Rivista Italiana di Paleontologia e Stratigrafia
(*Research in Paleontology and Stratigraphy*)
vol. 124(1): 91-104. **March 2018**

JOHNSON & KASKA 1965 FOSSIL CORALLINE ALGAE FROM GUATEMALA (REVISION OF THE JESSE HARLAN JOHNSON COLLECTION, PART 4)

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To cite this article: Basso D. & Granier B. (2018) - Johnson & Kaska 1965 fossil coralline algae from Guatemala (revision of the Jesse Harlan Johnson Collection, Part 4). *Riv. It. Paleontol. Strat.*, 124(1): 91-104.

Keywords: Rhodophyta; Corallinophycidae; fossil red algae; taxonomy.

Abstract. The original collections of eight species described by Johnson & Kaska (1965) from several Guatemalan localities and ages, have been examined, re-documented and critically revised. The generic placement of *Aethesolithon guatemalaensum*, *Lithothamnium? primitiva, Lithothamnium diagramaticum*, *Lithothamnium guatemalense*, *Lithothamnium toltecensum,* and *Jania occidentalis* resulted incorrect under modern taxonomic criteria, and changed accordingly, while a lectotype specimen was selected for *Amphiroa guatemalense* and *Amphiroa kaskaella*. We place tentatively *L. diagramaticum* in the new combination *Sporolithon? diagramaticum* on the base of the occurrence of secondary pit-connections and vegetative and reproductive anatomy corresponding to some extant species of the genus *Sporolithon*. *L. toltecensum* was based on few Miocene sterile thalli occurring with some fertile specimens of the same age - the latter incorrectly identified under the name *L. florea brassica* (Millet) Lemoine - both corresponding to the extant, long-lasting species *Lithothamnion crispatum* Hauck. The occurrence of large cell fusions and trichocytes, the shape and structure of the uniporate conceptacles and the dimerous construction collectively indicate that *Aethesolithon guatemalaensum* belongs to the genus *Hydrolithon,* with the new combination *H. guatemalaensum* (Johnson & Kaska) Basso & Granier. The vegetative anatomy of *Jania occidentalis* corresponds to that of a co-occurring *Corallina,* already identified as *C. matansa* Johnson. *Lithothamnium? primitiva* is not a coralline alga, since it is conspecific with *Marinella lugeoni* Pfender. The vegetative features of the sterile "*Lithothamnium guatemalense*" exclude it from the genus *Lithothamnion*, but the absence of important diagnostic characters suggests leaving it *incertae sedis* under the original binomial.

Introduction

Calcareous fossil algae from the Americas are not richly documented. Actually, most papers published before 1970 are authored by a single paleophycologist, the late Professor J.H. Johnson (1892-1974) of the Colorado School of Mines at Boulder (Wray 1985). He was a prolific contributor who introduced a significant number of new taxa among the fossil green and red algae. However, his production sometimes did not stand up to modern scientific scrutiny. There is a need to re-examine all the material he studied in light of the recent developments in paleophycology, which is partly achieved with the revision of some red calcareaous algae from Guatemala presented hereafter.

The "Fossil Algae from Guatemala" contribution (Johnson & Kaska 1965) deals with material collected in Guatemala (and Belize) during a first oil and gas exploratory period starting from 1956. Johnson was providing consultancy information to several oil companies operating there and his junior coauthor was an employee of Guatcal, a subsidiary of the California Exploration Company. "In the course of the geological work in Guatemala a nearly complete section of sedimentary rocks ranging in age from Permian to Miocene were encountered in various parts of the country..(omissis)..the collection grew until it amounted to approximately 25,000 slides" (Johnson & Kaska 1965, p. 1). Out of this collection acquired by Guatcal, Johnson & Kaska

Received: February 20, 2017; accepted: November 18, 2017

selected ca. 900 thin sections containing algal specimens for their study. In 1963, exploration almost abruptly ceased. The oil companies flew away from Guatemala and the fate of the remaining material is unknown. Just for the record, the first discovery of oil in Guatemala took place in 1971 on the Tortugas salt dome, near Rubelsanto and the border with Chiapas (Mexico). Oil production mainly from carbonate reservoirs of the Cretaceous Coban Formation reached and passed 20,000 barrels per day over almost a decade (1998-2007) but it is decreasing since then. A majority of those thin sections studied by Johnson and Kaska (1965) are deposited at the U.S. National Museum - Smithsonian Institution in Washington, D.C., where BG got the opportunity to organize a temporary loan to re-examine them. The results are presented in a series of contributions, including the revision of some fossil Dasycladales (Part 1; Granier et al. 2013; Part 5; Granier et al. 2017b), a revision of the status of *Marinella lugeoni* and synonyms (Part 2; Granier & Dias-Brito 2016), and a catalogue (Part 3; Granier et al. 2017a).

Material and methods

New observations and measuremens were performed at the UBO laboratories in Brest, on the original collection of thin sections that were illustrated and described by Johnson & Kaska (1965), later conserved in the Division of Paleobotany of the United States National Museum (USNM) in Washington, D.C. (Johnson & Kaska 1965). The collection should include 83 catalogued thin sections, but only 78 were actually found in the box (5 have been lost). Thin sections have been observed and photographed at low magnification (15-35x) under a stereo microscope Olympus SZX7 equipped with an Olympus Digital camera E620, and at higher magnification (90-230x) under an optical microscope Leizt Diaplan, equipped with a camera Canon EOS 350D. The cell length (L) is measured along the direction of elongation of the cell filament, as representing the distance between two primary-pit conections. The cell diameter (D) is measured normal to L. Other abbreviations follow Hrabovský et al. (2015). Growth forms are in agreement with Woelkerling et al. (1993).

Results

The original collection of calcareous algae, obtained from the oil exploration in Guatemala, was composed of specimens belonging to a wide range of taxonomic groups, from Permian to Miocene ages. Out of them, 61 thin sections that Johnson & Kaska (1965) listed for containing red calcareous algae are present in the USNM repository. They include 16 thin sections that presently constitute the original collections of the eight new species of fossil Corallinophycidae described by Johnson & Kaska (1965): *Aethesolithon guatemalaensum*, *Lithothamnium? primitiva, Lithothamnium diagramaticum*, *Lithothamnium guatemalense*, *Lithothamnium toltecensum, Jania occidentalis*, *Amphiroa guatemalense*, and *Amphiroa kaskaella*. During the present revision, the newly performed measurements in general conformed those reported in the 1965 protologue. However, according to a modern taxonomic approach, the microanatomical morphologies observable in Johnson & Kaska (1965) original collections were not sufficient for a proper identification of the coralline taxa, while in other cases they provided evidence that the original taxonomic placement was inadequate, as detailed below.

Systematic palaeontology

Division **RHODOPHYTA** Wettstein, 1901
Class **Florideophyceae** Cronquist, 1960
Subclass **Corallinophycidae** Le Gall & Saunders, 2007
Order **Sporolithales** Le Gall & Saunders, 2009
Family Sporolithaceae Verheij, 1993
Subfamily Sporolithoideae Verheij, 1993
Genus *Sporolithon* Heydrich, 1897
Type species: *Sporolithon ptychoides* Heydrich, 1897

Sporolithon? diagramaticum (Johnson & Kaska) Basso & Granier comb. nov.

Fig. 1

Basionym: *Lithothamnium diagramaticum* Johnson & Kaska 1965 (Fossil algae from Guatemala. Professional contributions of the Colorado School of Mines 1, pp. 34-35, tab. 8, pl. 34, figs 3-4)

Examined material: USNM 42531= thin section 12673, indicated as holotype in the protologue; USNM 42534 = thin section 12673B, paratype).

Lectotypification: Both the specimens figured in the protologue (pl. 34, figs 3,4) could not be found in the above mentioned thin sections of Johnson & Kaska's original collection. However, thin section USNM 42534 contains several fragments of a coralline species that fully conforms both the protologue and the few details observable in the original illustrations. According to Art. 8.5 and 9.2 of the Melbourne Code (McNeill et al. 2012) we select here a lectotype in USNM 42534 (thin section 12673B; Figs 1 a-b, e).

Derivation of name: The epithet *diagramaticum* derives from some sections of this species recalling the simplified diagram of *Lithothamnion* structure as reported in the early literature.

Age and locality: Early Eocene. On road Cadenas-San Luis, 4 km before San Luis (Johnson & Kaska 1965)

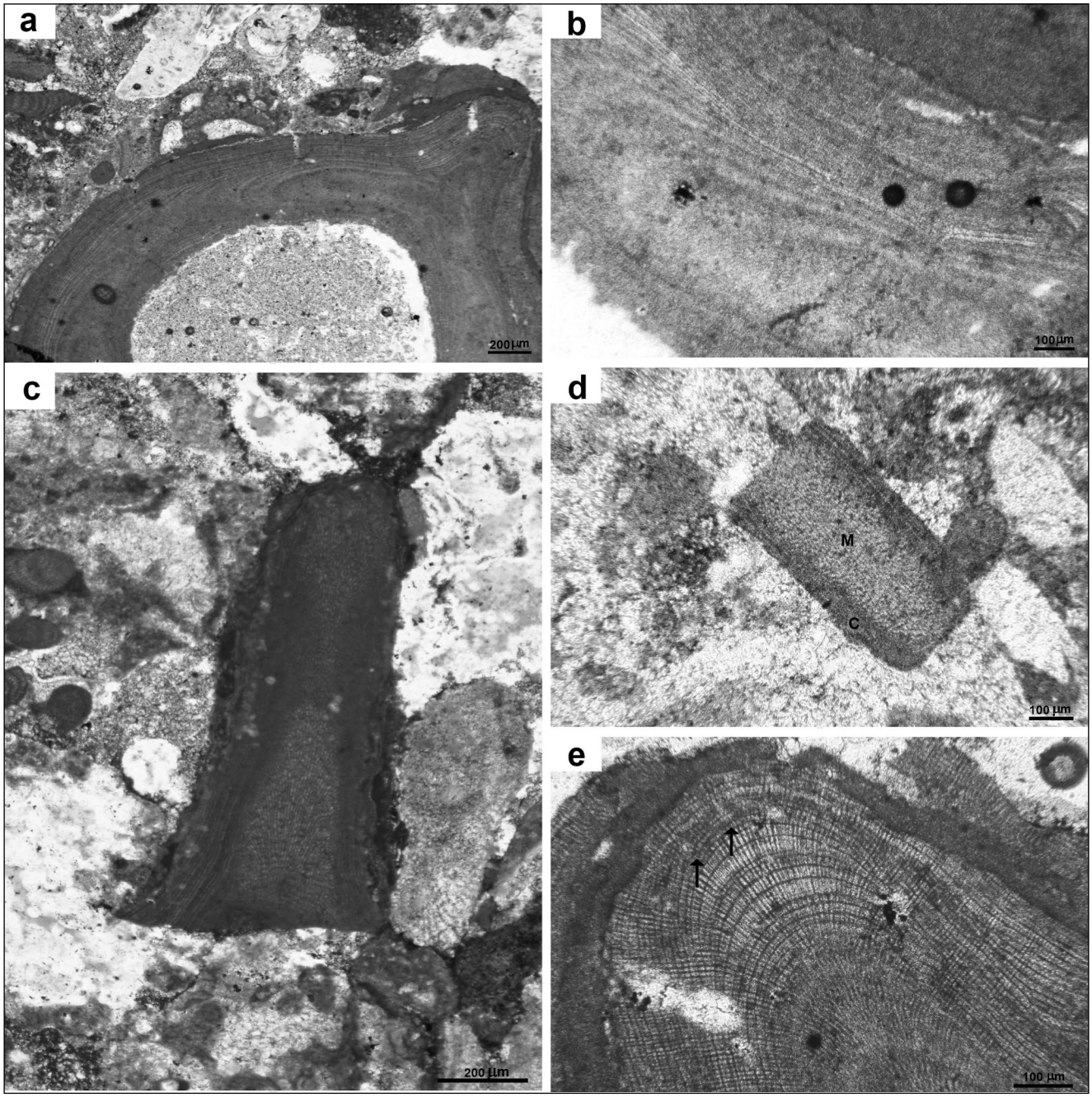

Fig. 1 - *Sporolithon? diagramaticum* (Johnson & Kaska) Basso & Granier comb. nov., USNM 42534 = thin section 12673B: a) lectotype specimen showing monomerous construction and a warty protuberance on the right; b) detail of a) to show the organization of cell filaments, producing the thallus elongation (evident in the "medulla") and thickening (growing toward the periphery to form the "cortex"); c) a fragmented protuberance; d) a fragmented protuberance showing cortex (C) and medulla (M). Note the different appearance of thallus organization due to orientation; e) magnification of the tip of a protuberance in a), showing two possible gametangial, uniporate conceptacles on the same layer (arrows below their base). Note the regular organization of the grid of cells due to uncommon cell fusions, typical of *Sporolithon*.

Growth form and vegetative anatomy. Thallus fruticose, with a monomerous construction (Figs 1a-d). Elongate protuberances up to 1 mm in maximum diameter (Fig. 1a, c-d). Protuberances with a central medulla ("central hypothallic tissue with a long plumose or water jet arrangement", Johnson & Kaska 1965: 34, fig. 3) about 300 µm thick, composed of rectangular cells (mostly L 15-31 x D 7-12 µm) apparently connected by secondary pit-connections (Fig. 1b, e). The medulla is surrounded by a variably developed perithallus (cortex), composed of cells L 7-15 x D 5-10 µm (Fig. 1b-d).

Reproductive structures. Rare and faint

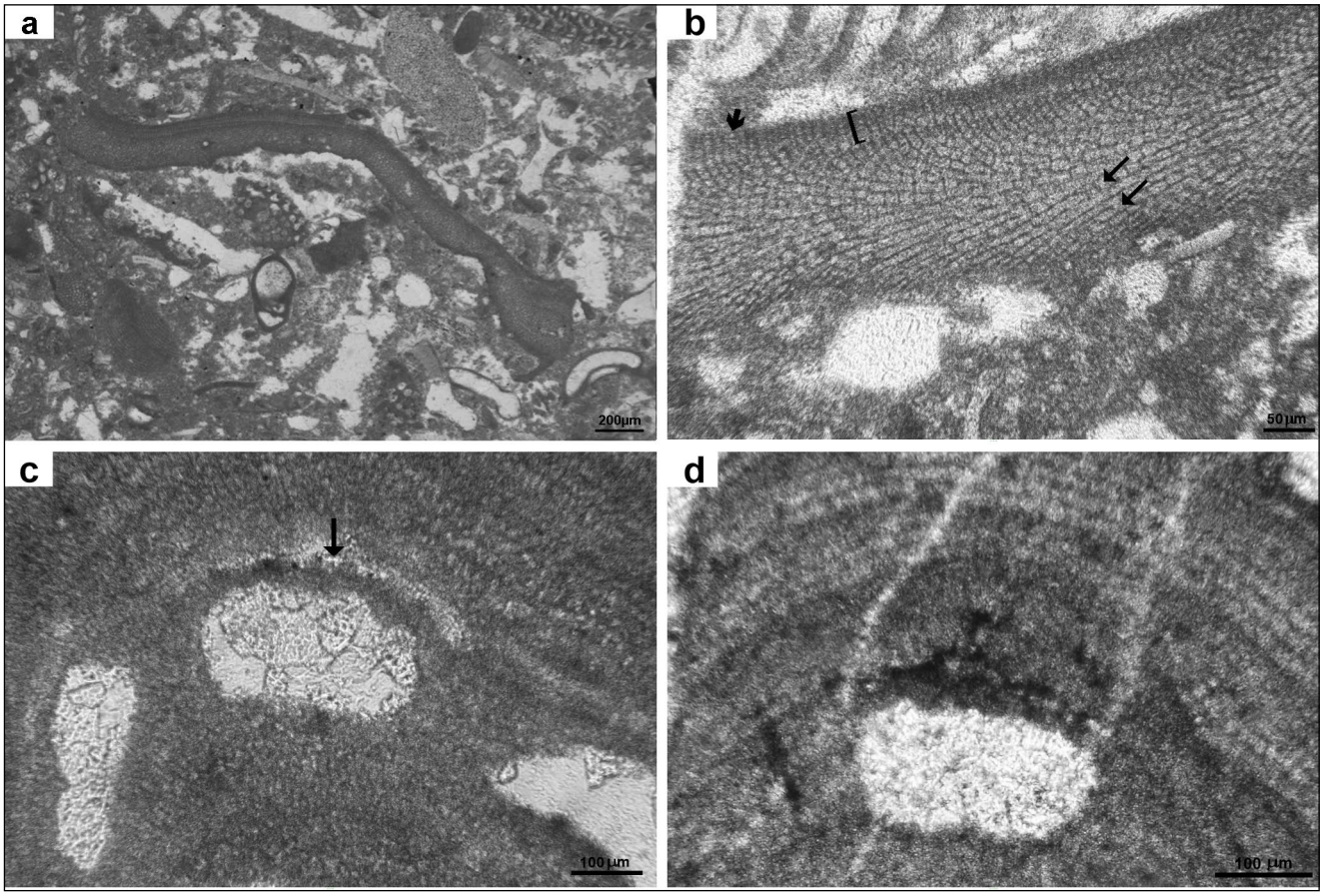

Fig. 2 - *Lithothamnion crispatum* Hauck: a) Holotype of *L. toltecensum* Johnson & Kaska 1965, USNM 42480= thin section 2205; b) Paratype of *L. toltecensum* Johnson & Kaska 1965: USNM 42481= thin section 2207. Note cell fusions (arrows), flattened epithallial cells (arrowhead), and thin perithallus (brace); c, d) Specimens originally identified as *L. florea-brassica* (Millet) Lemoine. Note the diagnostic shape of pore-canal cells (arrow); c USNM 42551= thin section 1309H; d USNM 42530= thin section 11260.

sub-circular to irregularly pear-shaped cavities about 100 µm in diameter opening toward the thallus surface, have uncertain nature (Fig. 1e). They are organised in a tier, just below the apex of a protuberance (Fig. 1a, e).

Remarks. This species has a very variable appearance depending on the section orientation, as Johnson & Kaska also probably noticed. Some fragments (Fig. 1c, d), as well as the lectotype, show good lateral alignment of cells in the cortex, but not in the medulla. Fragment in Fig. 1d, in particular, is also very similar to that illustrated by Johnson & Kaska (1965, plate 34, fig 3). All the described fragments collectively correspond to the original description in the protologue: "central hypothallic tissue with a long plumose or water jet arrangement". The occurrence of secondary pit-connections exclude the placement of this species in the genus *Lithothamnion*. The aspect of the vegetative thallus and the shape and size of the possible reproductive structures correspond to those observed in some species of extant *Sporolithon* (Bahia et al. 2015), therefore we place tentatively *Lithothamnium diagramaticum* Johnson & Kaska in the genus *Sporolithon* with the new combination *Sporolithon? diagramaticum*.

Order **Hapalidiales** W.A. Nelson, J.E. Sutherland, T.J. Farr & H.S. Yoon, 2015
Family Hapalidiaceae J.E. Gray, 1864
Subfamily Melobesioideae Bizzozero, 1885
Genus *Lithothamnion* Heydrich, 1897
Type species: *Lithothamnion muelleri* Lenormand ex Rosanoff, 1866

Lithothamnion crispatum Hauck, 1878

Fig. 2

1878 *Lithothamnion crispatum* Hauck, p. 289, pl. 3: figs 1-4
1965 *Lithothamnium toltecensum* Johnson & Kaska, p. 32, pl. 21, fig. 3; pl. 40, fig. 1
1965 *Lithothamnium florea brassica* - Johnson & Kaska, pp. 36-37, pl. 37, fig. 1; pl. 38, fig. 1
Other synonyms are listed in Basso et al. 2011.

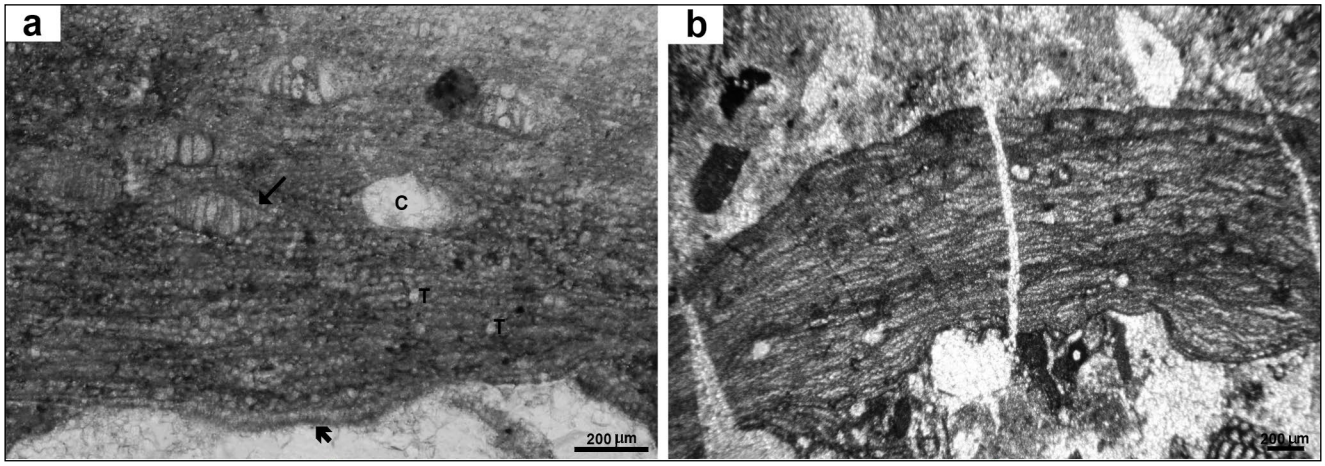

Fig. 3 - *Hydrolithon guatemalaensum* (Johnson & Kaska) Basso & Granier comb. nov.: a) holotype USNM 42477= thin section 1591, C = uniporate conceptacle chamber, T = single trichocytes, arrow = large irregular cells filling the empty conceptacles buried in the thallus, arrowhead = monomerous structure with monostromatic hypothallus; b) paratype USNM 42530A= thin section 11260.

Examined material: Holotype of *L. toltecensum* Johnson & Kaska 1965, pl. 21, fig. 3 (USNM 42480= thin section 2205; Fig. 2a); paratype of *L. toltecensum* Johnson & Kaska 1965, pl. 40, fig. 1 (USNM 42481= thin section 2207); *L. florea brassica,* Johnson & Kaska 1965, pl. 37, fig. 1, pl. 38, fig. 1 (USNM 42551= thin section 1309H and 42530= thin sections 11260).

Derivation of name: The epithet *toltecensum* is dedicated to the Toltec, the ancient Mesoamerican culture.

Age and locality: Miocene, possibly Early Miocene; 4 km SW of Livingston for *L. toltecensum* type material; Guatemalan localities 1309H and 11260, with no further detail, for *L. florea brassica* (Johnson & Kaska 1965).

Growth form and vegetative anatomy. *L. toltecensum* is a crustose thallus, with a monomerous construction and a dorsiventral organisation (Figs 2a, b). Hypothallus plumose, 160-255 µm thick, made of filaments of cells L 14-33 x D 11-18 µm, that give rise to a thin perithallus of cells L 9-15 x 11-15. Cells connected by fusions (Fig. 2b). Trichocytes not observed. Epithallial cells compressed (Fig. 2b).

Reproductive structures. The holotype of *Lithothamnium toltecensum* Johnson & Kaska is sterile (Fig. 2a)

Remarks. The material of *L. toltecensum* is very fragmentary and sterile, but fully corresponds to the vegetative anatomy of the living and fossil representatives of *L. crispatum* Hauck (Coletti et al. 2016). *L. crispatum* is easily recognized in the Miocene material from the distinctive shape of the pits, corresponding to the pore-canal opening through the multiporate conceptacle roof (Basso et al. 2011; Coletti et al. 2016, Fig. 2c-d). Since a fertile Miocene specimen of *L. crispatum* indeed occurs in the Johnson & Kaska collection (1965) under the name *L. florea brassica* (Millet) Lemoine, we confidently consider *L. toltecensum* as conspecific with *L. crispatum* Hauck.

Order **Corallinales** Silva & Johansen, 1986
Family Corallinaceae Lamouroux, 1812
Subfamily Hydrolithoideae A. Kato & M. Baba, 2011
Genus *Hydrolithon* (Foslie) Foslie 1909
Lectotype species: *Hydrolithon reinboldii* (Weber van Bosse & Foslie) Foslie

Hydrolithon guatemalaensum (Johnson & Kaska) Basso & Granier comb. nov.

Figs 3-4

Basionym*: Aethesolithon guatemalaensum* Johnson & Kaska (Fossil algae from Guatemala. Professional contributions of the Colorado School of Mines 1, pp. 49-50, tab. 13, pl. 45, figs 1-2).

Examined material: Holotype of *A. guatemalaensum* Johnson & Kaska 1965, pl. 45, fig. 2 (USNM 42477= thin section 1591; Fig. 3a); paratype of *A. guatemalaensum* Johnson & Kaska 1965, pl. 45, fig. 1 (USNM 42530A=thin section 11260; Fig. 3b).

Derivation of name: The name of the genus derives from *aethes* = unusual and *lithon* = stone; the specific epithet *guatemalaensum* means from Guatemala.

Age and locality: Early Miocene. The protologue reports four localities numbered 1222H, 1588, 1591, 11260. Out of these, only the 1222 is listed and marked in the map of Guatemala, for the area 4 km SW of Livingston (Johnson & Kaska 1965: 6 and attached map).

Growth form and vegetative anatomy. Thallus crustose, non-geniculate, protuberant, about 1200 µm thick. Thallus construction dimerous,

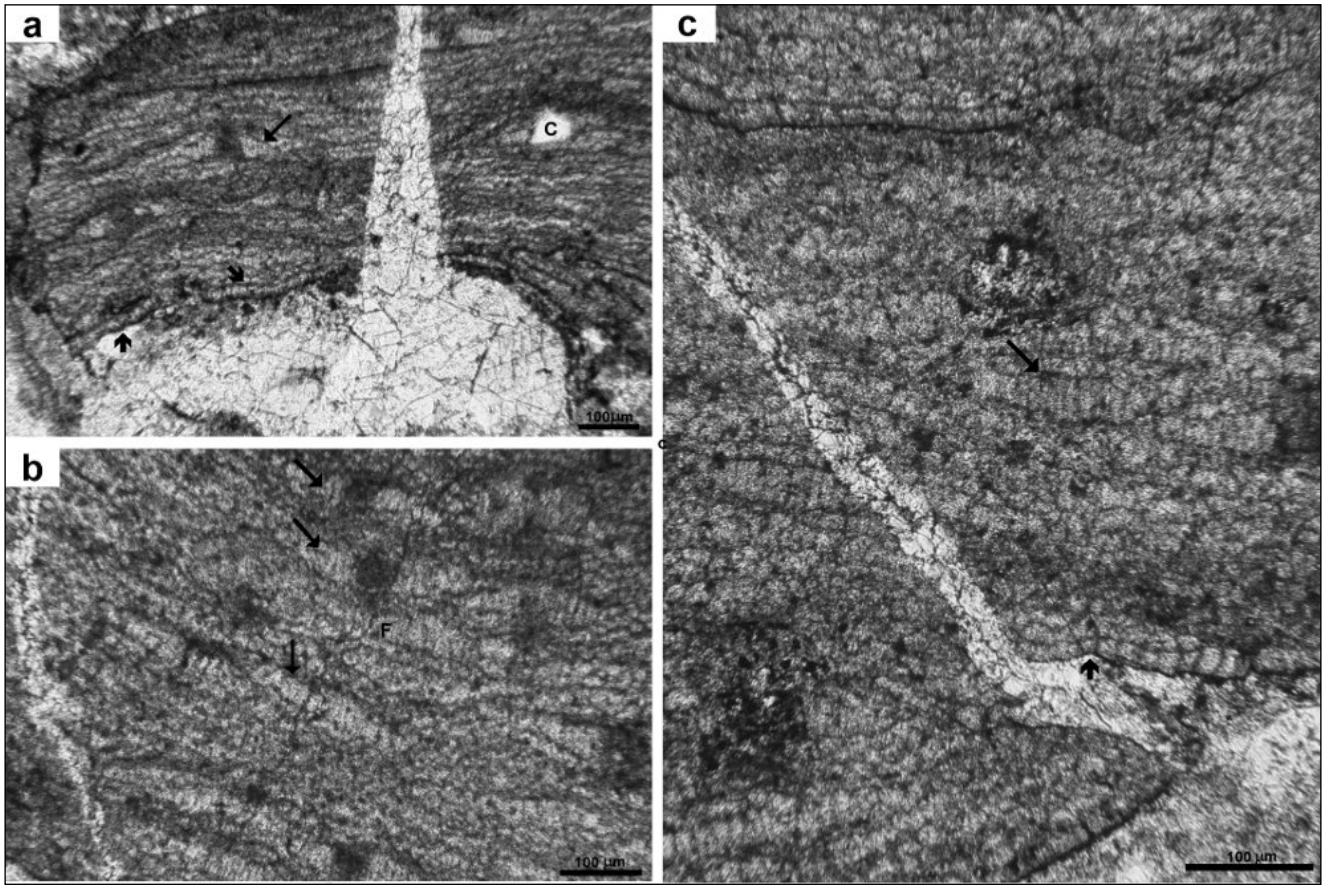

Fig. 4 - *Hydrolithon guatemalaensum* (Johnson & Kaska) Basso & Granier comb. nov.: paratype USNM 42530A: a) numerous conceptacle chambers (C) buried in the thallus (arrow). Note the dimerous construction and the monostromatic hypothallus (arrowhead); b-c) large adventitious cells filling the buried conceptacles (arrows), and monostromatic hypothallus (arrowhead).

thin hypothallus composed of one layer of irregularly rectangular cells, more frequently higher than broad, L 10-20 µm x D 15-40 µm (Figs 3a-b, 4a). The perithallus is composed of cells laterally connected by cell fusions. The perithallial cells are very variable in size and shape, because of the oblique cut, and thus the horizontal layering is ill-defined (Fig. 4a-b). Horizontal lenses of long and broad perithallial cells up to L 50 µm x D 30 µm alternate with cells as small as L 16 µm x D 10 µm (Fig. 4b, c). Large cells occur at the periphery of the numerous conceptacles (Figs 3a, 4a). Sparse single trichocytes are common.

Reproductive structures. Small uniporate conceptacles buried in the perithallus are common (Figs 3, 4a). They appear in the holotype section 42477 as ovoidal chambers about D 160-270 x H 80-110 µm, with a flat to concave floor developing on a layer of very small cells (Fig. 3a). The conceptacle chamber roof is not formed by cell filaments peripheral to the conceptacle and is compatible with a conceptacle development of Type 2 (Johansen 1981; Hrabovský et al. 2015). In section 42530 the conceptacles appear as lens-shaped areas 110-200 µm in diameter with an empty central area or more frequently filled by dark material (Figs 4a-b).

Remarks. The two thin sections are both obliquely cut, therefore the microanatomical features have an improper orientation and a deformed outline in the holotype. The distortion is even more severe in section 42530. This fossil coralline indeed possesses cells of different size and shape (cells at the periphery of conceptacles, adventitious cells inside conceptacles, and trichocytes), giving the thallus a distinctive chaotic appearance, but we could not ascertain the presence of the large polygonal cells, diagnostic for *Aethesolithon*. The occurrence of cell fusions and trichocytes, the shape and structure of the uniporate conceptacles and the dimerous construction collectively indicate that *Aethesolithon guatemalaensum* belongs to the genus *Hydrolithon* (Kato et al. 2011). Interestingly, published pictures of obliquely cut *Hydrolithon* fossil thalli show a striking similarity with the chaotic perithallus of *Aethesо-*

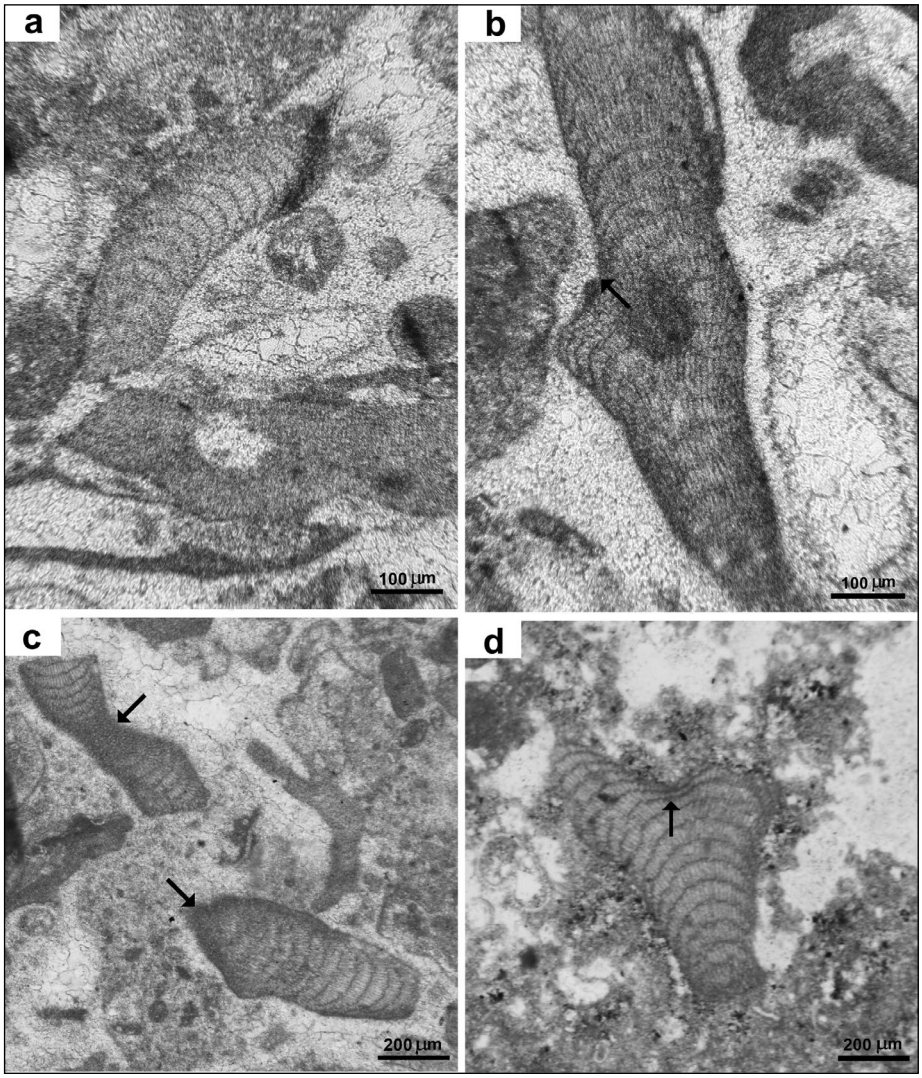

Fig. 5 - *Corallina matansa* Johnson, 1957: a) holotype specimen of *Jania occidentalis* Johnson & Kaska, 1965 in USNM 42523= thin section 8885; b, c) USNM 42519= thin section 8839; b - paratype specimen of *Jania occidentalis* Johnson & Kaska, 1965, note incipient bifurcation (arrow); c - other specimens with preserved genicula (arrows); d) USNM 42540= thin section 15971, specimen originally identified as *Corallina matansa* Johnson, note thallus bifurcation (arrow).

lithon guatemalaensum (e.g. Montaggioni 1979, pl. 2, fig. 3; Rösler et al. 2016, fig. 4). The disposition of the genus *Aethesolithon*, based on the type-species *A. problematicum* Johnson, 1964 would require further investigations on the relevant collection, and is outside the aim of this contribution.

Subfamily Corallinoideae (Areschoug) Foslie, 1908
Genus *Corallina* Linnaeus, 1758

Lectotype species: *Corallina officinalis* Linnaeus, 1758

Corallina matansa Johnson, 1957

Fig. 5

1957 *Corallina matansa* Johnson, pp. 238-239, pl. 44, figs 3-4
1965 *Jania occidentalis* Johnson & Kaska, pp. 56-57, pl. 26, figs 1-3.

Examined material: Holotype of *J. occidentalis* Johnson & Kaska, 1965, pl. 26, fig. 3 (USNM 42523= thin section 8885; Fig. 5a). Paratype of *J. occidentalis* Johnson & Kaska, 1965, pl. 26, fig. 2 (USNM 42519= thin section 8839; Fig. 5b). The specimens mentioned in the protologue and figured in Johnson & Kaska, 1965, pl. 26, fig. 1 and pl. 30, fig. 2 were not found. Other material: *Corallina matansa,* Johnson & Kaska, 1965, p. 54, pl. 21, fig. 1 (USNM 42540= thin section 15971).

Derivation of name: The specific epithet *matansa* derives from the Eocene Matansa limestone in Saipan, the type locality.

Age and locality: Paleocene-Eocene. The protologue of *J. occidentalis* reports the codes of five localities in Guatemala: 8839, 8840, 8885, 12673, 12673B (Johnson & Kaska 1965: 56). Out of these, 8839 and 8840 correspond to an area 3 km NW of San Luis; 12673 is on road Cadenas-San Luis, 4 km before San Luis; and the type locality 8885 is not indicated in the list of sample localities nor in the attached map (Johnson & Kaska 1965: 8). *Corallina matansa* is reported for the Lower Eocene of a series of locality codes (Johnson & Kaska 1965: 54) that are not indicated in the list of sample localities nor in the attached map (Johnson & Kaska, 1965: 8), with the exception of 15971, 15 km NE of Chinaja, and 12673, the same of *J. occidentalis* (on road Cadenas-San Luis, 4 km before San Luis).

Growth form and vegetative anatomy. Geniculate coralline. Fragments of isolated, scattered intergenicula, cylindrical to club-shaped. One complete geniculum, although not properly oriented,

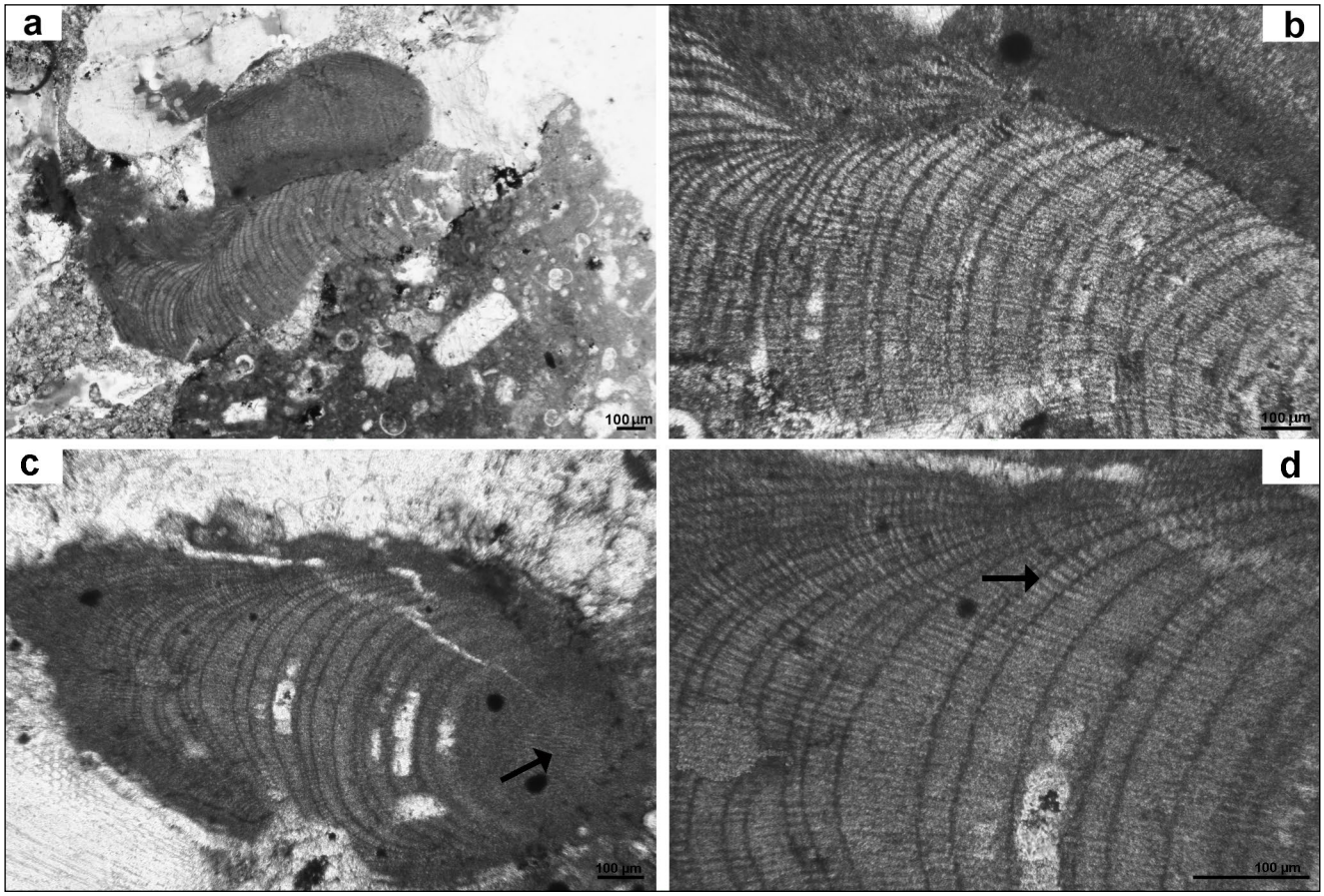

Fig. 6 - *Amphiroa guatemalense* Johnson & Kaska, 1965: a) lectotype specimen in USNM 42532=slide 12673A, note prostrate appearance of the thallus; b) magnification of **a** to show the row of short cells alternating with one-two rows of long cells; c) specimen in USNM 42534=slide 12673B, with a preserved geniculum (arrow); d) magnification of **c** to show the absence of fusion between cells of adjacent filaments (arrow). The occurrence of secondary pit-connections is testified by the regular shape of the longest cells of the cortex.

has been observed in a fragment occurring in thin section 42519 (Fig. 5c). The intergenicula show lateral branching (Fig. 5b, d), are about 800-1500 µm long and 180-330 µm broad, composed of 15-22 tiers of medullary cells of similar length (L 40-60 x D 9-17 µm; Fig. 5b).

Reproductive structures. Not observed.

Remarks. Within the modern concept of the genus *Jania*, intergenicula are unbranched or bearing two branches on broadened upper parts (Womersley 1996; Bressan & Babbini 2003). Therefore, the observed lateral branching of *J. occidentalis* Johnson & Kaska suggests that it does not belong to the genus *Jania*. Moreover, most of the extant species of *Jania* has few tiers of longer medullary cells in each intergeniculum, compared with *J. occidentalis*. The type material of *J. occidentalis* is quite poor for any certain assignment to any geniculate genus. However, on the basis of the few characters that can be observed, we can exclude some possible alternatives. In particular, the species cannot belong to *Arthrocardia*, because this genus is characterized by species showing mostly > 40 tiers of cells in the intergeniculum, and this character is not present in *J. occidentalis*. In the same paper, Johnson & Kaska (1965: 54, pl. 21, fig. 1) illustrated a fragment of *Corallina matansa* Johnson, 1957 showing identical structure and cell size, and report a wide and overlapping size range for *J. occidentalis* and *C. matansa* (tabs 17-18). Therefore, we consider *Jania occidentalis* as a heterotypic synonym of *C. matansa* Johnson, 1957, which has priority.

Subfamily Lithophylloideae Setchell, 1943

Genus *Amphiroa* Lamouroux, 1812

Lectotype species: *Amphiroa tribulus* (Ellis & Solander) Lamouroux, 1812

Amphiroa guatemalense Johnson & Kaska, 1965

Figs 6-7

1965 *Amphiroa guatemalense* Johnson & Kaska, pp. 52-53, pl. 24, figs 1-3.

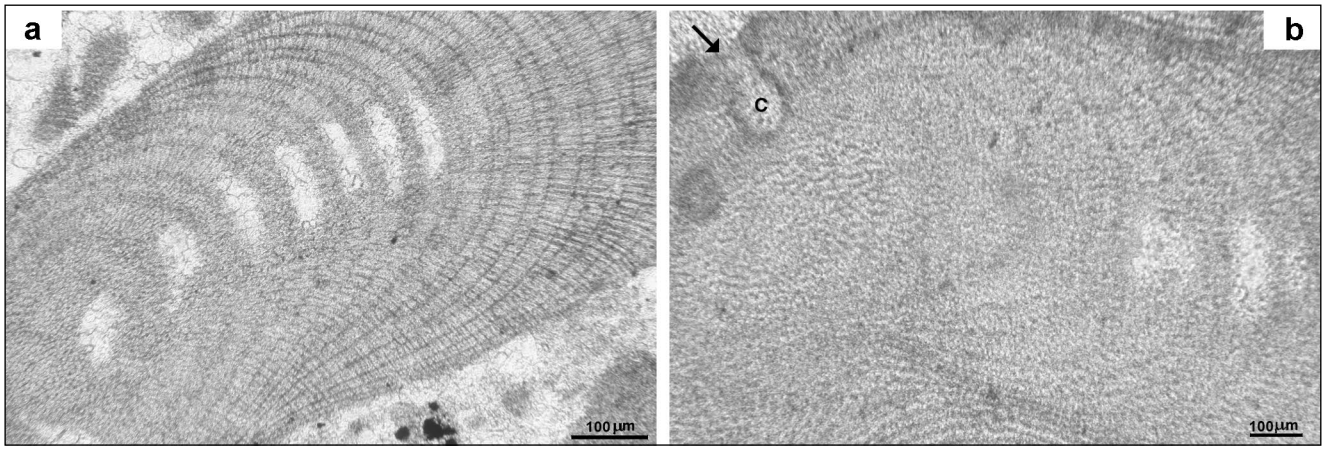

Fig. 7 - *Amphiroa guatemalense* Johnson & Kaska, 1965: a, b) two young apices in USNM 42517=thin section 8802; a - paratype specimen, detail of the regular cell arrangement, showing one row of short cells alternating with one row of long cells; b - a small uniporate conceptacle with ovoid chamber (C) and pore canal opening at the thallus surface (arrow).

Examined material: Syntype specimen of *A. guatemalense* Johnson & Kaska, 1965 pl. 24, fig. 1 (USNM 42532= thin section 12673A; Fig. 6a, b); the other syntype specimen in USNM 42534= thin section 12673B (Johnson & Kaska 1965, pl. 25, fig. 1) was not found. Paratypes of *A. guatemalense* Johnson & Kaska, 1965, pl. 24, figs 2-3 (USNM 42517= thin section 8802 and USNM 42538=slide 15134 respectively).

Lectotypification: The specimen of *A. guatemalense* Johnson & Kaska, 1965 illustrated in pl. 24, fig. 1 (USNM 42532= thin section 12673A) is here selected as lectotype (Fig. 6a-b).

Derivation of name: The specific epithet *guatemalense* means Guatemalan.

Age and locality: Late Paleocene and early Eocene. The lectotype locality is on road Cadenas-San Luis, 4 km before San Luis. No information is provided in the protologue about the other localities (8802 and 15134).

Growth form and vegetative anatomy. Geniculate coralline with intergenicula up to 1.8 mm long and 0.6 mm wide, possibly also decumbent (Fig. 6a). Structure of intergenicula with a medulla of one short–celled tier (L 13-28 x 7-10 µm) alternating with one or two long-celled tiers (commonly observed 30-40 tiers in each segment) (Fig. 6b). Cells connected by secondary pit-connections (Figs 6b, d). Intergenicular cortex absent to thick, made of several cells L 9-12 x D 5-10 µm (Fig. 6b).

Reproductive structures. On the same thin section USNM 42517, another specimen shows presumed uniporate conceptacles with a coarsely spherical chamber, about 100-110 µm in diameter, developed within the cortical cells (Fig. 7). The conceptacles are immersed, and open at the thallus surface with a pore up to 90 µm long and 30-50 µm broad (Fig. 7b).

Remarks. The conceptacle in Fig. 7 shows well-defined boundaries, unlike bioperforations, and the cells of the periphery of the conceptacle chamber are visible inside. The uniporate conceptacles are of unknown origin, but their shape and size are similar to the carposporangial conceptacles described for *A. rigida* in Baja California, Mexico (Riosmena-Rodriguez & Siqueiros-Beltrones 1996, fig. 9).

Amphiroa kaskaella Johnson & Kaska, 1965

Fig. 8

1965 *Amphiroa kaskaella* Johnson & Kaska, pp. 53-54, pl. 25, figs 2-3

Examined material: Syntypes of *A. kaskaella* Johnson & Kaska 1965 pl. 25, figs 2-3 (USNM 42498= thin section 4262). USNM 42516 (thin section 8798), mentioned and figured in the protologue (p.54, pl. 26, fig. 4), is lost.

Lectotypification: Johnson & Kaska selected USNM 42498= thin section 4262 as type material, indicating that it contains "two good specimens". According to Articles 8.2, 8.5 and 9.15 (Melbourne Code) the type of a name of a fossil species is the specimen (or one of the specimens) on which the validating illustrations are based. Since a specimen is a gathering of a single species made at one time, disregarding admixtures, and since thin section 4262 contains an admixture of species, the whole thin section cannot be considered as the type specimen. Out of the two fragments illustrated in the protologue, and still present in the type collection, the one figured in Johnson & Kaska (1965) pl. 25, fig. 2 is a complete, fertile intergeniculum. Therefore, the specimen illustrated in Johnson & Kaska (1965) p. 121, pl. 25, fig. 2, is here selected as lectotype of *Amphiroa kaskaella* Johnson & Kaska.

Derivation of name: The origin of the specific epithet *kaskaella* was not explained in the protologue. The species was possibly dedicated to a member of Harold V. Kaska's family.

Age and locality: Paleocene. Type locality is 4262, 6 km NE of San Luis.

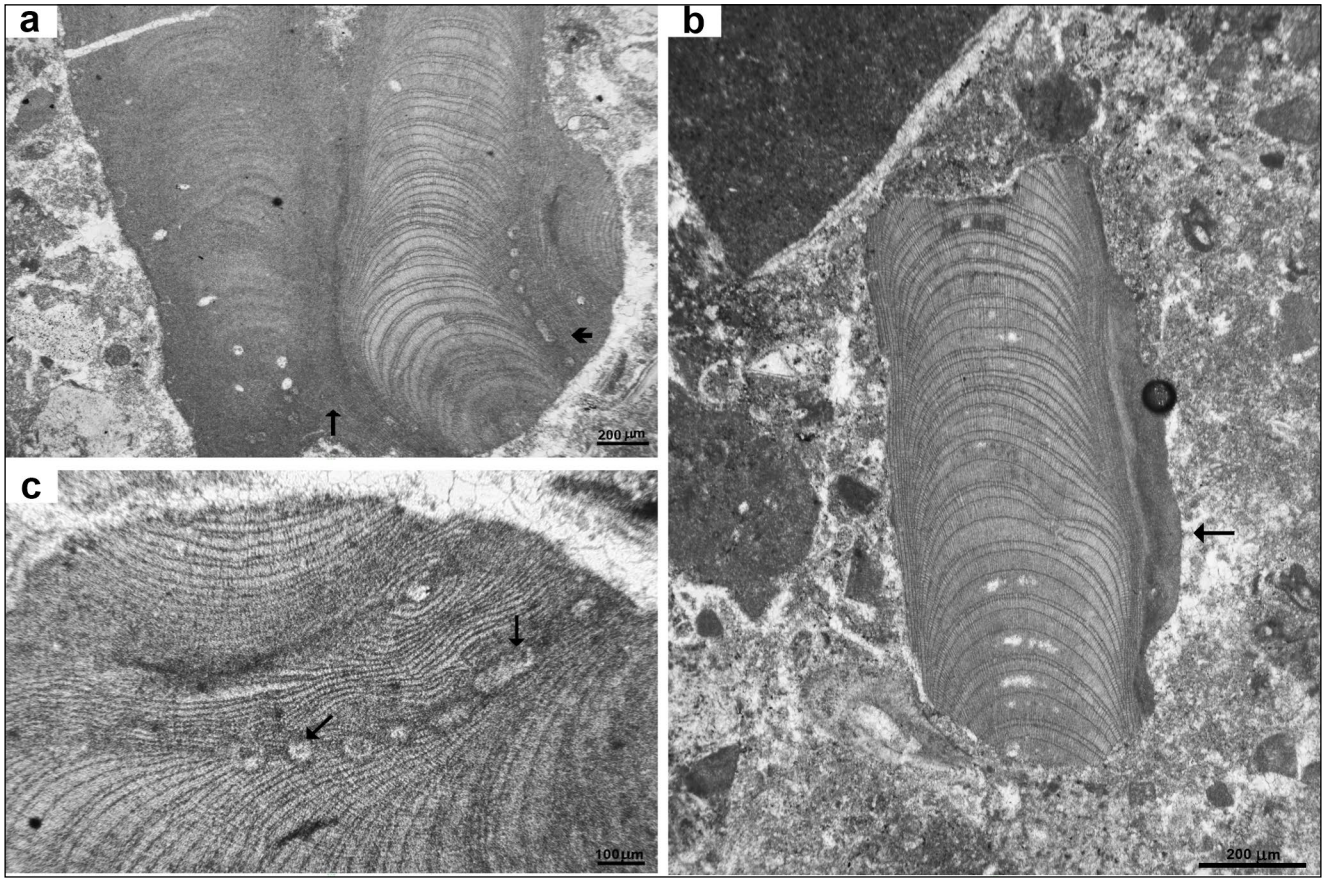

Fig. 8 - *Amphiroa kaskaella* Johnson & Kaska, 1965, USNM 42498= thin section 4262: a) two intergenicula partially fused at the base (arrow). The lectotype specimen is on the right. Note the small conceptacles aligned at the base of the cortical thickening (arrowhead), and the alternation of one tier of short cells with two-three tiers of long cells; b) paratype specimen, with characteristic cortical thickening (arrow); c) magnificatiton of the presumed conceptacles in the lectotype specimen (arrows).

Growth form and vegetative anatomy. Geniculate coralline. Intergenicula up to 3.5 mm long and 1.2-1.4 mm wide. Intergenicula composed of a medulla of one short–celled tier (L 18-46 x 6-13 µm) alternating with two or three long-celled tiers (L 53-102 x 6-13 µm, with about 50-60 tiers in each segment) (Figs 8a-b). Intergenicular cortex absent to thick, made of several cells L 10-20 x D 6-11 µm. Secondary pit-connections visible in largest cells. Cortex of adjacent intergenicula partially fused at their base.

Reproductive structures. Uniporate conceptacle chambers immersed in the intergenicular cortex are aligned in a row (Fig. 8a, c). The chambers are rounded to elliptical in section, D 80-170 µm x H 65-70 µm, with the largest chambers possibly resulting from the fusion of adjacent small ones. Pore not observed (Fig. 8c).

Remarks. Within the limits of this investigation based on few but important specimens, we have presently no elements to support a different generic attribution. Future investigation on newly collected, abundant and well preserved material will hopefully provide full details of this fossil coralline species.

Subclass **Corallinophycidae** Le Gall & Saunders, 2007
Incertae sedis

"Lithothamnium guatemalense" Johnson & Kaska, 1965

Fig. 9

1965 *Lithothamnium guatemalense* Johnson & Kaska, 1965, pp. 29-30, pl. 29, figs 1-3.

Examined material: Holotype of *L. guatemalense* Johnson & Kaska, 1965, pl. 29, fig. 2 (USNM 42518= thin section 8807). Paratypes of *L. guatemalense* Johnson & Kaska 1965, pl. 29, fig. 1 (same thin section USNM 42518) and pl. 29, fig. 3 (USNM 42517A= thin section 8802).

Age and locality: Early Eocene. Johnson & Kaska (1965) report four localities numbered 8796, 8802, 8807, 8798. Out of these, only the 8796 was listed and marked in the map, for the area 4.5 km NE of San Luis (Johnson & Kaska 1965: 8 and attached map).

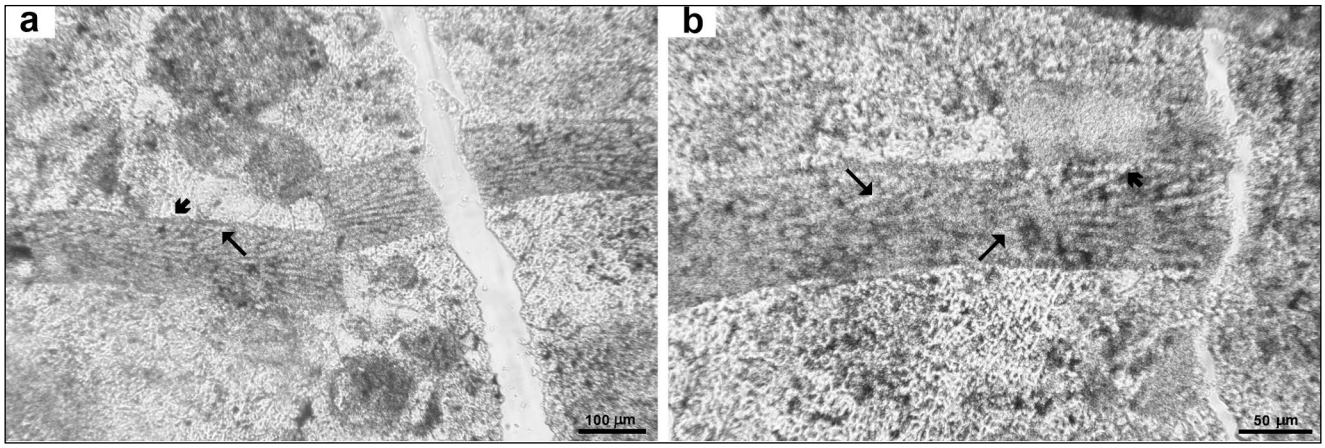

Fig. 9 - "*Lithothamnium guatemalense"* Johnson & Kaska, 1965, USNM 42518= thin section 8807: a) the holotype is a fragmented laminar thallus mostly composed of hypothallus. Note the ovate epithallial cells (arrowhead) and the large, probably meristematic, subepithallial cells (arrow); b) magnification of the holotype showing cell fusions (arrows) and large meristematic cells (arrowhead). Perithallial cells are not visible.

Growth form and vegetative anatomy. Thallus foliose, non protuberant, up to 110 µm thick. Thallus construction monomerous, with dorsiventral organisation. Hypothallus composing most of the total thickness (Fig. 9a-b), apparently plumose because of the oblique cut, made of long cells (mostly L 20-50 x D 7-10 µm) directed toward the thallus margin and diverging upward and downward to both thallus surfaces. Cells of adjacent filaments connected by cell fusions (Fig. 9b). Perithallus very reduced, made of few cells, or absent, terminating with an ovoidal epithallial cell (Fig. 9b). Meristem intercalary below epithallial cells, appearing as a clear line of long cells, connected by cell fusions.

Reproductive structures. Not observed, the thalli are sterile.

Remarks. The specimen with perithallus of 130 µm thick mentioned in the protologue could not be found in the original material of *"Lithothamnium guatemalense"*.

Although Johnson & Kaska (1965) assigned the above described sterile coralline fragments to the genus *Lithothamnion* (at that time spelled *Lithothamnium*), the occurrence of ovoidal epithallial cells and the aspect of the meristem collectively point to a different generic placement. In particular, some analogies can be found with extant species of *Neogoniolithon*, including the growth-form, and the aspect of the intercalary meristem (Mateo-Cid et al. 2014). Following the modern concept of the genus (Penrose 1996; Kato et al. 2013), *Neogoniolithon* may show a coaxial or non-coaxial hypothallus, although the coaxial arrangement of the hypothallus is considered diagnostic in the fossil (Braga et al. 1993; Hrabovský et al. 2015). Moreover, the oblique cut, also reported in Johnson & Kaska protologue (1965), may hide a coaxial hypothallus, as demonstrated in *Neogoniolithon contii* (Quaranta et al. 2007, pl. 1, fig. 7). Nevertheless, the fragmentary material and the lack of diagnostic characters prevent a taxonomic placement of this fossil coralline, therefore we leave the species *incertae sedis*, and thus we report its original name in quotation marks.

Order ? **Rhodogorgonales** Fredericq & Norris, 1995

Family Elianellaceae Granier in Granier & Dias-Brito, 2016

Genus *Marinella* Pfender, 1939

Type species: *Marinella lugeoni* Pfender, 1939

Fig. 10

Marinella lugeoni Pfender, 1939, nomen cons.

1939 *Marinella lugeoni* Pfender nomen cons., pp. 215-216, pl. II, figs 1-2.
1965 *Lithothamnium? primitiva* Johnson & Kaska, pp. 30-31, pl. 6, fig. 1.
1965 *Marinella lugeoni* - Johnson & Kaska, p. 74, pl. 6, fig. 2.
1965 *Girvanella minuta* - Johnson & Kaska, p. 96, pl. 30 fig. 1.
Other synonyms are listed in Granier & Dias-Brito (2016).

Examined material: Holotype of *Lithothamnium? primitiva* Johnson & Kaska, 1965, pl. 6, fig. 1 (thin section USNM 42547=slide 18587); *Marinella lugeoni*, Johnson & Kaska, 1965, pl. 6, fig. 2 (same thin section USNM 42547); *Girvanella minuta*, Johnson & Kaska, 1965, pl. 30, fig. 1 (same thin section USNM 42547).

Derivation of name: The epithet refers to the primitive "generalized structure" of this fossil red alga.

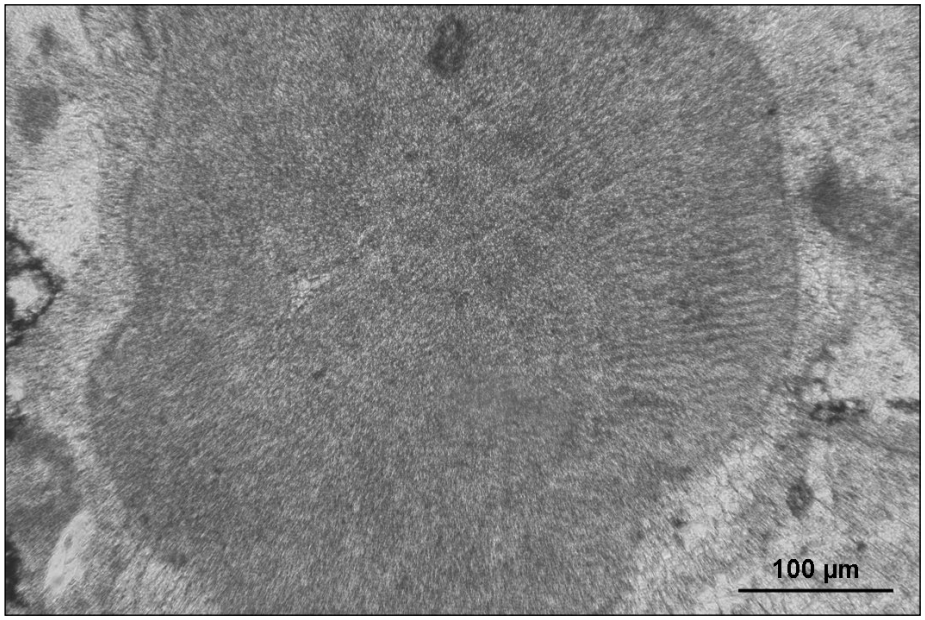

Fig. 10 - *Marinella lugeoni* Pfender, USNM 42547= thin section 18587: specimen originally selected as holotype of *Lithothamnium? primitiva* Johnson & Kaska, 1965. Note the lack of connection between adjacent filaments, the absence of cell layering, and the typical "pipe puff" appearance.

Age and locality: Late Jurassic to early Cretaceous. The Guatemalan locality 18587 was not listed in the table of the investigated areas, nor indicated in the attached map (Johnson & Kaska 1965: 5-10).

Growth form and vegetative anatomy. A cluster of fan-shaped thalli, radiating from a sub-central empty area, looking like a "pipe puff" (Pfender 1939). The thallus consists of juxtaposed filaments with aligned constrictions, but with non-obvious cell partitions. Filaments are 6 to 9 µm in diameter, composing a hairy fabric (Fig. 10).

Reproductive structures. Not observed.

Remarks. In agreement with the recent revision (Granier & Dias-Brito 2016), we confirm that Johnson & Kaska misidentified *Marinella lugeoni* with two different species, although the relevant specimens occurred in the same thin section. This was a consequence of the systematic approach of the sixties, when different orientations of the sectioned material were not fully appreciated, and, on the contrary, great importance was given to subtle variations in cell size.

Conclusions

The original collections of eight red algal species described by Johnson & Kaska (1965) from several Guatemalan localities and ages, have been examined, re-documented and critically revised. For most of the examined taxa, Johnson & Kaska (1965) clearly indicated and illustrated the type specimen on which the names of their new species were based, and these names have been accepted here (Melbourne Code Art. 9.1, McNeill et al. 2012). In three cases we had to select a lectotype. The type of fossil taxa is always a specimen (Melbourne Code Art. 8.5). Moreover, the holotype (or lectotype) of a name of a fossil-species is the specimen on which the validating illustrations are based and when a type specimen is indicated but not identified among the validating illustrations, a lectotype must be designated from among the specimens illustrated in the protologue (Art. 9.15). In agreement with the mentioned Articles, we selected a lectotype for the name of the two species that were based on syntypes, namely *Amphiroa guatemalense* and *A. kaskaella*. In the case of *Sporolithon? diagramaticum* nov. comb. the holotype was lost: we selected a lectotype from the original material in agreement with Johnson & Kaska protologue, according to Art. 9.2 (McNeill et al. 2012).

We had to modify the generic placement of the revised species that resulted incorrect under modern taxonomic criteria, that is to say in most cases, with the exception of *Amphiroa guatemalense* and *A. kaskaella*. This is not surprising, as new diagnostic criteria at high taxonomic ranks (i.e. type of cell anastomoses) were unknown at the time of Johnson & Kaska's contribution. Some fragmentary and sterile thalli, in some cases as unique specimen, would be presently considered insufficient for the erection of a new species, and "*Lithothamnium guatemalense*" is emblematic of an obsolete approach to

systematic Palaeontology. Further studies will hopefully be able to describe the missing, essential details of the vegetative and reproductive anatomy of this fossil alga.

Acknowledgements. DB is grateful to the UBO (Université de Bretagne Occidentale) for the invitation as visiting professor in Brest during February 2014. BG benefited of a Smithsonian Fellowship for the study of the Collection Jesse Harlan Johnson conserved in the Smithsonian Institution in Washington, D.C. The Department of Paleobiology of the Smithsonian National Museum of Natural History is warmly acknowledged for the loan of the Johnson & Kaska collection.

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