14–15; section through two specimens showing the branching pattern of cortical siphons that are recognizable in part (black arrow); white arrow indicates a swelling of the thallus; *3*, sample SS–16–99,8CT; CL photomosaic of encased area of *1* (rotated 180°), showing cortical siphons oriented perpendicular to the surface of the thallus and developed symmetrical at both sides of a central line; note the clear branching pattern of the cortical siphons; *4*, sample SS–14–15; plane polarized light image showing the branching pattern of the cortical siphons; 5, sample SS–16–99,8CT; CL photomosaic showing the diagenetic obliteration of the "upper" cortex of a plate; *5*, sample SS–16–99,8CT; CL photomosaic of a slightly oblique section of a thallus; note that in this case, the "lower" cortex is absent probably due to the 2-D cut of the blade.

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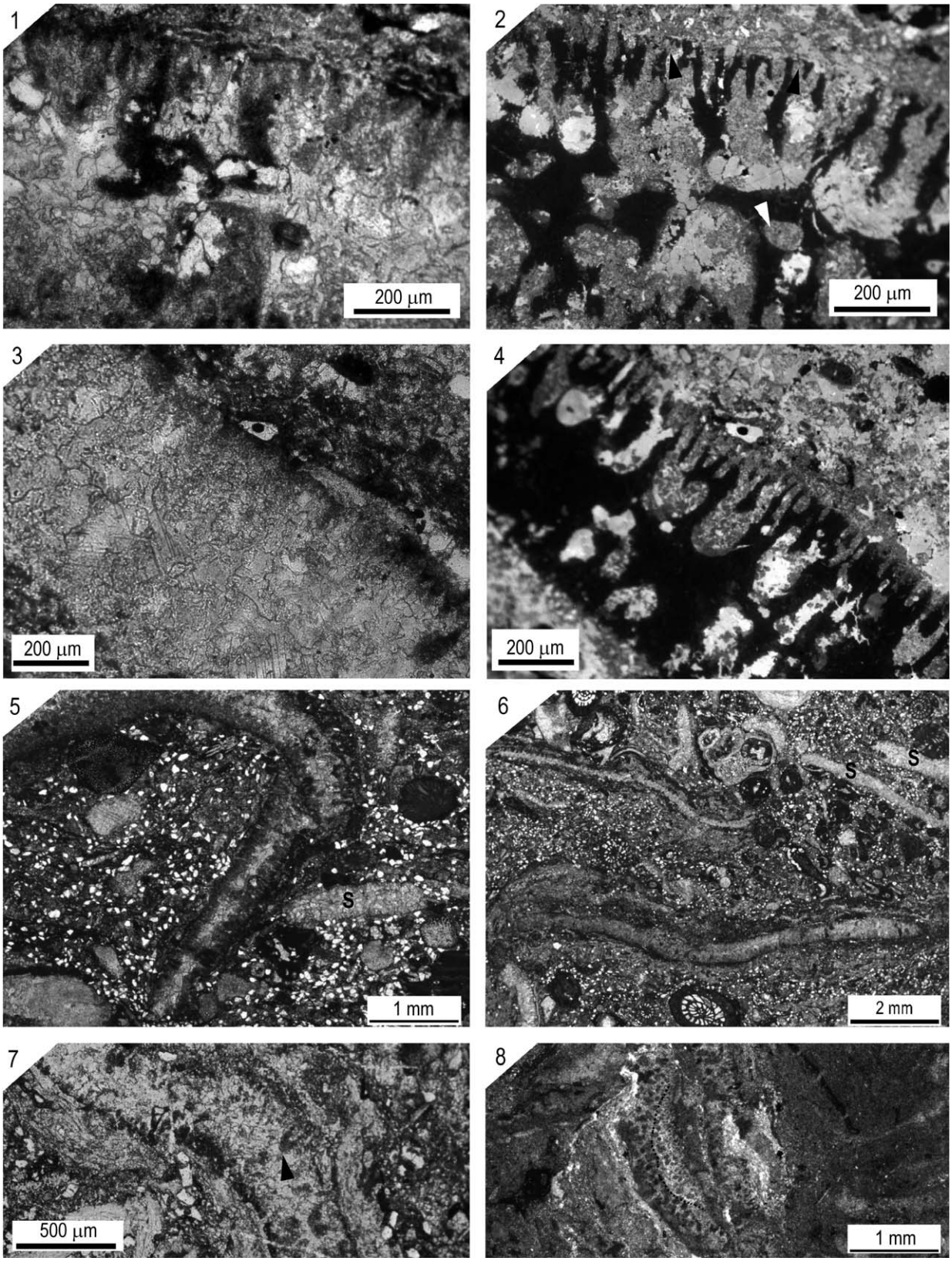


FIGURE 7—Photomicrographs of *Anchicodium magnum* Endo, 1951, from the Dueñas Formation, Myachkovian, NW Spain. *1*, *3*, *5–8*, plane polarized light images; *2*, *4*, cathodoluminescence (CL) images. *1*, *2*, sample SS–16–99,8CT; plane polarized light and CL photomicrographs of the same area enlarged from Figure *6.3*; note the different aspect of the large and dichotomized cortical siphons seen under conventional microscopy versus CL; black arrow points to hair-like siphonous structures developed at the margin of the thallus; white arrow is pointing to an oval section interpreted as an oblique cut of a medullar siphon; *3*, *4*, sample SS–16–99,8CT; plane polarized light and CL photomicrographs of another specimen showing the branching pattern of the cortical siphons and bulbous nature of the primary siphons; note that the cortical siphons under CL are clearly evident, despite neomorphism; *5*, *6*, sample SS–16–99,8; different preservational stages of *Anchicodium*; most specimens show micrite-filled siphons, whereas others (S) consist of a mosaic of sparite (their taxonomic affinity has

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seawater. On the other hand, it is generally assumed that anchicodiacean "phylloid algae" produced aragonite on the external surfaces of individual cortical siphons, as the modern genus *Halimeda*. This assumption is supported by Dickson et al. (1991) and Kirkland et al. (1993), who reported *Eugonophyllum* specimens with preserved primary aragonitic skeletons from the Pennsylvanian Holder Formation (New Mexico). In addition, tangential sections of anchicodiacean algae can exhibit net-like zones of polygonal features that are very similar to the net-like pattern of modern *Halimeda* (Kirkland et al., 1993).

If the mineralization in *Anchicodium* was analogous to that of modern siphonous algae (e.g., *Halimeda*, *Udotea*, *Penicillus*), the intersiphonal spaces were calcified in photosynthetic parts of the thalli of the medullar and cortical regions (Borowitzka and Larkum, 1977). The most heavily calcified algae of Recent Bryopsidales are found in some species of *Halimeda*, and the extent of calcification increases with the age of the alga. Natural concentrations of $CaCO_3$ found in the form of aragonite needles in Bryopsidales range from 60–80% in *Halimeda*, to 32–47% in the weakly calcified *Udotea* (Hillis-Colinvaux, 1980). It is thought that calcification is probably in direct relation for increased rigidity in turbulent hydraulic regimes, for maintaining an erect thallus position to maximize exposure to sunlight, and as a possible defense against grazers, especially when combined with toxic secondary metabolites and nocturnal growth of new and non-calcified segments (Wray, 1977; Paul and Alstyne, 1988; Schupp and Paul, 1994).

In the Dueñas Formation, *Anchicodium* occurs as elongate and undulating blades that under transmitted plane polarized light are preserved as non-ferroan calcitic mosaics of equant and anhedral to subhedral crystals (up to 210 μm wide) that are generally coarser towards the center of the thallus. Most thalli are 2–4 mm long and the maximal length is 1.81 cm, although most of the specimens seem to be broken. Under plane polarized light, the cortex of *Anchicodium* is partially preserved through infilling of cortical siphons by micrite or by microsparite. In the latter, the siphonous structure is almost imperceptible due to neomorphism and just staining reveals the microstructure of the algae when ferroan calcite fills the skeletal pores (Fig. 7.8), but CL microscopy often reveals more details. Algal thalli exhibit a variety of preservational stages, even throughout the same specimen (Fig. 5); preservation is always better at the edges of the thalli and decreases in quality towards the center. In the same thin section, specimens range from relatively well preserved to completely obliterated by diagenesis (e.g., Fig. 7.5, 7.6). Such different preservational stages of *Anchicodium* remain enigmatic, although perhaps reflect differences in thoroughness of calcification related to the age of the specimens or to different positions on the thalli, as occurs in modern *Halimeda* or related anchicodiacean algae, such as *Eugonophyllum* (Kirkland et al., 1993).

In some specimens, cortical siphons could be seen on both sides of the thallus (e.g., Figs. 4.4, 4.5, 6.3), in others only on one side (e.g., Figs. 5, 6.5, 6.6). Some authors have suggested that some anchicodiacean algae (*Ivanovia*, *Kansaphyllum*, *Iranicodium*) developed different skeletal elements in opposite surfaces of the thallus. For example, Torres (1995, 2003) suggested that the inner and outer cortices of the cyathiform alga *Ivanovia* were dimorphic, that is, "the inner cortex of the cup consisted of densely packed columnar utricular casts quite different from the loose, spongy casts of the outer cortex of the cup" (Torres, 2003, p. 36). Baars (1992) erected the genus *Kansaphyllum* on the basis of the two layer arrangement of the thallus that exhibited a lower medulla of intertwining siphons and only an upper photosynthetic cortex composed of closely packed siphons occurring normal to the surface. As mentioned above, a similar dimorphism is apparently obvious in some *Anchicodium* specimens of the Dueñas material. However, a close examination revealed that the differences of the "lower" and the "upper" cortex are only locally present in some specimens and even change along the thallus of a single specimen (Fig. 5). This suggests that the "dimorphism" may be related to differences in the way the section was cut through an undulating blade (e.g., Fig. 6.6) or to differential deformity of cortices during diagenesis rather than an anatomical feature as Torres (1995, 2003) and other workers suggested. Therefore, it is assumed that *Anchicodium* had a bilateral symmetry developing the same elements with the same sizes and morphologies at both sides of the thallus.

Cold CL has revealed with great detail the structure of the cortex of *Anchicodium* (e.g., Figs. 4.4, 4.5, 6.3, 7.2, 7.4). The preservation of the (moldic) siphonous structures in the studied samples is probably related to micritic envelop processes along the siphons or to micritic infillings of these cavities. If calcification in *Anchicodium* proceeded in a similar way to that of *Halimeda*, dark lines and spaces (non luminescent) should represent the original intersiphonal acicular aragonite, whereas light gray areas (dull to bright luminescent calcite) correspond to post-mortem infilling of siphonal spaces, originally occupied by algal cytoplasm. The common obliteration of the medullar zone suggests that its calcification was apparently faint, although in some specimens, transverse sections of the medullar siphons could be observed (Figs. 4.4, 4.6, 4.8, 7.2). Dragastan et al. (2002) suggested that the differences in calcification between the medulla and the cortex (incomplete calcification) in modern *Halimeda* represent a response to a physiological balance in two ways: 1) cytoplasmic streaming is facilitated in the uncalcified medulla, which also provides flexibility during times of hydrodynamic disturbances; and 2) photosynthesis occurs in the cortical pigmented areas where chloroplasts are concentrated, resulting in precipitation of aragonite mostly in the intersiphonal spaces of the cortex. Additionally, experimental laboratory studies have demonstrated that $CaCO_3$, even in the absence of increased hardness, can decrease feeding by herbivores by changing pH conditions and neutralizing acid in the guts of herbivores (Hay et al., 1994).

Following the diagenetic pathways established in the Salamón Gold District for *Archaeolithophyllum* accumulations (Corrochano et al., 2013), the non-luminescent phase representing original intersiphonal spaces probably indicates an early diagenetic transformation process (dissolution-precipitation) from aragonite to calcite under oxidizing conditions in a mixing zone or a marine phreatic environment. These conditions are consistent with their CL signal and the inferred Mn and Fe relative compositions, because oxidizing conditions favored the Mn presence in marine cements mainly as Mn^{4+}, and the Fe presence as Fe^{3+}, rather than the divalent forms Mn^{2+} and Fe^{2+}.

←
been confirmed with CL images); *7*, sample SS–16–99,8CT; section through neomorphosed specimen; note that at the left side of the image, morphological features resemble those observed in some *Ivanovia* specimens; cortical siphons are sporadically visible at the right side due to the micritic infill (black arrow); *8*, sample SS–14–15; chemical staining revealing the skeletal microstructure of a recrystallized zone (light area bordered by dashed line) of a tangential cut though a thallus; dark spots in this area correspond to ferroan calcite.

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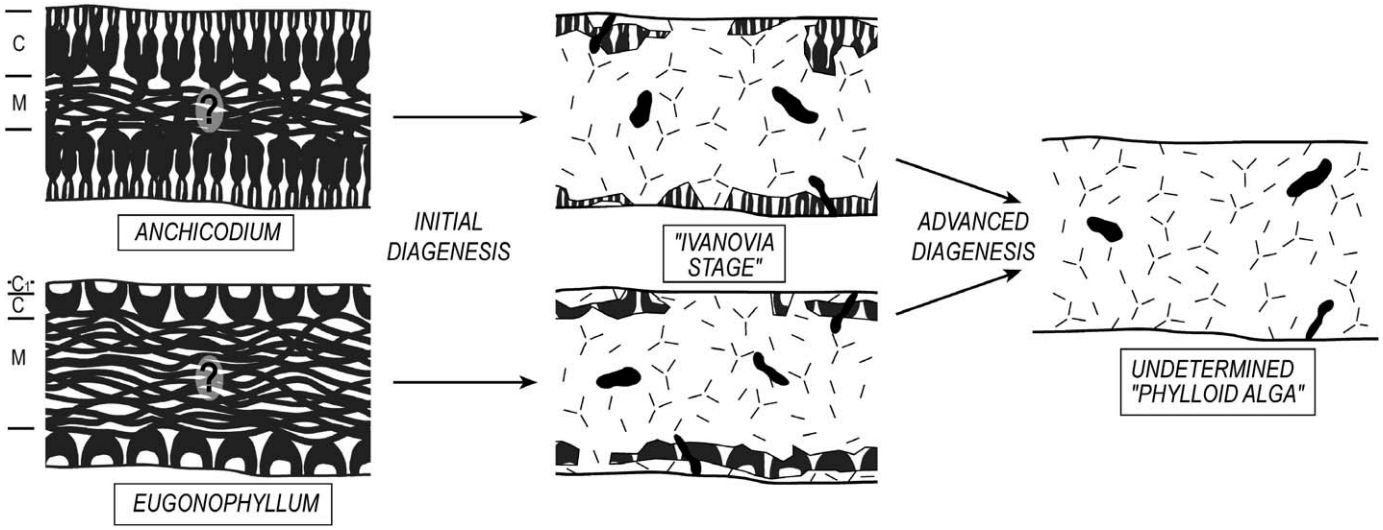


FIGURE 8—Schematic diagram illustrating successive diagenetic transformations of *Anchicodium* and *Eugonophyllum* and appearance of the "*Ivanovia* diagenetic stage" and the "undetermined phylloid alga." Abbreviations: M=medulla; C=cortex; C_1=subcortex.

DISCUSSION

Elliott (1982) suggested that the evolution of udoteaceans appears to have consisted of variations and different combinations of the medullar and cortical siphons, from the early Paleozoic onwards. *Anchicodium* and related anchicodiacean differ from other Paleozoic siphonous algae by the gross external morphology of the thallus (leaflike or membranous) and the particularly weak calcification of the medullar zone.

The thalli of anchicodiacean algae consist of undulating membranes or plates about 1 mm thick composed of a central medulla sandwiched between a peripheral cortex. The cortical system consists of dichotomously branched multi-seried (2–4) cortical siphons. *Eugonophyllum* is distinguished from *Anchicodium* and *Ivanovia* by having oval reproductive structures (conceptacle-like) randomly distributed over the surface of the thallus or in the terminal margins of the blades (Konishi and Wray, 1961; Kirkland et al., 1993; Forsythe, 2003). Reproductive organs in *Ivanovia* specimens have only been reported in the questionable Triassic form *I. triassica* Torres, 2003, and remain unknown in *Anchicodium. Eugonophyllum* is also distinguished from both *Ivanovia* and *Anchicodium* by having a well differentiated inner (subcortex) and outer cortex with short peripheral utricular molds recessed from the surface of the thallus (Fig. 8). In contrast, the cortical structure of *Anchicodium* and *Ivanovia* is not differentiated in two layers. Cortical siphons in *Ivanovia* (dark streaks of Khvorova, 1946) and *Anchicodium* are marginal, elongate, dichotomously branched and arranged perpendicularly to the surface of the thallus (Figs. 2, 8). Based on literature data, the most important difference between both genera consists of the degree of calcification and preservation of the algae; whereas *Anchicodium* is heavily to lightly calcified throughout, *Ivanovia* is in most cases highly neomorphosed showing indistinct relicts of utricular molds.

In addition to the differences in the skeletal microstructure and the mode of calcification, the growth habit of these algae also differs. All of them presumably grew as erect calcareous plants (e.g., Wray, 1968) acting as bafflers and trappers, but some species of *Eugonophyllum* and *Ivanovia* have been described as cyathiform algae (e.g., Cross and Klosterman, 1981; Torres, 1995, 1997, 2003; Torres et al., 2003), whereas *Anchicodium* has only been reported as fragmented remains of leaflike thalli. The morphotaxon *Calcipatera* erected from previously described *Anchicodium*, shares numerous morphological features with this genus, and was only justified on the basis of its cup-shaped form, identical to that of the Holocene genera of brown algae *Lobophora* and *Padina* or the green alga *Udotea cyathiformis* (Sawin and West, 2005).

Because "phylloid algae" usually occur in a poor stage of internal preservation, many reported examples in the literature have probably been erroneously identified, and some of them are probably synonymous (Wray, 1977; Vachard et al., 2012). Hence, usage of generic names has become "more territorial than realistic" (Baars and Torres, 1991). Furthermore, some elements of descriptions might be applied to several genera, and it seems that many of them represent in reality diagenetic stages rather than botanical taxa. While the differences between *Eugonophyllum* and *Anchicodium* are well established, the validity of *Ivanovia* is controversial. Although the common obliteration of the skeletal microstructure of *Ivanovia* apparently indicates basic differences in biochemical activity and presumably warrant the existence of the genus, most relatively well-preserved specimens of *Ivanovia* resemble *Anchicodium* (compare some *Anchicodium* illustrations of Johnson [1946], Endo [1951], Senowbari-Daryan and Rashidi [2010], and this study, with some *Ivanovia* illustrations of Toomey [1991b, pl. 32, figs. 2–5], Mamet [1994, pl. 1, fig. 8], Torres [1995, fig. 5], Torres [2003, fig. 4], Mamet and Villa [2004, figs. 12a, 12j–12n]). In these examples, both algae exhibit long secondary or tertiary cylindrical, marginal, dichotomously branched cortical siphons perpendicularly arranged to the surface of the thallus; furthermore, the siphons become thinner after branching and the dichotomization is evident in one-third the total thickness of the thallus (e.g., Torres, 1995). In addition, other shared morphological features are the presence of protuberances (nodes of Reid, 1986) and apparent thallus bifurcation (Johnson, 1946; Reid, 1986; Torres and Baars, 1992a). Therefore, the synonymy of these taxa seems to be unequivocal and it can be suggested that the minor morphological differences between both genera are related to different diagenetic transformations (Fig. 8). On the other hand, Vachard et al. (1989, 2001, 2012) suggested that the morphotaxon *Ivanovia* represented the latest diagenetic stage affecting some *Archaeolithophyllum* from the middle Permian of Tunisia. Nevertheless, based on cathodo-

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luminescence data reported here, it is proposed that most *Ivanovia* specimens represent a diagenetic stage of *Anchicodium* or *Eugonophyllum* instead of the red alga *Archaeolithophyllum*.

CONCLUSIONS

The cortical structure of the late Paleozoic siphonous alga *Anchicodium* can be characterized using cold cathodoluminescence microscopy. The cortical system of *Anchicodium* exhibits in thin section a bilateral symmetry and is composed of up to three (four?) orders of dichotomized cortical siphons that are usually swollen at the center; primary siphons are bulbous and are followed by elongate cylindrical siphons. These structures are preserved as non-luminescent molds that contrast sharply with the dull micrite infilling the intersiphonal spaces. The recognition of such detailed anatomic characteristics allows us to establish a solid taxonomic scheme for fossil "phylloid algae", and further corroborates the green affinity of anchicodiacean "phylloid algae."

Based on cathodoluminescence observations, morphologic features, biometric data, and an intensive review of the literature, it is suggested that *Ivanovia* represents a diagenetic stage of related anchicodiacean algae, such as *Anchicodium* or *Eugonophyllum*.

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