

## UPPER TRIASSIC CALCAREOUS ALGAE FROM THE PANTHALASSA OCEAN

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*Abstract.* Upper Triassic calcareous algae, abundant and well-diversified in Tethyan deposits, have rarely been described in rocks of Panthalassan origin. Over the past ten years, several studies were performed on Upper Triassic carbonate deposits of Panthalassan affinity in North America, Japan and Far East Russia, revealing unexpectedly rich and diversified assemblages. The samples were collected from nine localities situated on both sides of the Pacific Ocean. The identified algal assemblage consists of green and red algae, including fourteen dasycladaleans, rare bryopsidaleans, and several rhodophyceans. This paper describes the main algal taxa, including six new species: *Holosporella? rosanae* Bucur & Del Piero n. sp., *Holosporella magna* Bucur & Fucelli n. sp., *Griphoporella minuta* Bucur & Peybernes n. sp., *Patruliuspora pacifica* Bucur, Del Piero & Peyrotty n. sp., *Patruliuspora oregonica* Bucur & Rigaud n. sp. and *Collarecodium? nezpervae* Bucur & Rigaud n. sp. Rivulariacean-like cyanobacteria and thaumatoporellacean algae are also present. The whole Panthalassan algal assemblage comprises both unknown (?endemic) and common taxa of the Tethyan domain. To explain the cosmopolitan distribution of various Upper Triassic benthic organisms (scleractinian corals, calcified sponges, foraminifera), a close connection with the Tethys Ocean was hypothesized by different authors. During the Late Triassic, the Tethys was open to the east on the Western Panthalassa but not to the west, suggesting that Triassic calcareous algae were able to efficiently colonize environments that are estimated to be more than 10'000 km apart. An adventitious transport of calcareous algae and/or their spores is proposed to explain this long-range algal dispersal.

## INTRODUCTION

The Late Triassic represents a time-period with a relatively high abundance of calcareous algae (Flügel 1985, 1991; Barattolo 1991; Bucur 1999; Granier & Grgasović 2000; Nose et al. 2018). This seems related to the re-emergence and increasing development of reefal and associated environments from the Middle to the Upper Triassic (Flügel 2002).

Most known species of calcareous algae in the Upper Triassic (including dasycladaleans, udoteaceans, and “solenoporaceans”) have been identified in limestone rocks from Europe, mainly in the Alps and Carpathians, but also in central and southern Italy, Greece and the Dinarides. They were first described at the end of the nineteenth century (e.g., Gumbel 1872; Salomon 1895) and then widely studied in the twentieth century and over the last twenty years (Pia 1912, 1920; Bistricky 1964; Ott 1967, 1968; Flügel 1961, 1975; Senowbary-Daryan 1980; Di Stefano 1981; Barattolo et al. 1993, 2008;

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Parente & Climaco 1999; Senowbari-Daryan & Zamparelli 2005; Grgasovič 2007). Outside of Europe, Upper Triassic calcareous algae are known from Indonesia (Timor and Moluccas) (Vinassa de Regny 1915; Pia 1924), Eastern Tibet (Flügel & Mu 1982), Turkey (Senowbari-Daryan & Link 2005; Senowbari-Daryan et al. 2006), Iran (Senowbari-Daryan & Hamadani 2000), and Oman (Berneker 1996, 2005). In contrast with this relative abundance, only few manuscripts dealing with Triassic limestone deposits from North and South America mentioned or described calcareous algae. A report of phylloid-like algae from Lime Peak, Yukon was published by Reid (1986), and later the species was re-described by Torres (2003) as *Ivanovia triassica* Torres, 2003. In her PhD Thesis, Reid (1985), also illustrated calcareous algae from Lime Peak assigned to Cyanophyceae (*Garwoodia* or *Cayenxia*), “Solenoporaceae” (*Parachaetetes* sp., and *Parachaetetes triassicus* (sic) (Vinassa de Regny, 1915), and dasycladales (*Chypeina*). These *Chypeina* specimens were interpreted by Flügel et al. (1989) as bryozoans although their structure is typical of dasycladales with laterals arranged around a central cavity and sparitic calcification of the lateral’s wall. The dasycladalean *Diplopora oregonensis* Flügel, Senowbari-Daryan & Stanley, 1989 was described from the Excelsior Gulch Conglomerate (Hurwal Formation, Wallowa Mountains, Oregon) (Flügel et al. 1989). The Triassic reef limestone from Summit Point (Oregon), and Mina (Nevada) studied by Martindale et al. (2012, 2015) contain “solenoporacean” red algae (the authors mention seven species: *Solenopora* cf. *alcicornis* Ott, 1966, *S.* cf. *undata* Senowbari-Daryan & Link, 2005, *S.* cf. *endoi* Flügel, 1975, *S.* cf. *simionescui* Dragastan, 1969, *Parachaetetes* cf. *tauricus* Senowbari-Daryan & Link, 2005, *P.* cf. *cassianus* Flügel, 1961, *Tauristorea* cf. *discursa* Senowbari-Daryan, Link & Isintek, 2006) as well as unspecified Dasycladacean green algae.

For the past ten years, in the frame of the REEFCADE Project (to R.M.), several studies made on Upper Triassic deposits of North America, as well as far East Russia and Japan (Chablais et al. 2010a, b, c, 2011; Heerwagen & Martini 2018, 2020; Khalil et al. 2018; Onoue et al. 2009; Peybernes et al. 2015, 2016a, b; Peyrotty et al. 2020; Rigaud 2012; Rigaud et al. 2012, 2013a, b, 2015a, b, 2016; Sano et al. 2012; Senowbari-Daryan et al. 2010) revealed the existence of distinct calcareous algae in many of the studied sections, but none of

these publication discussed in detail the algal assemblages or gave a systematic description of the observed algae. The aim of our study is to describe and illustrate Panthalassic algae found by all the above-mentioned authors and examine their palaeobiogeographical distribution. The whole association is rich and consists of algae known already from the Tethys as well as of new species, possibly endemic to Panthalassa.

## GEOLOGICAL FRAMEWORK

The studied samples containing algae were collected from nine localities situated on the Circum-Pacific region: seven from North America, and two from Eastern Asia (Fig. 1 and Tab. 1).

### North America

#### Yukon, Oregon and Idaho

The material from the northwestern part of North America comes from three distinct Upper Triassic localities: (1) the Black Marble Quarry in Oregon, USA (lower-middle parts), (2) the Mission Creek Quarry in Idaho, USA (base of the Quarry), and (3) Lime Peak in Yukon, Canada (West side of the Peak) (Tab. 1). All these localities are part of allochthonous terranes that originated in the Panthalassan Ocean and accreted onto the American continental margin in the Mesozoic (Coney et al. 1980). Lime Peak is part of Stikinia (Bordet 2016a, 2016b) whereas the Black Marble Quarry and, with less certainty, the Mission Creek Quarry (both tectonically isolated blocks) are regarded as part of the Wallowa terrane (Hoover 1991; Stanley et al. 2008; Rigaud 2012), possible southern prolongation of Stikinia (Mortimer 1986; Oldow et al. 1989; Yancey & Stanley 1999). The samples used in this study come from bedded, fossiliferous shallow-water limestones of lagoonal facies that are notably rich in molluscs, foraminifers, ostracodes, echinoderms, and possibly associated with small coral and/or sponge thickets. The preservation of originally aragonitic components (e.g., gastropods, scleractinian corals, involutinid foraminifers, green algae) is quite atypical: although fully recrystallized, specimens are often pervasively impregnated by hydrocarbons (now metamorphosed into graphite) so that their original structure is still visible (see Rigaud

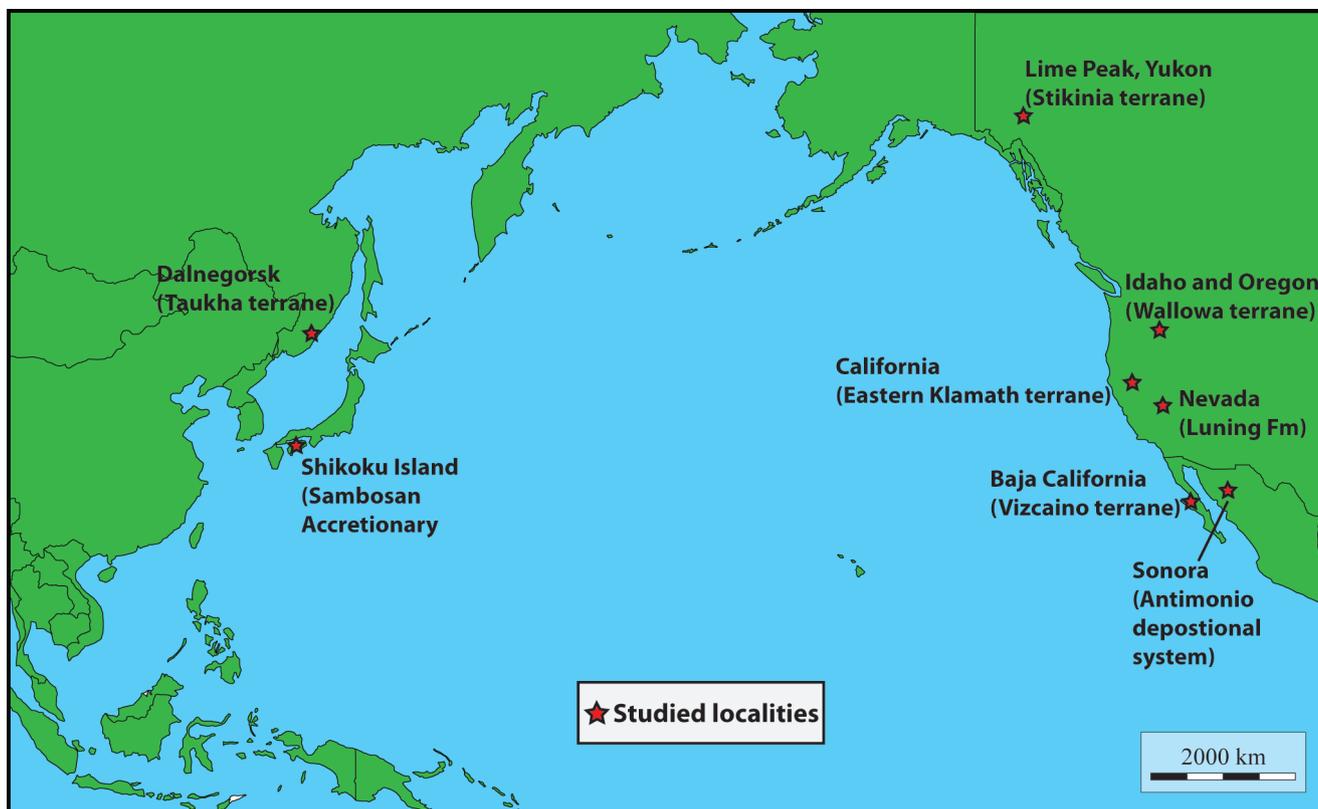


Fig. 1 - Location of the studied areas providing calcareous algae in the circum-Pacific domain (base map modified after d-map.com).

et al. 2015a for details). The Black Marble Quarry (BMQ) is well-known for its foraminiferal content, particularly rich in involutinids (Kristan-Tollmann & Tollmann 1983; Rigaud et al. 2010, 2012, 2013a-b, 2015a-b, 2016) and for its giant wallowaconchid bivalves (Stanley 1979; Yancey & Stanley 1999). It presents a foraminiferal assemblage typical of the Norian (see Koehn-Zaninetti 1969; Blau & Schmidt 1990), including the Norian marker *Aulosina oberhauseri* (Koehn-Zaninetti & Brönnimann 1968). The dark grey to black, restricted lagoon limestone beds in which algae have been discovered are found in the first fifty meters of the quarry, below the transition to a more open marine facies (Scotch Creek Member) of the Martin Bridge Formation (see Rigaud 2012 for details). Age-diagnostic fossils (ammonoids) found by Nolf (1966, p. 54) would position such levels within the Lower Norian, Kerri Zone.

The Mission Creek Quarry or Lapwai Quarry (LQ) is particularly famous for its fossil-rich silicified beds that contain a rich and diversified invertebrate lower upper Norian (Sevastian: age based on the ammonite *Gnomobalorites cordilleranus* Tozer, 1979, see Nützel & Erwin 2004) fauna, including bivalves (Newton, unpublished data), brachiopods

(Cooper 1942; Hoover 1991), corals (Squires 1956; Stanley 1979, 1986), and gastropods (Haas 1953; Nützel & Erwin 2001, 2004). Only few authors have investigated the quarry and most studies are based on the collection of J. S. Williams, J. Reed, and Norman D. Newell (see Squires 1956 for details). These silicified beds are found south of the quarry, near a zig-zagging gravel road, few meters below the transition to a Hurwal-type (red/brown argillite) lithology (see Rigaud 2012 for details). The here described algae/porostromate-rich wackestone-floatstone/rudstone levels were recovered from other, slightly older sedimentary strata (in a stratigraphic position estimated to be 55–65 meters below the silicified beds). The preservation of these older levels is uneven and marbled limestone rocks are majoritarily observed. However, in some levels, usually darker (dark gray) or yellowish, fossils such as corals (Stanley 1986) and foraminifers (Rigaud et al. 2015a) are preserved and may abound. The here reported algae come from yellowish levels found at the foot of the quarry.

Lime Peak is one of the Upper Triassic limestone bodies which form a northeast trending belt along the East side of Lake Laberge. These massive

to stratified carbonates, are part of the Hancock Member of the Aksala Formation (Bostock & Lees 1938; Hart 1997; Tozer 1958). The Lime Peak area is the place where Hancock Member carbonates are better exposed and preserved (Tab. 1). The samples were collected on the north-west side of the peak: there, a 20-m-thick outcrop is formed by ca 12 m massive limestones which are underlain by ca 8 m of medium to thick-bedded (20-40 cm) algae-bearing strata. Based on conodont assemblages the age of the deposits is late Norian (Lei et al. 2019).

### California

Hosselkus Limestone material comes from a series of outcrops located north of the city of Redding in Shasta County, USA (Tab. 1). These outcrops are part of the Eastern Klamath terrane, a sequence of Palaeozoic and Mesozoic island arc deposits that were built upon oceanic crust (Irwin 1977) and accreted onto the American continental margin during the Mesozoic (Coney et al. 1980). It is worth to notice that the best-preserved limestone units crop out in the Shasta Lake area and not at the type locality (Taylorsville, Plumas County). In the Shasta area, the lower part of the Hosselkus Limestone shows a great variety of open basin facies (e.g., deep environment with radiolarians, condensed levels of halobid-like bivalves, crinoids packstone, calciturbidites with ammonoids). After a progressive transition toward shallower basinal facies, the whole succession is covered by several meters of breccia composed of centimetric to decimetric limestone clasts within a radiolarian-rich fine matrix. The limestone clasts derive from an Upper Triassic carbonate platform that no longer exists. Facies mostly reflect platform top to foreslope environments, with mud-dominated and grain-dominated elements associated with shallow-water organisms; the last are observed in millimetric to decametric reworked elements, and notably comprise the here-described algae and coral-rich facies. Conodonts recovered in all three types of facies indicate a late Carnian age.

### Nevada

The Luning Formation crops out in a wide area of Western Nevada and is part of the Luning Allochthon, a series of nappes composed of Triassic and Jurassic sedimentary rocks and Permian to Triassic volcanic rocks (Oldow 1981). The thickest succession of the Luning Formation is loca-

ted north of the Pilot Mountain (Tab. 1) where it shows a total thickness exceeding 2000 m (Sandy & Stanley 1993), divided in three members: Lower, Middle and Upper. The Lower Member is an alternation of shales and coral and sponge biostromes, while the middle member is fully terrigenous, showing alternation of shales, sandstones and conglomerates. The Upper (algae-bearing) Member shows a regular alternation of lagoonal-peritidal facies, with abundant bivalves, gastropods and megalodonts, alternated with decimeter-thick coral horizons and nodular marls. Muller & Ferguson (1936) had already evidenced the abundance of fossils in the Upper Member of the Luning Formation. Preliminary conodont results indicate a middle Norian age for this portion of the formation.

The presence of a thick terrigenous member, around 600 m (Sandy & Stanley 1993) plus the occurrence of marls with variable percentage of clay minerals, might suggest that the Luning Formation was probably deposited close to the American continental margin and not in the middle of Panthalassa.

### Mexico

Outcrops of Upper Triassic carbonates of shallow-marine facies are rare in Mexico. They are limited to two areas in Sonora and in Baja California Sur (Tab. 1).

In Sonora, the Antimonio depositional system (ADS) encompasses the El Antimonio Group, generally considered as part of the northwest-southeast trending tectonostratigraphic Antimonio terrane (González-León et al. 2009 and references therein). The shallow-marine strata that yielded the studied algae belong to the Upper Triassic Rio Asunción Formation. Outcrops in northern Sonora are located near the cities of Caborca and Hermosillo (Herwagen & Martini 2018). The main localities are Sierra del Álamo and Barra los Tanques (Tab. 1). At Sierra del Álamo, the Rio Asunción Formation (upper part of the El Antimonio group succession, ca. 109 m), consists of shallow-marine limestone, siltstones to fine grained sandstones, some intercalated volcanics, and shales. A distinct carbonate interval, dated by ammonoid and bivalve biostratigraphy as Norian in age (Damborenea & González-León 1997 and references therein; González-León 1997), contains sponge-coral biostromes with algae. At Barra los Tanques, a precise biostratigraphic fra-

Locality	Geological context	GPS Points	Lithology / Facies	Age	Samples
<b>ASIA</b>	Taukha terrane	44°23'47.86"N 135°46'45.04"E	Lagoonal limestone (Involutinid-Megalodontid Wackestone to Rudstone)	lower-middle Norian	GP-152; GP-153; GP-157; GP-206C; GP-206C-2; GP-206C-3; GP-206C-4
			Reefal limestone (sponge-algae Boundstone and Grainstone)		CP-259A; CP-259B; CP-261 (Sambosan Type locality)
<b>ASIA</b>	Sambosan Accretionary Complex (SAC)	33°34'45.2"N 133°42'7.33"E	Lagoonal limestone (Involutinid-algae Wackestone)	Upper Triassic	CP-94A; CP-94B (Wajiki locality)
			Open lagoon (peloid-bioclust Packstone to Grainstone)		JC231a (Takayama locality)
<b>Yukon</b> (Canada)	Stikinia terrane	61° 3' 57.35"N 134° 54' 57.95"W	Lagoonal limestone Wackestone to rudstone	late Norian	WH-227a; WH-227b; WH-232a; WH-232b; WH-233a; WH-233b; WH-234; WH-235a; WH-235b; WH-236a; WH-259; WH-260; WH-261 (Lime Peak)
<b>Idaho</b> (USA)	? Wallowa terrane	46° 17' 34.37"N 116° 42' 02.69"W	Lagoonal limestone (Dasydiadacean-Porostromate Wackestone-Packstone and Floatstone-Rudstone)	Norian (?Sevastian)	LQ-5; LQ-6; LQ-23; LQ-24; LQ-27; LQ-39A; LQ-39B; LQ-39C; LQ-39D; LQ-39F; LQ-39G; LQ-39I (Mission Creek Quarry)
<b>Oregon</b> (USA)	Wallowa terrane	45° 22' 23.27"N 117° 21' 16.40"W	Organic-rich limestone, restricted lagoonal facies (Involutinid-rich Mudstone to Packstone)	lower Norian (Kerr Zone)	BMQ-33R4; BMQ-36-9; BMQ-48; BMQ-48R2; MQ-7D; MQ-16; MQ-16D; MQ-18R-2; MQ-19-1; MQ-33R3; MQ-34b-17; MQ-34b; MQ-34-9; MQ-36; MQ-38R; MQ-41; MQ-41-10; MQ-41D; MQ-48-2; MQ-48-3; MQ-48-4; MQ-48D; MQ-48R-2; MQ-49R; MQ-77; MQAC-17b; MQVIC-41 (Black Marble Quarry)
<b>California</b> (USA)	Eastern Klamath terrane	Reef facies locality: 40°46'45.24"N 122° 0'9.62"W	Debris dominated foreslope Shallow organisms reworked in open basin environment as centimetric breccia; matrix indicate a deep environment with radiolarians	upper Carnian (based on Conodonts)	FA48b; FA-50-2A; FA-129; FA-210; FA-217 (Shasta County)
<b>Baja California Sur</b> (Mexico)	Vizcaíno terrane	San Hipólito locality: 26°59'36.04"N 113°59'12.19"W	Patch reef margin to back reef (echinoid-lithoclast-peloid Grainstone to Rudstone and Wackestone)	late Norian	EH-509 (San Hipólito Formation)
<b>Nevada</b> (USA)	Attached, or really close to American Craton	Holosporella magna bed: 38°29'12.96"N 118°13'1.89"W	Lagoonal to tidal environment (mostly Wackestone and Packstone)	middle Norian (based on Conodonts)	FA-81a; FA-81c (north-east flank of Garfield Hills)
<b>Sonora</b> (Mexico)	Antimonio depositional system (ADS)	Barra los Tanques locality: 30°29'41.91"N 112°50'48.24"W	Sand sheets and sand shoals (siliciclastic ostracod-gastropod-lithoclast Grainstone to Rudstone)		EH-118A (Barra los Tanques)
			Sand sheets and sand shoals, agitated water (lithoclastic echinoid-gastropod-sponge-peloid Grainstone to Rudstone)	late Norian	EH-212a; EH-216a; EH-216b (Sierra del Álamo - SA)
		Sierra del Álamo (EA) locality: 30°41' 40"N 112°33' 9.30"W	Sand sheets and sand shoals, agitated water (siliciclastic lithoclastic ostracod/rich Wackestone to Grainstone)		EH-306a; EH-311a; EH-319A (Sierra del Álamo - EA)
		Sierra del Álamo (EA) locality: 30°41' 40"N 112°35'7.00"W			

Repository: All the samples and thin sections are stored in the Museum d'Histoire Naturelle de Genève, Switzerland (MHNG-GEP1-2020-0001 to MHNG GEP1-2020-0082).

Tab. 1 - Coordinates of the investigated localities, together with their geological context, lithologies and facies content, ages, and collected samples.

mework has not been established yet. The shortly exposed section (ca 29 m) is predominantly composed of limestones with terrigenous material including sponge-coral biostromes and patch-reefs with algae, comparable to those at Sierra del Álamo. Intercalated in the succession are lumachelle beds,

and carbonate-cemented siltstones to fine sandstones (Heerwagen & Martini 2018).

In Baja California Sur, the studied algae come from the San Hipólito Formation on the Vizcaíno terrane. The Vizcaíno terrane is a northwest-southeast trending tectonostratigraphic unit, which

constitutes the entire Vizcaíno Peninsula. However, its classification as a terrane is somewhat unclear (Heerwagen & Martini 2020 and references therein). The San Hipólito Formation (ca 2400 m thick marine succession) is named after the nearby village and represents an arc-ophiolite assemblage (Busby 2004; Morán Zenteno et al. 1994) with basinal to slope facies spanning from the Norian to the Pliensbachian (Orchard et al. 2007). The formation comprises a limestone breccia (ca 105 to 260 m thick), which includes re-worked upper Norian shallow-water limestones. According to Heerwagen & Martini (2020), the breccia itself consists of volcanoclastic sandstones containing limestone clasts in a poorly sorted, massive to weakly bedded, fine to medium-coarse litharenite matrix. The size of the clasts ranges from several decimeters up to few meters in diameter. Lithologically, the limestone clasts are composed of light gray to gray, sometimes with a pinkish hue, micritic limestone. The macrofossil assemblage is dominated by brownish-weathered coral colonies; subordinate are fragments of thalamid sponges and fossil debris including echinoids, gastropods, bivalves, brachiopods, ostracodes, and foraminifers. Only in some samples red algae and dasycladalean algae, serpulids, bryozoans, coprolites, and fragments of calcimicrobe colonies were found. Less commonly found were blocks of micritic limestone that contain megalodontid bivalves.

## Asia

On the Asian part of the Circum-Pacific region, the algae described in this paper have been found in Far East Russia in the Taukha terrane and in Japan in the Sambosan Accretionary Complex (SAC) (Tab. 1).

### Far East Russia

The Russian outcrops are located in the southern part of the Sikhote-Alin orogenic belt (Primorsky Krai), defined as an upper Tithonian-Hauterivian accretionary prism (Kemkin et al. 1997). The Tetyukha suite (Kojima 1989; Khanchuk et al. 2016), situated in the northern part of the Taukha terrane (Dalnegorsk area) is made of Norian atoll-type carbonates from the Panthalassa ocean (Peyrotty et al. 2020). The sedimentology and biostratigraphy of the limestone have been studied and described in detail by Peyrotty et al. (2020). The algae presented in this paper have been observed in involu-

tinids-megalodontids wackestone to rudstone facies interpreted as lagoonal limestones. Algae are associated with megalodontids, involutinids (dominated by *Parvalamella friedli* (Kristan-Tollmann, 1962)), gastropods and undetermined calcimicrobes. The age of this facies is defined as early-middle Norian on the basis of foraminifers. According to Kojima (1989), the Taukha terrane represents the northern extension of the SAC but the here-described algae differ, possibly suggesting a different origin or depositional environment of the Upper Triassic shallow-water limestone from Japan and Russia.

## Japan

The material from South West Japan comes from three localities of the Sambosan Accretionary Complex (SAC) in western, central and eastern Shikoku Island. The SAC is an Upper Jurassic-Lower Cretaceous subduction-generated accretionary complex which contains Upper Triassic deep and shallow-water carbonates units (Kanmera 1969; Matsuo-ka & Yao 1990; Onoue & Sano 2007; Peybernes et al. 2016b). Samples CP-259 and CP-261 have been found in limestone breccias with volcanoclastic matrix that crop out at the Sambosan type locality, near Kochi. This locality is described in detail in Peybernes et al. (2015, 2016a, 2016b; Peybernes et al. under review). Microfacies and associated fauna (e.g., hypercalcified sponges) point to reefal depositional environments. Conversely, sample CP-94 is a lagoonal involutinid wackestone that comes from the Wajiki area and has been retrieved from a limestone breccia with siliceous mudstone matrix (Peybernes et al. 2016b). Limestone clasts and blocks from these two localities range from the Ladinian?-Carnian to the Rhaetian (Peybernes et al. 2016b). Sample JC231A is a peloid-bioclast grainstone to packstone, found in Upper Triassic limestones outcropping on the seashore in Takayama area. Limestone units from this locality were studied by Chablais (2010) and Peybernes et al. (2016b).

## MATERIAL AND METHODS

We selected 82 thin sections containing calcareous algae coming from these nine localities in North America and Asia (Tab. 1). The thin sections were studied under a Carl Zeiss Axioscop petrographic microscope. Microphotographs of algae were made using a Canon Power Shot A640 Digital Camera. All thin sections are stored in the Museum d'Histoire Naturelle de Genève (Switzerland) under the numbers MHNG-GEPI-2020-0001 to MHNG GEPI-2020-0082.

### Calcareous algae assemblage

The studied thin sections are characterized by an algal assemblage consisting of chlorophyceans and rhodophyceans, two major groups of the so called "calcareous algae" or algae characterized by calcium carbonate skeletons which favored their preservation as fossils. The assemblage occurs on both sides of the Pacific Ocean (North America, Japan and Far East Russia), and consists of fourteen dasycladaleans (Pl. 1-12) (*Pseudodiplopora borzai* (Bystrycki, 1978), *Pseudodiplopora?* sp., ?*Thyrsoporella multipora* (Bilgütay, 1968), *Holosporella?* *rossanae* Bucur & Del Piero n. sp., *Holosporella magna* Bucur & Fucelli n. sp., *Griphoporella curvata* (Gümbel, 1872), *Griphoporella minuta* Bucur & Peybernes n. sp., *Physoporella jomdaensis* Flügel & Mu, 1982, *Salpingoporella* sp., *Gyroporella* div. sp., *Macroporella* sp., *Chypeina* cf. *besici* Pantič, 1965, *Patrulinspora pacifica* Bucur, Del Piero & Peyrotty n. sp. and *Patrulinspora oregonica* Bucur & Rigaud n. sp.), rare bryopsidaleans (one possible udoteacean, *Collarecodium?* *nezpercae* Bucur & Rigaud n. sp., Pl. 4K-M; Pl. 13, and rare gymnocodiaceans *Permolcalculus* sp., Pl. 6I (Pm); Fig. 5), and several rhodophyceans (Pl. 14-15) (*Noritbannium madoniensis* Senowbari-Daryan, Keupp, Abate & Vartis-Matarangas, 2002, "*Parachaetetes*" sp., and "*Solenopora*" sp.). Some microfossils with algal affinity were also observed within the limestone of the Black Marble Quarry (Oregon), but in a state of preservation which does not allow a taxonomic identification. They belong to rivulariacean-like cyanobacteria (Pl. 16A-D), to udoteaceans (Pl. 16E-F), dasycladaleans (Pl. 16G-K) and to a problematic microfossil with possible algal affinity (Pl. 16L-I). Thamatoporellacean fragments have also been identified (Pl. 16L-M).

### PALAEONTOLOGICAL DESCRIPTION

Phylum **CHLOROPHYTA** Pascher, 1914  
 Class **ULVOPHYCEAE** Stewart & Mattox, 1978  
 Order **Daycladales** Parscher, 1931  
 Family **Diploporaceae** Pia, 1920  
 Genus *Pseudodiplopora* Bucur & Enos, 2001

#### *Pseudodiplopora borzai* (Bystrycki, 1978) Bucur & Enos, 2001

Pl. 1A-E; Pl. 2A-H; Pl. 3A, B, F; Pl. 4A, D-H

1978 *Diplopora borzai* nov. spec., Bystrycki, p. 328, pl. 1, fig. 1-4; pl. 2, fig. 1-4.

1981 *Diplopora panormitana* n. sp., Di Stefano, p. 74, pl. 1, fig. 1-3; pl. 2, fig. 1-3; pl. 3, fig. 1-4; pl. 4, fig. 1-4.

? 1989 *Diplopora oregonensis* n. sp., Flügel et al., p. 376, Fig. 2-4.

2001 *Pseudodiplopora borzai* (Bystrycki, 1978) nov. comb. - Bucur & Enos, p. 328.

#### Description

Thallus cylindrical with a maximum observed length of 15.6 mm. Well defined axial cavity, most probably corresponding to the central stem of the alga. Laterals tubular slightly flared at the distal end (phloiophorous type) with metaspondyle arrangement (e.g., Pl. 1C; Pl. 2E, H; Pl. 3F; Pl. 4A, D). Most specimens have the axial cavity filled with reproductive cysts (gametangia) of

generally spherical shape. In longitudinal (Pl. 1A; Pl. 2A, C; Pl. 2A, B) as well as in oblique (Pl. 1B-D; Pl. 2E, H; Pl. 3F; Pl. 4A) or transverse (Pl. 3B) sections, cysts are predominantly arranged more or less on the margins of the axial cavity leaving an empty space in the center. However, the cysts occasionally occupy almost the whole space of the central stem (Pls. 1E, 2B, D, F). The cysts are not directly welded to the external surface of the axial cavity. Between the cysts and the calcareous wall, there is a very narrow free space (Pl. 2A, C, F, G). Sterile specimens were also identified (Pl. 4D-H) which, except for the lack of cysts, have the same characteristics as the fertile ones.

#### Dimensions (in mm)

Fertile specimens:

L (maximum observed length) = 15.600

D (external diameter) = 1.300-2.600 (mean = 1.890)

d (internal diameter) = 0.550-1.500 (mean = 0.910)

d/D (%) = 27.77-63.15 (mean = 47.48)

e (thickness of the calcareous wall,  $D-d/2$ ) = 0.270-0.800

Cysts diameter = (0.043) 0.060-0.100

Sterile specimens:

D = 0.870-1.800 (1.270)

d = 0.280-1.100 (0.610)

d/D (%) = 28-68.18 (47.70)

$D-d/2$  = 0.170-0.550 (0.320)

#### Discussion

The specimens identified in Idaho present all the characteristics described and illustrated by Bystrycki (1978) for *Diplopora borzai*. Bystrycki (1978) described the laterals (branches) as being spindle-shaped ... "with a sharp tip at both edges, and maximum thickness closely before the mouth or, which is the most common, at the mouth leading out the sleeve. In the latter case the pores of the branches are open outside and resemble the pores of the branches of the phloiophore type." (Bystrycki 1978, p. 328). Di Stefano (1981) and Di Stefano & Senowbari-Daryan (1985) also considered the laterals of the Sicilian specimens as phloiophorous. Accordingly, Bucur & Enos (2001) transferred *Diplopora borzai* Bystrycki, 1978 into the new genus *Pseudodiplopora* (metaspondyle arrange-

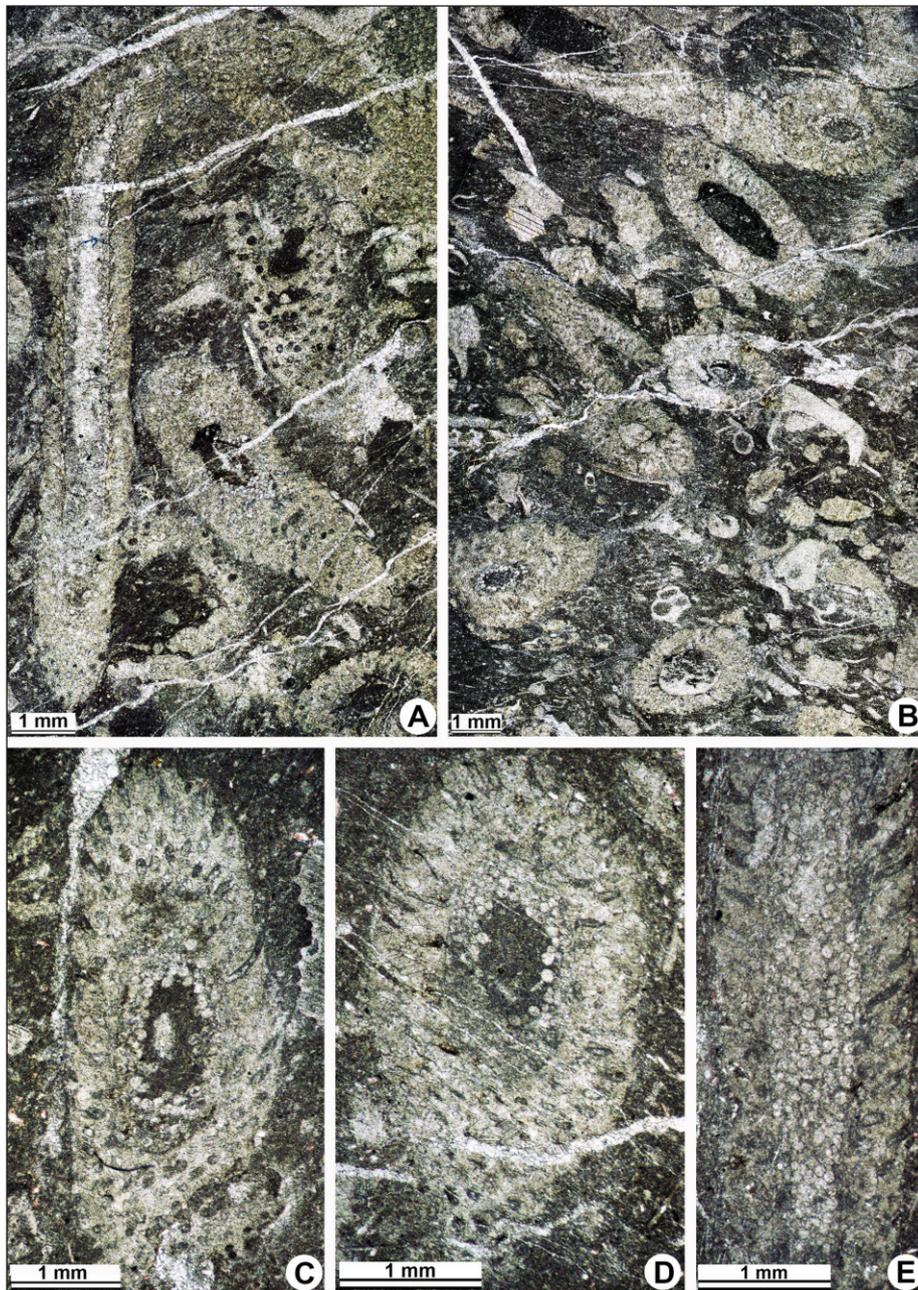


PLATE 1

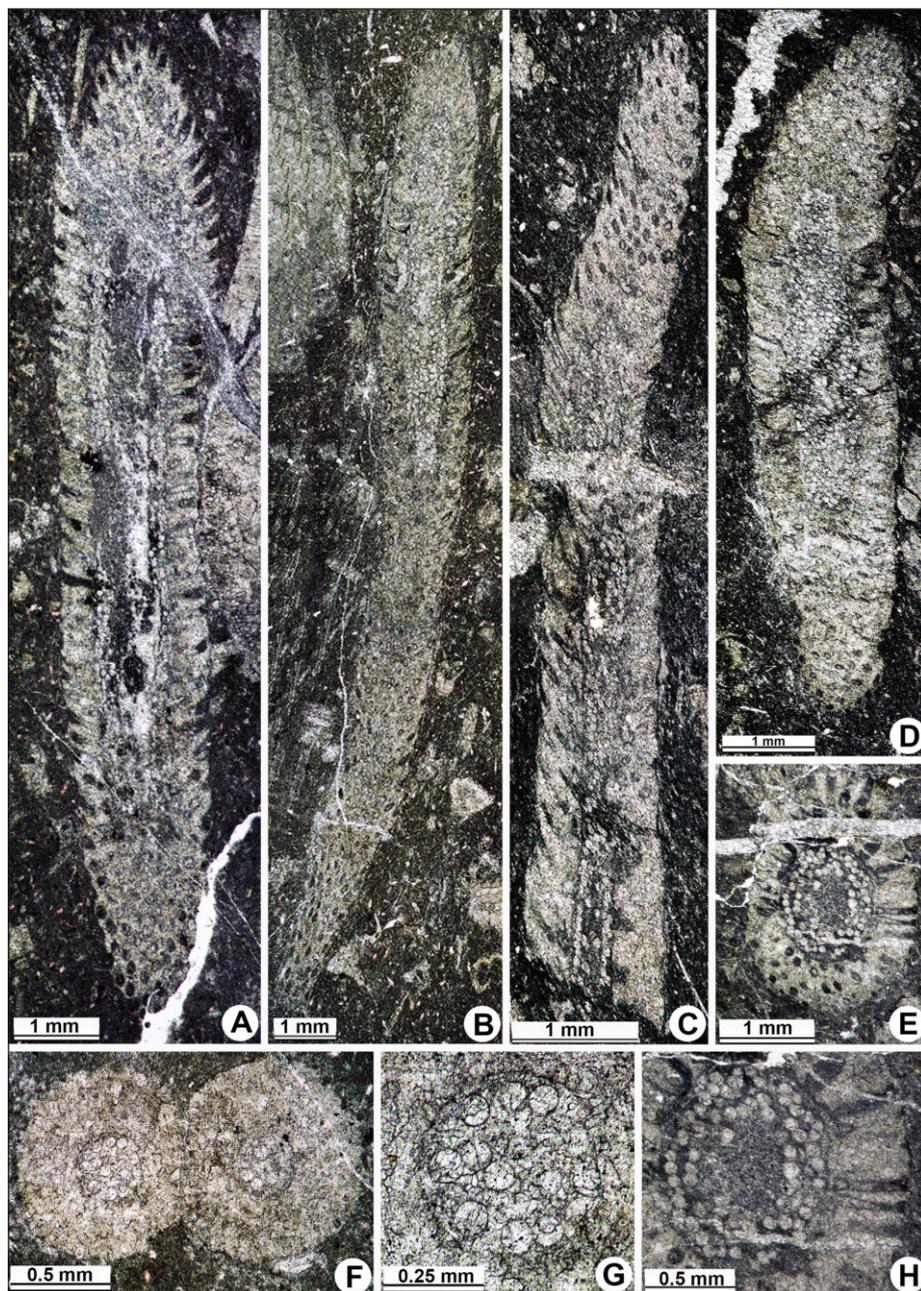
A-E - *Pseudodiplopora borzai* (Bystricky).  
 A, B) Microfacies with *Pseudodiplopora*; rudstone-floatstone with dasycladalean, mollusc and echinoderm fragments. C, D) oblique sections; E) longitudinal section (close-up view of the specimen in Pl. 2C showing the central cavity filled with gametangia). A, thin section LQ-39I; B, thin section LQ-39F; C, thin section LQ-39b; D, E, thin section LQ-39C; Idaho, U.S.A.

ment and phloioporous laterals) under the new combination *Pseudodiplopora borzai* (Bystricky, 1978) (see also Barattolo & Romano 2005). The thallus dimensions of the American specimens match the dimensions given by Bystricky (1978), Di Stefano (1981) and Di Stefano & Senowbari-Daryan (1985) except for the mean values of the cyst diameter (larger in the American specimens). Flügel et al. (1989) described *Diplopora oregonensis* from the Red Gulch conglomerates, Wallowa Mountains, northeast Oregon, and compared the new species with *Diplopora borzai*. The former should differ from the latter by the "... type of the thallus (segmented versus non-segmented in *Diplopora borzai* ...), the

scarcity of typical metaspondyle branching patterns (most whorls exhibit an euspondyle pattern), and also the dimensions." (Flügel et al. 1989, p. 378). Dimensions differences are emphasized in regard to the pore diameter (smaller in *D. oregonensis*) and the size of the cysts (*D. oregonensis* having two different size ranges). We must emphasize that the specimens illustrated by Flügel et al. (1989) show an advanced degree of diagenesis which strongly obliterates the structure of the skeleton. The illustrated specimens in Figs. 3, 4 (Flügel et al. 1989) do not show a proper segmentation of the thallus. It is possible that advanced dissolution process along the pores (e.g., Fig. 3/1, 3, Flügel et

## PLATE 2

A-H - *Pseudodiplopora borzai* (Bystricky). A-D) longitudinal-oblique sections; E) oblique section; F) transverse section of two specimens; G) close-up view of the left specimen in F showing the gametangia filling the whole central cavity; H) close-up view of the specimen in E showing the gametangia filling a large part of the central cavity, as well as the external enlargement of the laterals. A, F, G, thin section LQ-39A; B, thin section LQ-39C; C, D, thin section LQ-39D; E, H, thin section LQ-39F; Idaho, U.S.A.



al. 1989) resulted in such an interpretation, but the longitudinal sections from Fig. 4/1-3 (Flügel et al. 1989) do not confirm it. Regarding the thallus dimensions, even if small differences exist, the general thallus dimensions of *D. oregonensis* match the dimensions given by Bystricky (1978) for *D. borzai*. The smaller diameter of the pores could also be a feature related to the strong diagenesis. In respect to the cysts dimensions, there is a wide dimensional range from 0.030-0.066 in *D. borzai* (Bystricky 1978) to 0.050-0.070 in the Sicilian specimens (Di Stefano 1981) and to 0.043-0.100 in the specimens described in the present paper. This variability could be partially due to the fact that these small

corpuscles are cut randomly, but could also be a natural feature related to habitat. The existence of two different range of sizes for cysts in *D. oregonensis* illustrate in fact this variability. In view of the above considerations we think that *Diplopora* (*Pseudodiplopora*) *oregonensis* is a probable junior synonym of *Pseudodiplopora borzai*.

**Stratigraphic range:** Carnian (Bystricky 1978); Carnian-Norian (Di Stefano & Senowbari-Daryan 1985; Granier & Deloffre 1994; Granier & Grgasovič 2000). Norian (Flügel et al. 1989) for *D. oregonensis*. Our specimens from Idaho are early to early late Norian in age (most probably middle Norian).

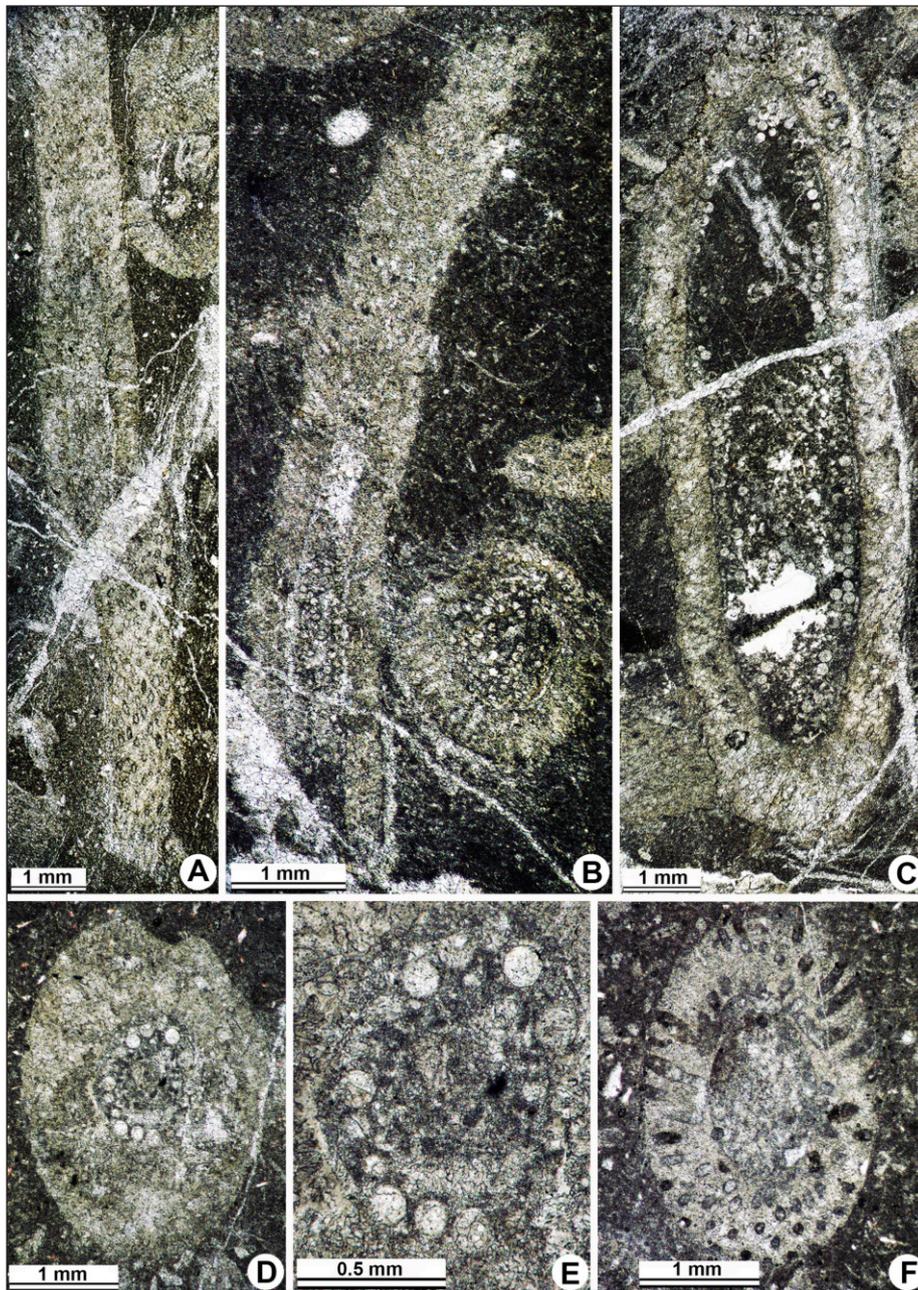


PLATE 3

A, B, F - *Pseudodiplopora borzai* (Bystricky). A) longitudinal-oblique-tangential section; B) longitudinal-oblique and transverse sections; F) oblique section. A, thin section LQ-39C; B, thin section LQ-39G; F, thin section LQ-39A; Idaho, U.S.A.

C, D, E - *Pseudodiplopora?* sp. C) longitudinal-oblique section; D) transverse section; E) close-up view of the specimen in D showing the shape and arrangement of gametangia. C, thin section LQ-39I; D, E, thin section LQ-39B; Idaho, U.S.A.

*Pseudodiplopora?* sp.

Pl. 3C, D; Pl. 4B, C

Associated with *P. borzai* we found some specimens of a large dasycladalean displaying a very recrystallized calcareous wall surrounding the central cavity. For this reason, the shape of the laterals cannot be observed adequately, but they probably were phoiophorous as suggested by some laterals "ghosts" (Pl. 3C). By contrast, the reproductive cysts inside the central cavity are very well preserved. They are arranged around the margin of the central cavity in 2 or 3 rows (Pl. 3D, E; Pl. 4B, C) but probably occupied more space inside the stem (Pl. 3C).

**Dimensions (in mm):**

L (maximum observed) = 11.800

D = 3.200-3.600

d = 1.550-2.000

cyst diameter = 0.140-0.180

Family Thyrsoporellaceae Granier & Bucur in  
Granier et al., 2013

Genus *Thyrsoporella* Gumbel, 1872

?*Thyrsoporella multipora* (Bilgutay, 1968)

Pl. 4I, J

1968 *Placklesia multipora* n. gen., n. sp., Bilgutay, p.71, text-fig 4, pl. 3, figs. 1-9.

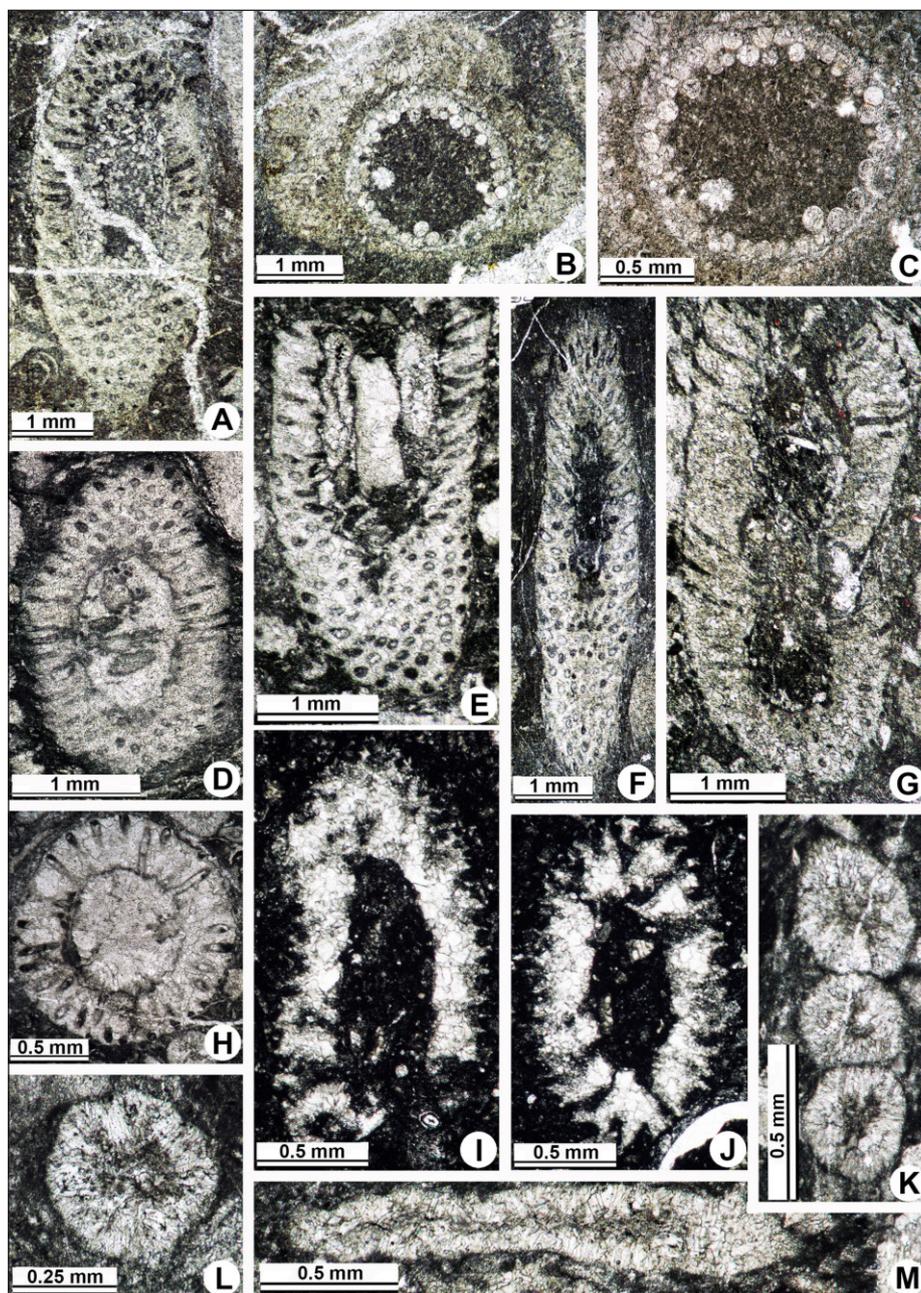
## PLATE 4

A, D-H - *Pseudodiplopora borzai* (Bystriky). A) oblique section of a fertile specimen; D-G) oblique and longitudinal-oblique sections of sterile specimens; H) transverse section of a sterile specimen. A, thin section LQ-39I; D, thin section LQ-6; E, thin section LQ-24; L, thin section LQ-39F; G, thin section LQ-23; H, thin section LQ-27; Idaho, U.S.A.

B, C - *Pseudodiplopora?* sp. Transverse section; C is a close-up view of the specimen in B showing the shape and arrangement of gametangia. Thin section LQ-39G; Idaho, U.S.A.

I, J - *Thyrsoporella multipora* (Bilgütay), oblique sections. Thin section MQ-34B, Oregon, U.S.A.

K-M - *Collarecodium? nezpercae* Bucur & Rigaud n. sp., paratypes. Transverse (K, L) and longitudinal-oblique (M) sections. K, L, thin section LQ-27; M, thin section LQ-24; Idaho, U.S.A.



1978 *Placklesia multipora* Bilgütay 1968 - Senowbari-Daryan, p.200, pl. 30, figs. 1-6.

2006 *Thyrsoporella multipora* (Bilgütay 1968) nov. comb. - Schlagintweit, in Gawlick et al., p.110, fig. 4.1-2.

### Description

Bilgütay (1968) and Senowbari-Daryan (1978) gave a detailed description of this alga. Essentially, it has a cylindrical thallus bearing laterals with five order of dichotomous branching. Unfortunately, most identified specimens were subjected to a strong diagenesis, and the branching of the laterals is difficult to follow. The rare exceptions are represented by the oblique sections illustrated in Pl. 4I, J.

### Dimensions (in mm):

L (maximum observed) = 6.600

D = 0.630-1.150 (mean = 0.970)

d = 0.220-0.470 (mean = 0.370)

d/D (%) = 32-47 (mean = 37)

e (D-d/2) = 0.210-0.420 (mean = 0.30)

**Locality:** Black Marble Quarry in Oregon (Lower Norian).

### Discussion

Schlagintweit (in Gawlick et al. 2006) considered that either the criteria used by Bilgütay (1968) to distinguish the genus *Placklesia* from the genus *Thyr-*

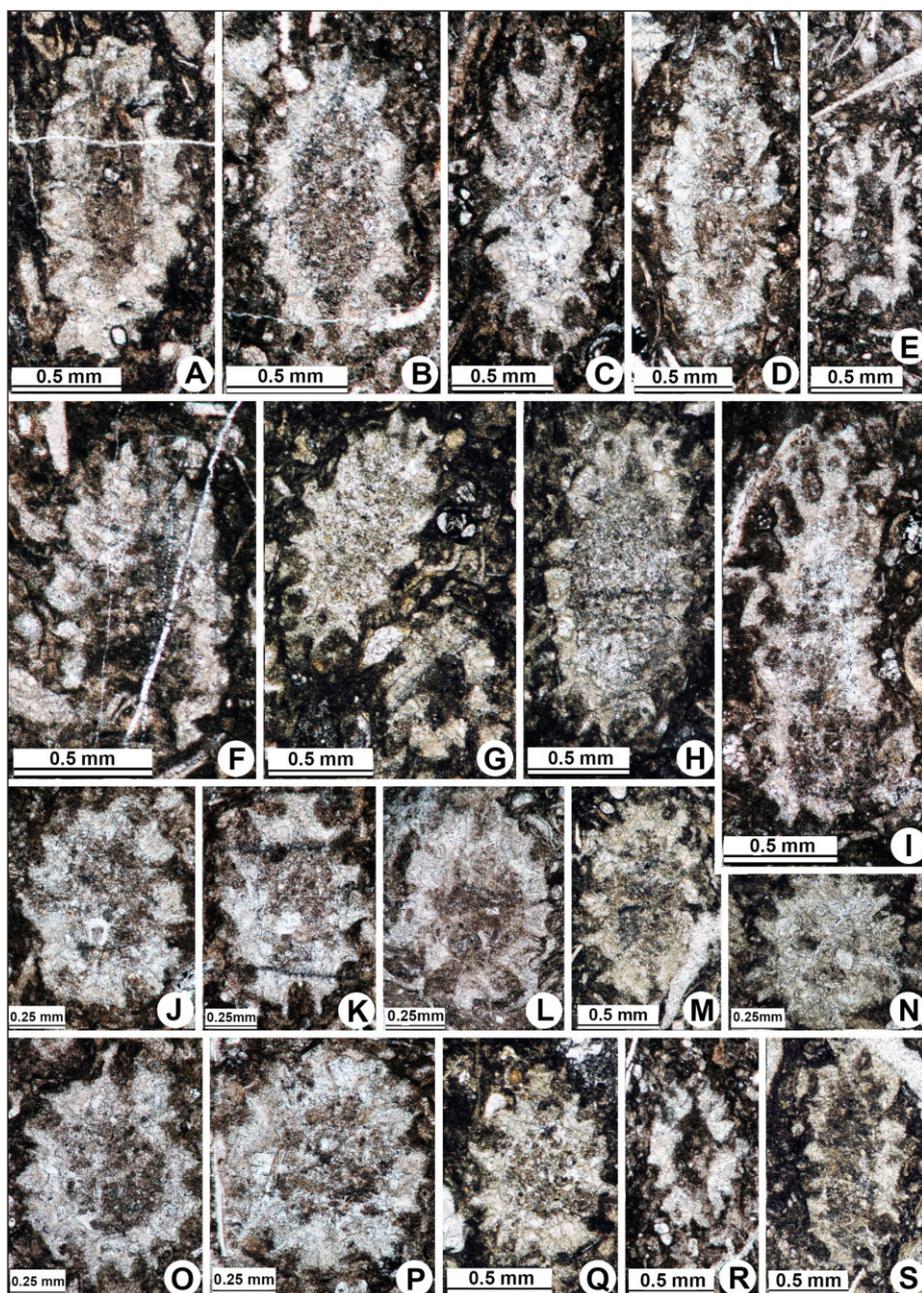


PLATE 5

A-S - *Holosporella? rossanae* Bucur & Del Piero n. sp. A-I, S) oblique sections; J-M, R) transverse-oblique sections; N-Q) transverse sections. A-C, K, R, thin section WH-227a; E, L-N, S, thin section WH-227b; D, F, G, thin section WH-235a; H, I, J, P, Q, thin section WH-235b; Yukon, Canada. K - holotype; A-C, R - paratypes.

*soporella* (i.e., 1, the existence of 5 order of lateral branching; 2, segmentation of the calcareous skeleton; and 3, thallus branching) are inconsistent (e.g., segmentation), or they are characteristic for other species of the genus *Thyrsoporella*. Thus, as a consequence, he transferred the species *P. multipora* to the genus *Thyrsoporella* in the new combination *Thyrsoporella multipora* (Bilgütay). Granier & Bucur (in Granier et al. 2013) disagreed with this synonymy because they considered that these genera differ in the division formula of the branching pattern. However, as emphasized by Schlagintweit (in Gawlick et al. 2006), the Late Jurassic species *Thyrsoporella pseudoperplexa* Granier & Braik (Granier & Braik 2002)

has the same division formula as *Placklesia multipora* and we consider here the synonymy proposed by Schlagintweit as acceptable.

**Stratigraphical range:** Rhaetian (Bilgütay 1968; Senowbari-Daryan 1978; Granier & Gragovic 2000; Schlagintweit in Gawlick et al. 2006); upper Norian-Rhaetian (Granier & Deloffre 1994; Bucur 1999). Until now, *T. multipora* was known only from the Northern Calcareous Alps (Schlagintweit in Gawlick et al. 2006). Its presence in the lower Norian of Oregon would be remarkable.

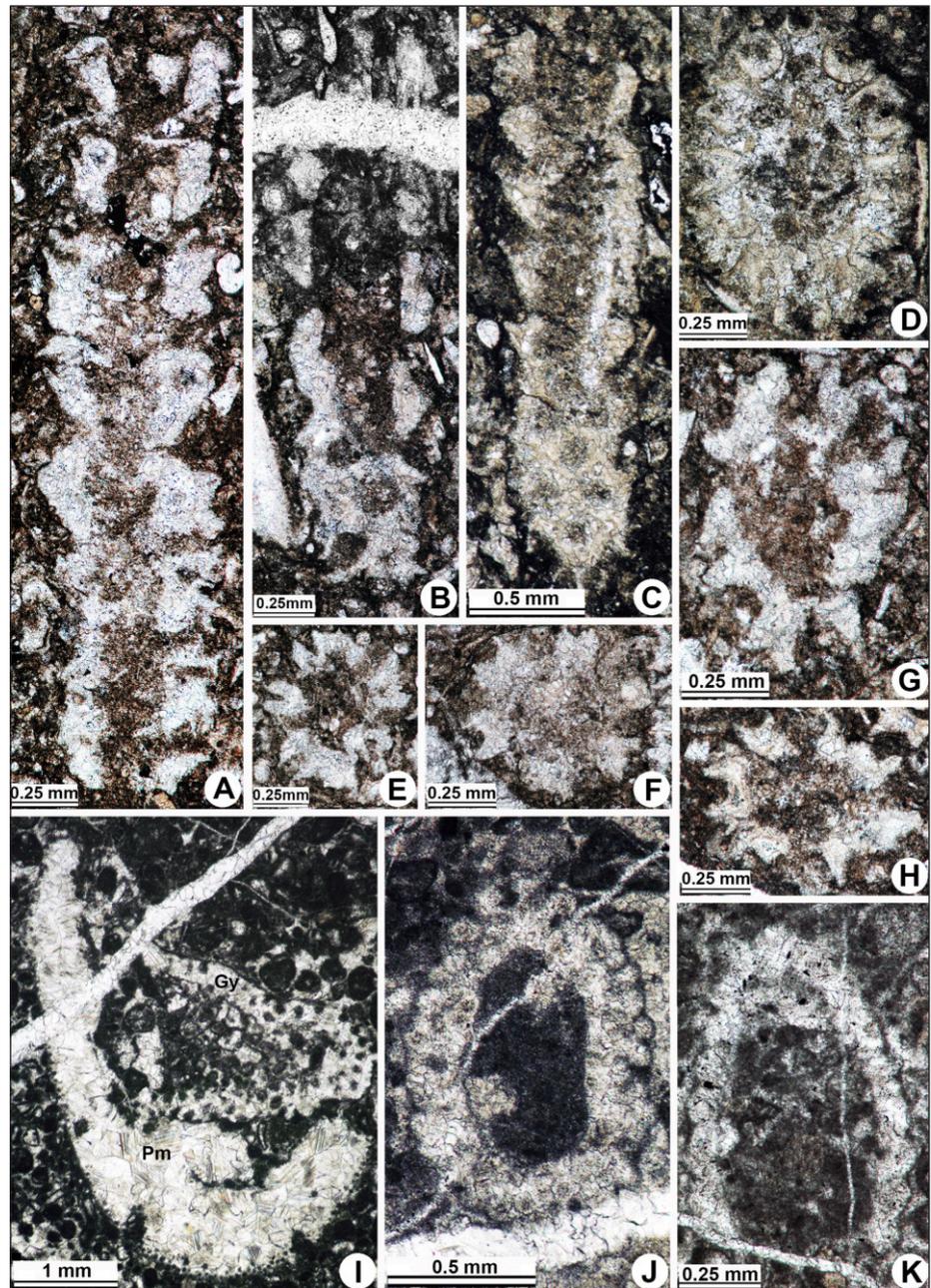
Family Triploporaceae Pia 1920, emend Granier & Bucur in Granier et al., 2013

## PLATE 6

A-H - *Holosporella?* *rossanae* Bucur & Del Piero n. sp. A) longitudinal section; B, C) longitudinal-oblique sections; E, F) transverse sections; H) transverse-oblique section. A, B, E, G, thin section WH-227b; C, D, thin section WH-235b; H, thin section WH-235a, Yukon, Canada.

I - *Gyroporella* sp. (Gy) and *Permocalculus* sp. (Pm), oblique sections. Thin section GP-152; Dalnegorsk, Far East Russia.

J, K - *Gyroporella* sp., oblique sections. J, thin section GP-157; K, thin section GP-153; Dalnegorsk, Far East Russia.

Genus *Holosporella* Pia, 1930*Holosporella?* *rossanae* Bucur & Del Piero n. sp.

Pl. 5A-S; Pl. 6A-H

**Origin of the name:** species dedicated to Prof. Dr. Rossana Martini, University of Geneva, for her contributions to the study of Triassic deposits all over the world.

**Holotype:** specimen in Pl. 5K, thin section WH-227a [MHNG-GEPI-2020-0014].

**Paratypes:** specimens illustrated in Pl. 5A-C, R (thin section WH-227a [MHNG-GEPI-2020-0014]), Pl. 5L, M, O, S; Pl. 6A-G (thin section WH-227b [MHNG-GEPI-2020-0015]).

**Type locality:** Lime Peak, Yukon (Canada), Stikinia terrane (GPS: 61° 3' 57.35"N; 134° 54' 57.95"W).

**Type level:** late Norian.

**Material and repository:** More than 50 specimens identified in four thin sections (WH-227a, WH-227b, WH-235a, WH-235b) stored in the Museum d'Histoire Naturelle de Genève under the numbers MHNG-GEPI-2020-0014, 0015, 0021 and 0022.

**Diagnosis:** Thallus cylindrical bearing whorls of spheroidal to ovoid laterals arranged in quincunx. Laterals, communicating with the axial stem through a peduncle enlarge distally in a blister. Calcification weak as a distinct wall around the laterals and occasionally between the whorls. The distal end of the laterals is frequently non-calcified.

**Description**

The cylindrical thallus consists of successive whorls arranged in quincunx (Pl. 6B, C). Calcification is variable and is mainly located around the proximal part of the laterals (Pl. 5J, L, O-Q) but

does not seem to reach the main stem. Due to this type of calcification, the thallus presents occasionally a sort of articulation visible in some longitudinal sections (Pl. 6A-C). The laterals communicate with the axial cavity through a short tubular proximal part (Pl. 5A, B, H, J-S; Pl. 6E, H). Distally, the laterals enlarge becoming spheroidal (Pl. 6D, E) or ovoid (Pl. 5C, E-G, I). No reproductive structures have been detected, but probably they were located inside the laterals (cladospore type).

**Dimensions (in mm):**

L (maximum observed) = 2.920

D = 0.650-1.000 (mean = 0.760)

d = 0.250-0.450 (mean = 0.339)

d/D% = 32.05-55.00 (mean = 44.58)

e = (D-d)/2 = 0.170-0.270 (mean = 0.207)

p (lateral's diameter) (max.) = 0.170-0.220 (mean = 0.190)

l (lateral's length) = 0.250

h (distance between whorls) = 0.190-0.250 (mean = 0.230)

w (number of laterals in a whorl) = 8-9

**Comparisons:** So far, eight species attributed to the genus *Holosporella* are known and only one was described from Triassic (Norian) deposits (i.e., *Holosporella conradii*, Barattolo et al. 2008). The type of calcification (usually calcification surrounded the laterals up to their distal ends in *H. conradii*) as well as arrangement of laterals (bending upwards and downwards in *H. conradii*) differentiate the two Triassic species. The type species *Holosporella siamensis* was described by Pia (1930) from deposits initially assigned to the Triassic. Subsequently, the age of these deposits was reconsidered as Middle Jurassic (Bassoulet 1987). Most of the *Holosporella* species have laterals characterized by a short proximal peduncle and a spherical (e.g., *H. siamensis*, *H. senegalensis*, *H. conradii*) or ovoid (e.g., *H. oblonga*, *H. arabica*, *H. farsica*) distal blister (Pia 1930; Bernier 1984; Granier 1991, 1992; Barattolo et al. 2008; Bucur et al. 2012). Except for *Holosporella sarda* (Pecorini), a large species considered by Barattolo et al. (2008) as more conveniently to be placed in the genus *Humiella*, the other species of *Holosporella* have a calcareous skeleton more or less compact. The lower Cretaceous *Holosporella farsica* and, partially, the middle Jurassic *Holosporella siamensis* have a similar calcification with that of *Holosporella? rossanae* n. sp. have. The shape

of the laterals in *H. siamensis* and the general dimensional parameters differentiate the two species from the new species described here. *Holosporella? rossanae* exhibits a weak calcification related to the proximal part of the laterals. Consequently, it is difficult to define the complete outline of the laterals, and hence the uncertainty regarding the generic assignment. The calcification and the dimensional parameters differentiate *Holosporella? rossanae* n. sp. from the other *Holosporella* species (for comparisons see also Bucur et al. 2012, table 1).

**Micropalaeontological assemblage:** *Holosporella? rossanae* n. sp. is found in association with abundant molluscs (bivalves and gastropods), abundant ostracodes, brachiopods, calcimicrobes (*Girvanella* sp.) and rare corals and sponges, abundant foraminifers. The foraminifers include abundant verneulinidae: *Siphonvalvulina*, common mesoendothyridae: *Wernlina*, common nodosariidae, minor involutinidae: *Aulosina*, *Aulotortus*, rare Robertinida: *Robertonella*, *Falsoreinholdella*, as well as rare Trocholinidae: *Frentzenella*, and rare miliolids.

**Palaeoenvironment:** *Holosporella? rossanae* is found in wackestones to packstones limestone microfacies, which were deposited in shallow open ramp environments.

***Holosporella magna* Bucur & Fucelli n. sp.**

Fig. 2, Pl. 7A-H

**Origin of the name:** from the latin magna, referring to the large dimensions of this alga.

**Holotype:** Specimen in Pl. 7A, thin section FA-81A [MHNG-GEPI-2020-0073].

**Paratypes:** specimens in Pl. 7C (thin section FA-81A [MHNG-GEPI-2020-0073]) and Pl. 7E (thin section FA-81C [MHNG-GEPI-2020-0074]).

**Type locality:** The north-east flank of Garfield Hills, Nevada (U.S.A.) (GPS 38°29'12.96"N; 118°13'1.89"W).

**Type level:** middle Norian.

**Material and repository:** two thin sections, containing the holotype and paratypes, stored in the Museum d'Histoire Naturelle de Genève under the numbers MHNG-GEPI-2020-0073 and 0074.

**Diagnosis:** Large specimen of *Holosporella* (outer diameter of the thallus is about 1 cm) bearing club- to spindle-shaped laterals arranged in quincunx. Calcification represented by a thin layer around the laterals. Most frequently found as dispersed laterals in the sediment.

**Dimensions (in mm):**

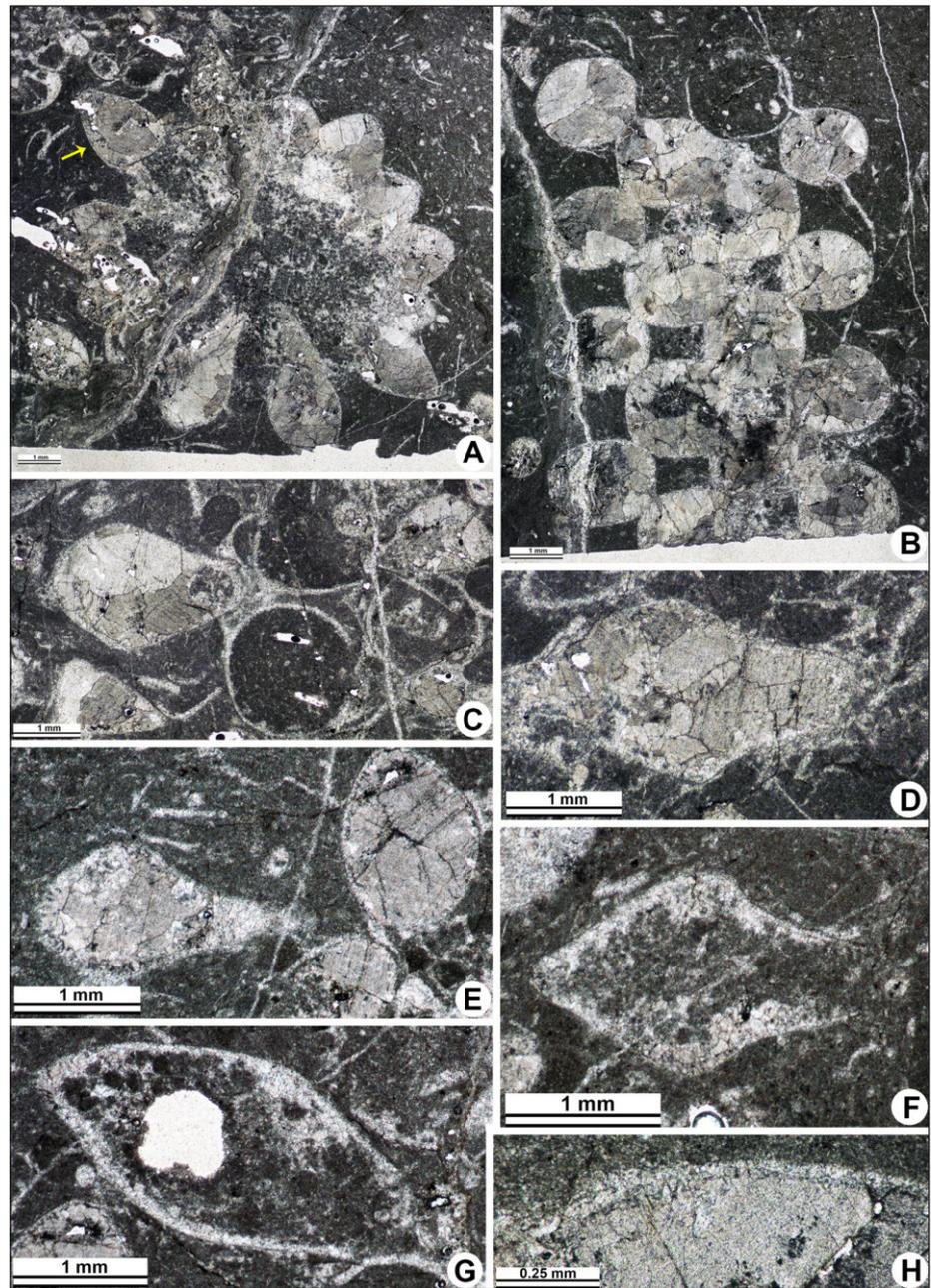
L (maximum observed) = 10.000 (probably much larger in the living alga)

D = 9.600

d = 2.400

## PLATE 7

A-H - *Holosporella magna* Bucur & Fucelli n. sp. A) transverse section; B) tangential section; C) tangential-oblique section through several laterals; D-G) different sections of isolated laterals in sediment; H) close-up view of the specimen in A (arrow) showing the structure of the wall. A, C, D, H, thin section FA-81A; B, E-G, thin section FA-81C; Nevada, U.S.A. A - holotype; C, E - paratypes.



$$d/D = 25\%$$

$$e = (D-d)/2 = 3.600$$

$$l = 2.050-3.600$$

$$P \text{ (max.)} = 1.520-2.080$$

$$h = 1.200-1.500$$

$$w = 12$$

### Description

We found only one well preserved specimen (Fig. 2, and Pl. 7A, B), two fragments containing 3 or 4 laterals (Pl. 7C, E), and many dispersed laterals in the sediment (Pl. 7D, F, G). The shape of the laterals seems to be variable, from classical club-shaped (Pl. 7A, lower part; Pl. 7C, left part)

to spindle-like (fusiform) (Pl. 7D, E, G) with an acuminate distal end. The wall of the laterals is thin. The laterals are grouped in whorls arranged in quincunx (Fig. 2, Pl. 7B). Reproductive structures have not been observed, but most probably they were situated inside the laterals (cladosporate type).

**Comparisons:** *Holosporella magna* n. sp. is the largest known species of *Holosporella*. It can be compared with *Holosporella sarda* (Pecorini 1972) Cherchi & Schroeder (1985), having a relatively similar morphology of the laterals but with a short evident peduncle, and much smaller general dimensions (e.g.,  $D = 1.5$  mm compared to 9.6 mm



Fig. 2 - Limestone sample with *Holosporella magna* Bucur & Fucelli n. sp. in transverse and tangential sections, as well as numerous fragments of laterals spread in the rock. Sample FA-81, Nevada (U.S.A.).

in *H. magna* n. sp.). Senowbari-Daryan & Hamadani (2000, p. 114, Pl. I, figs. 8, 9) described and illustrated specimens of a dasycladalean alga assigned with question mark to the genus *Holosporella*. The laterals of this alga (“Zisten” in the original paper) have globular to ovoid-piriform shape and are arranged around a central stem (Senowbari-Daryan & Hamadani 2000). From the provided illustrations we estimate the outer diameter (D) at about 1.5 mm. The maximum diameter of the laterals reaches 0.5-0.6 mm. *Holosporella*? sp. from Iran differs from *Holosporella magna* n. sp. by its dimensions and the shape of the laterals (piriform, with a wide proximal portion and a narrower distal portion).

### Discussion

Barattolo & Romano (2008) mentioned that *Holosporella sarda* (Pecorini) would be more conveniently placed in the genus *Humiella* Sokac & Velić 1981b. The genus *Humiella* comprises five relatively large dasycladaleans (Granier & Deloffre 1993): *H. cateniformis* (Radoičić), *H. dalmatarum* (Sokač & Velić), *H. piriformis* (Sokač & Velić), *H. sardinensis* (Ott & Flaviani) and *H. tentae* (Sokac & Velić) all from Lower Cretaceous rocks (Radoičić 1967; Sokač & Velić 1981a, b; Ott & Flaviani 1983). Masse et al. (1984) considered the presence of small pores within the wall of the central stem and the wall of the laterals as a defining characteristic of the genus *Humiella*. Species similar to *Humiella* species but devoid of such pores should therefore

not be classified with the genus *Humiella* (see also Sokač 1987). If we follow this reasoning the newly described species belongs to the genus *Holosporella*, together with *H. sarda*. The calcareous wall surrounding the laterals of *Holosporella magna* n. sp. is made of small sparite crystals (Pl. 7H), and is devoid of perforations. Regarding the species *Humiella japodica* Sokač (Sokač 2001), Barattolo et al. (2008) consider that the laterals of this species arranged in closed whorls have to be considered piriferous, and the species have to be assigned more conveniently to the genus *Physoporella*.

**Micropalaeontological assemblage:** *Holosporella magna* was found in a centimetric bed of mudstone facies, where no other organisms were found. In the beds below and above, conodonts of middle Norian age occur, together with thin lumachelle layers bearing bivalves and gastropods.

**Palaeoenvironment:** lagoonal-peritidal facies (cycles) with abundant bivalves including megalodontids, and gastropods, alternated with decimetric corals horizons and nodular marls, probably deposited on a broad carbonate platform.

Genus *Griphoporella* Pia, 1915, emend. Barattolo et al., 1993

***Griphoporella curvata* (Gümbel, 1872) Pia 1915, emend. Barattolo et al., 1993**

Pl. 8A-F; Pl. 10A

1872 *Gyroporella curvata* n. sp., Gümbel, 1872, p. 280, Pl. D.IV, fig. 2a-d.

1915 *Griphoporella curvata* n. comb. - Pia in Spitz & Dyrenfurth, Pl. I, fig. 11.

1993 *Griphoporella curvata* (Gümbel 1872) Pia 1915 - Barattolo et al., p. 26, pl. 1-7.

2000 *Griphoporella curvata* (Gümbel, 1872) Pia 1915, emend Barattolo et al., 1993 - Granier & Grgasović, p.67 (with extended synonymy list).

2000 *Griphoporella curvata* (Gümbel, 1872) Pia, 1915 (emend Barattolo et al., 1993) - Senowbari-Daryan & Hamadani, p.102, pl. I, figs. 1, 2A, 4, 6, 7; pl. II, figs. 1B, 2B, 3B; pl. III, figs. 2B, 4; pl. IV, fig. 9).

**Material:** Several specimens found in three thin sections coming from Shikoku Island (Japan), and one thin section from Sonora (Mexico).

### Dimensions (in mm):

L (maximum observed) = 12

D = 1.050-3.000

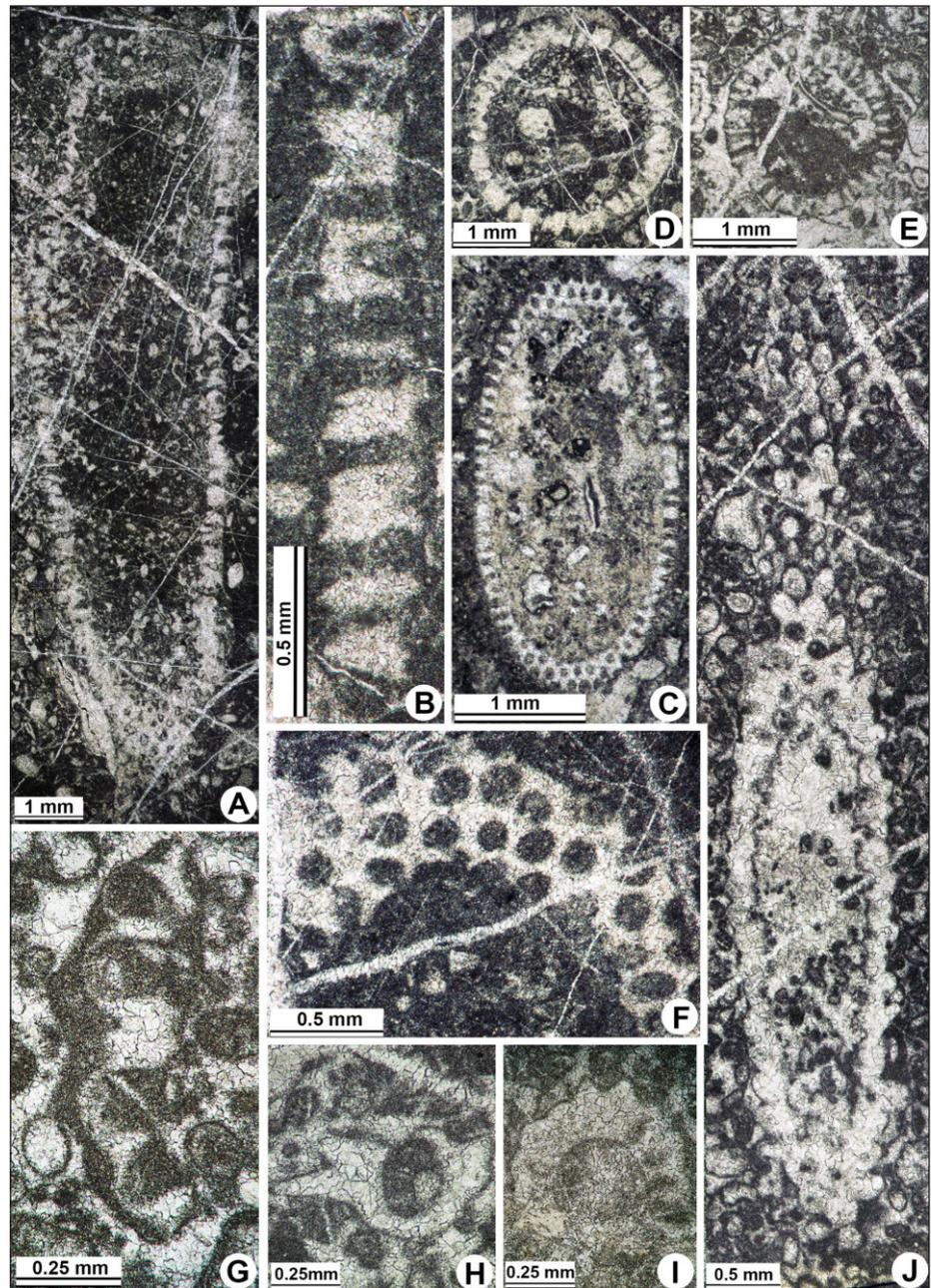
d = 0.700-2.200

(D-d)/2 = 0.150-0.300

p (distal) = 0.100-0.200 (0.162)

## PLATE 8

- A-F - *Griphoporella curvata* (Gümbel). A) longitudinal, slightly oblique section; B) fragment in longitudinal section showing the calcareous wall and the distal end of the laterals; C) oblique section; D, E) transverse sections. A, thin section CP-94a; B, D, F, thin section CP-94b; C - thin section CP-261; E, thin section JC-231a; Sambosan, Shikoku Island, Japan.
- G - *Gyroporella* sp., fragment in transverse section. Thin section JC-231a; Sambosan, Japan.
- H, I - *Chypeina* cf. *besici* (Pantić). Transverse-oblique (H) and transverse (I) sections. Thin section JC-231a; Sambosan, Shikoku Island, Japan.
- J - *Physoporella jomdaensis* Flügel & Mu., longitudinal-oblique section. Thin section JC-231a; Sambosan, Shikoku Island, Japan.



### Discussion

*Griphoporella curvata* is one of the most frequent species identified in the Tethyan Upper Triassic. Barattolo et al. (1993) studied thoroughly this species, designated a neotype and gave the following emended diagnosis (Barattolo et al. 1993, p. 33): "Cylindrical or slightly club-shaped thallus. Primary branches only, arranged in very close, alternate whorls. The branches are phloiophorous, with a subterminal narrowing; their transverse section is subcircular. The inclination of the branches is  $45^{\circ}$ - $60^{\circ}$  in the proximal portion then it gradually increases outwards up to  $70^{\circ}$ - $80^{\circ}$ . The distal portion of the branches form a cortex with polygonal meshes

horizontally compressed. Reproductive organs unknown (not calcified) probably situated in the central stem or in the primary branches (endospore or cladospore). The calcification constitutes a calcareous skeleton continuous, very thin and enveloping to a various degree different portions of the primary branches. As a consequence, the pores show different morphologies, both in different specimens and in different portions of the same specimen". The specimens identified in Japan (Pl. 8A-F) as well as rare fragments of thallus from Sonora (Mexico) (Pl. 10A) correspond to this diagnosis. Senowbari-Daryan et al. (2011) described *Griphoporella curvata* from Upper Triassic Nayband Formation in Iran.

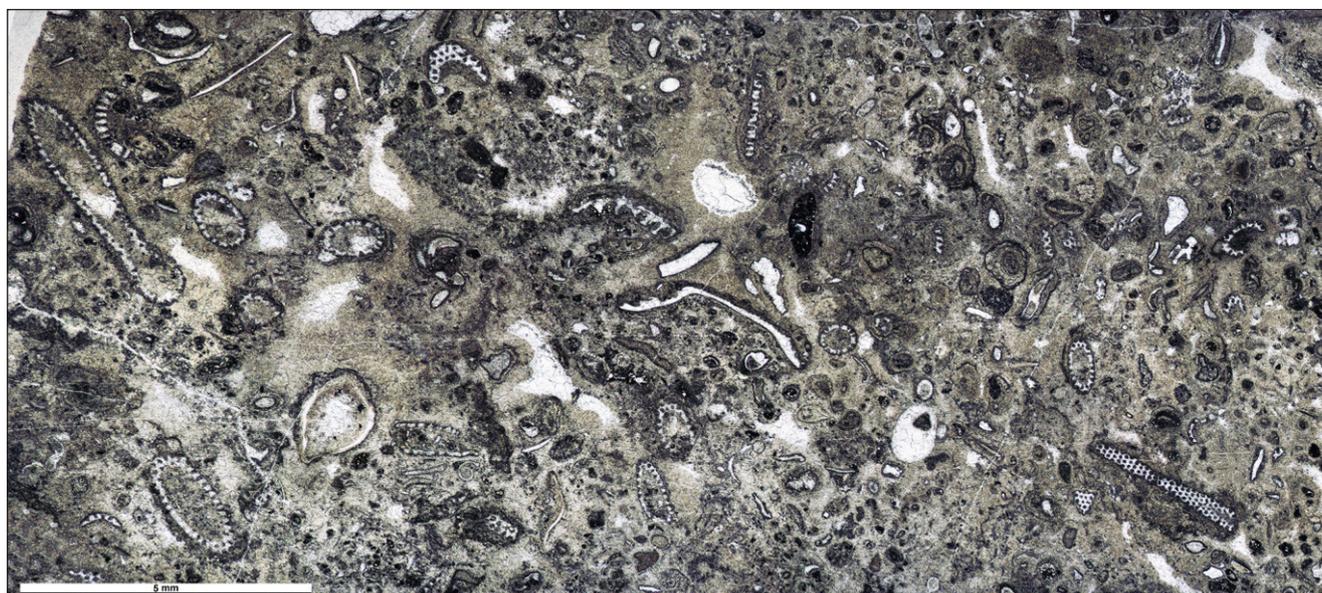


Fig. 3 - Bioclastic grainstone containing numerous specimens of *Griphoporella minuta* Bucur & Peybernes n. sp. Sample CP-259a, Sambosan, Shikoku Island (Japan).

Most of the illustrated specimens show a thin calcareous envelope covering the external part of the laterals. The laterals have also frequently a vesiculiform shape (e.g., Fig. 4F, Fig. 5E, H, J, Fig. 6E-G, Fig. 7H, etc. in Senowbari-Daryan et al. 2011). These authors (Senowbari-Daryan et al. 2011) recognized two types of *Griphoporella*: with open, and with closed pores. Senowbari-Daryan & Hamadani (2000) also described specimens with open pores. In discussing the specimens with closed pores, Senowbari-Daryan et al. (2011) noted also the presence of closed pores in the type specimen of *Macroporella retica* (Zanin-Buri, 1965), a species synonymized by Barattolo et al. (1993) with *G. curvata*. In fact, the appearance of such closed pores in the type specimen of *M. retica* represents an effect of sectioning, many pores in this specimen being open to the exterior. In our opinion, the specimens illustrated by Senowbari-Daryan et al. (2011) have laterals of vesiculiform shape characteristic for a *Gyroporella* and should be assigned to this genus (compare also Fig. 3d in Gümbel, 1872 with fig. 4F in Senowbari-Daryan et al. 2011).

### *Griphoporella minuta* Bucur & Peybernes n. sp.

Fig. 3, Pl. 9A-Z

**Origin of the name:** from the latin *minuta*, meaning small.

**Holotype:** specimen in oblique section illustrated in Pl. 9D, thin section CP-259a [MHNG-GEPI-2020-0008].

**Paratypes:** specimens in Pl. 9A, B, E, F, H, I, R, S, X, thin section CP-259a [MHNG-GEPI-2020-0008].

**Type locality:** Sambosan, Shikoku Island (Japan). GPS coordinates: 33° 34.452'N; 133° 42.733'E.

**Type level:** Upper Triassic.

**Material and repository:** About 30 specimens identified in one thin section (CP-259a) stored in the Museum d'Histoire Naturelle de Genève under the number MHNG-GEPI-2020-0008.

**Diagnosis:** Thallus cylindrical bearing phloioforous primary laterals disposed in whorls with euspondyle arrangement. Large central cavity and very thin calcareous wall. Calcification around the distal part of the primary laterals but probably not reaching their most distal end.

### Dimensions (in mm):

L (maximum observed) = 3.500

D = 0.360-0.740 (mean = 0.550)

d = 0.220-0.470 (0.360)

d/D% = 52.38-72.30 (65.10)

e - (D-d)/2 = 0.065-0.135 (0.095)

p (distal) = 0.050-0.090 (0.069)

h = 0.080-0.100 (0.094)

w = 11-17 (15)

### Description

The thallus is cylindrical, but a slightly club-shaped form is not excluded (Pl. 9A, L, Q). The laterals are phloioforous with a thin proximal part and a larger distal part. Some of them seem to present a constriction in their distal portion just before the final enlargement (Pl. 8H, M, O, arrows) a feature characteristic of the genus *Griphoporella* Pia, emend Barattolo et al. (1993) which differen-

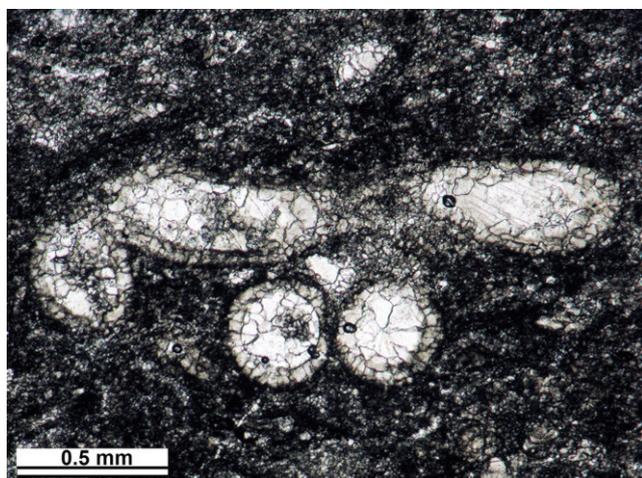


Fig. 4 - *Collarecodium? nezpercae* Bucur & Rigaud n. sp. showing a very discrete marginal zone probably corresponding to the cortical zone of the alga. Specimens from the Black Marble Quarry (sample MQ-7D), Oregon (U.S.A.)

tiates this genus from *Salpingoporella* Pia in Trauth, 1918. The laterals are arranged in close alternating whorls (Pl. 9B, N) (euspondyle arrangement). They probably represent only the distal calcified part of much longer laterals (see Barattolo et al. 1993 p. 40-41, Text figs. 6-7, reconstruction of *Griphoporella curvata*). As a consequence of this type of calcification the central cavity is very large (more than 65 % of the thallus diameter). The outline of the central cavity is smooth, as emphasized by longitudinal (Pl. 9A), oblique (Pl. 9D, M) and transverse (Pl. 9T, X) sections.

**Comparisons:** Four valid species are known from the Triassic (*Griphoporella bechstedti*, *G. curvata*, *G.? guembeli* and *G. kuenzelsauensis*) and six from the Jurassic-Cretaceous (*G.? aurigerica*, *G. ellenbergeri*, *G. minima*, *G. perforatissima*, *G. jurassica* and *G. cretacea*) (Granier & Deloffre 1993; Granier & Grgasović 2000; Bucur & Schlagintweit 2009). *Griphoporella minuta* n. sp. is morphologically similar to *G. curvata* from the Upper Triassic. The consistent difference between the two species is related to the general dimensions. As emphasized by Table 2, the largest specimens of *G. minuta* have smaller dimensions than the smallest specimens of *G. curvata*. A comparable species regarding the dimensions is *Griphoporella minima* Nikler & Sokač from the lower part of the Upper Jurassic of Velebit (Croatia) (Nikler & Sokač 1967). It differs from *G. minuta* n. sp. by the type of calcification (yellowish cryptocrystalline calcite in *G. minima*) and by the shape and number of laterals. *Griphoporella kuenzelsauensis* (Flügel & Hag-

	<i>Griphoporella curvata</i> (Gümbel, 1872) in Barattolo et al. 1993	<i>Griphoporella minuta</i> Bucur & Peybernes n. sp
L(max.)	> 20	3.400
D	0.730-3.120 (1.860)	0.360-0.740 (mean 0.550)
d	0.420-2.600 (1.370)	0.220-0.470 (0.360)
(D-d)/2	0.100-0.360 (0.240)	0.065-0.135 (0.095)
p	0.0630-0.110(0.089)	0.050-0.090 (0.069)
h	0.075-0.120 (0.091)	0.080-0.100 (0.094)
w	16-21 (18.6)	11-17 (15)

Tab. 2 - Comparative dimensions (in mm) of *Griphoporella curvata* (Gümbel, 1872) and *Griphoporella minuta* Bucur & Peybernes n. sp.

dorn, 1993) is another small species having general dimensions close to that of *Griphoporella minuta* n. sp. The differences consist in the shape of the laterals (cylindrical, slightly enlarged distally, but occasionally also narrowed distally in *G. kuenzelsauensis*; see Fig. 6 in Pl. 2, holotype in Flügel & Hagdorn 1993), as well as in the shape of the thallus (supposed moniliform in *G. kuenzelsauensis*). The shape of the thallus and general dimensions differentiate *G. minuta* n. sp. from the other species mentioned above.

**Micropalaeontological assemblage:** n. sp. has been found in a bioclastic grainstone containing microproblematica (*Baccanella floriformis*), small foraminifers, ostracodes, sponge fragments, echinoderms and undetermined shell fragments.

**Palaeoenvironment:** biotic content and microfacies of associated samples (e.g., CP259B is a sponge-algae boundstone) suggest deposition in a reefal environment.

Genus *Physoporella* Steinmann, 1903, emend.  
Grgasović, 1995

*Physoporella jomdaensis* Flügel & Mu, 1982  
Pl. 8j

### Discussion

Only one specimen of *Physoporella* was found in the thin section JC-231a from Shikoku Island (Japan). It shows the characteristic cylindrical thallus with a relatively large central cavity and pyriform laterals with horn-like distal ends. The laterals are arranged in alternating whorls. The Japanese specimen is a little bit smaller than the type specimens from Tibet, but it fits the dimensions given by Grgasović (1997) for *Physoporella jomdaensis* from

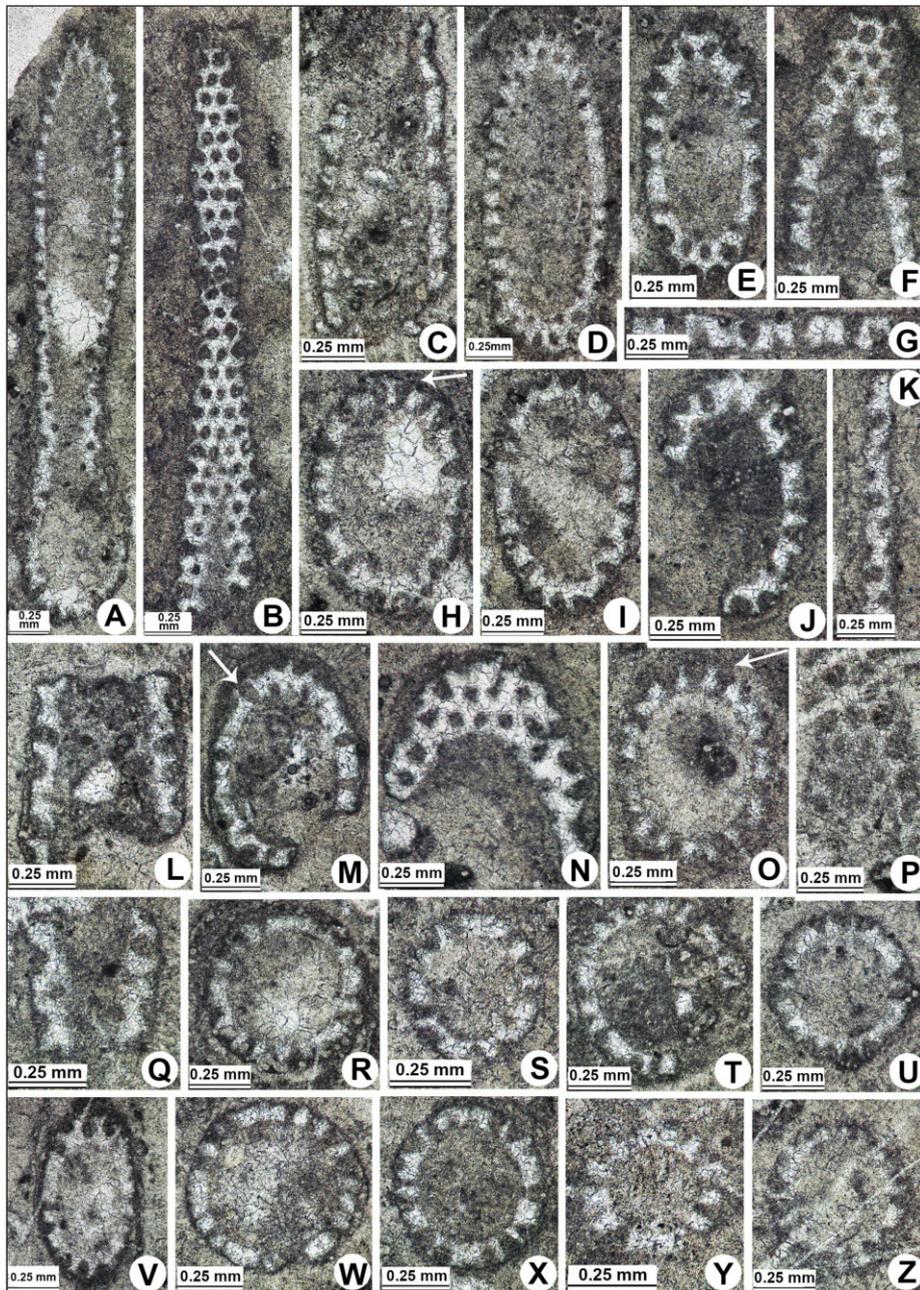


PLATE 9

A-Z - *Griphoporella minuta* Bucur & Peybernes n. sp. A) longitudinal-oblique section; B) longitudinal-tangential section. C, G, K, L, Q) fragments in longitudinal section. D, E, H-J, M-P, V) oblique sections. A-Z, thin section CP-259a; Sambosan, Shikoku Island, Japan. D - holotype; A, B, E, F, H, I, R, S, X - paratypes.

Croatia (see table 3 for comparisons). As noted by Grgasović (1997, p. 207) the differences in dimensions are consistent with the limits of variation known in the other species of the genus *Physoporella*.

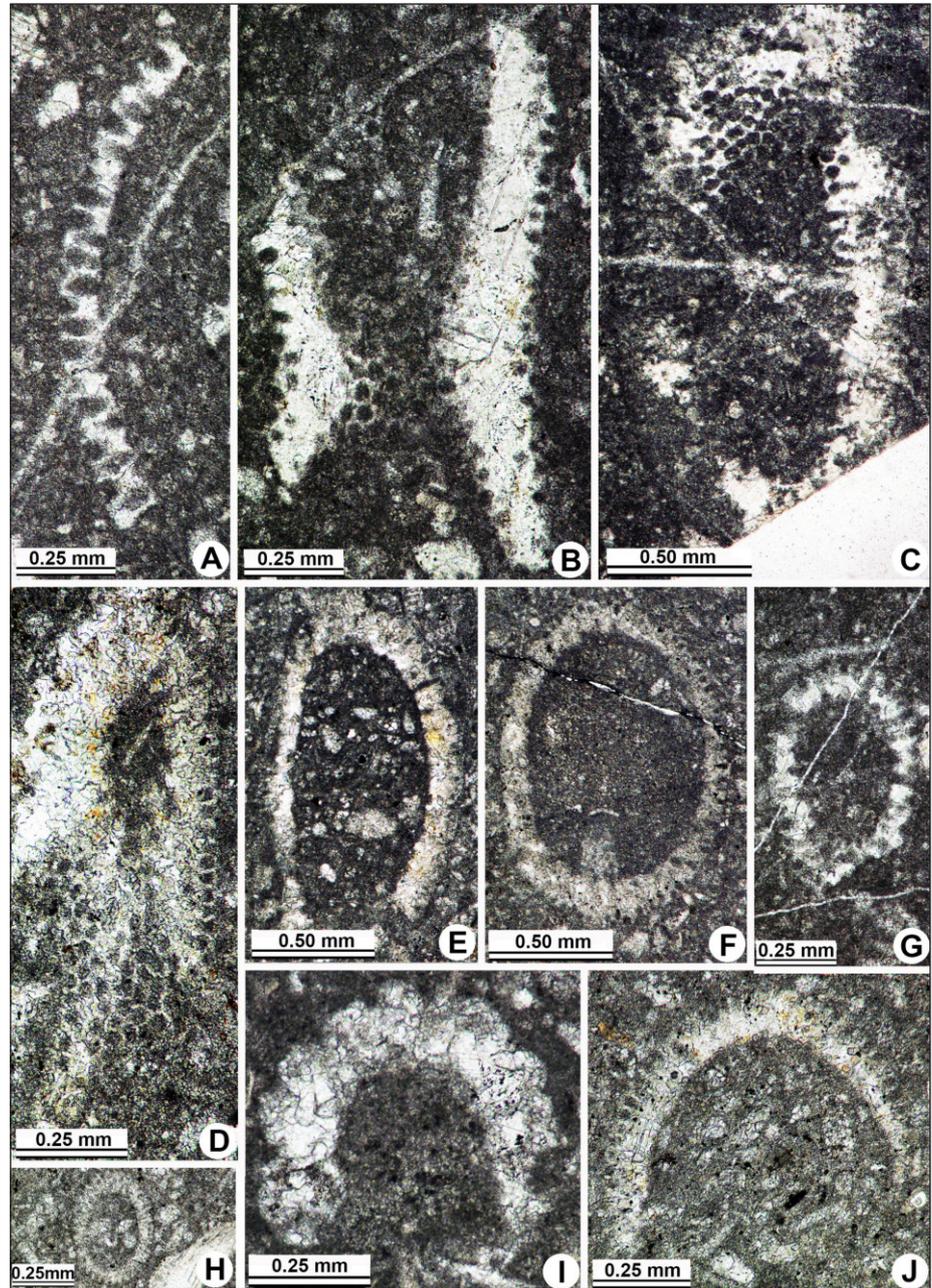
**Stratigraphical range:** *Physoporella jomdaensis* was described by Flügel & Mu (1982) from Carnian limestone of eastern Tibet. The Croatian specimens of Žumberak have a Norian age (Grgasović 1997).

	Flügel & Mu 1982	Grgasović 1997	This paper
L (max. observed)	11.7	4.9	6.600
D	1.5-1.75	0.85-1.06	1.100
d	0.8-1.3	0.47-0.68	0.700
d/D %	63-77	49-64 (57)	63.6
p	0.15-0.22	0.11	0.150
h	0.12-0.25	0.23-0.25	0.200
w	15	14	15-16 (estimated)

Tab. 3 - Comparative dimensions (in mm) of *Physoporella jomdaensis* Flügel & Mu, 1982 from Tibet, Croatia and Japan.

## PLATE 10

- A - *Griphoporella curvata* (Gümbel), fragment in oblique section. Thin section EH-306A; Sonora, Mexico.
- B-D - *Macroporella?* sp., longitudinal oblique (B) and oblique (C, D) sections. B, C, thin section EH-306A; D, thin section EH-216b; Sonora, Mexico.
- E-G, I, J - *Gyroporella* div. sp., oblique sections. E, thin section EH-212A; F, thin section EH-311A; G, thin section EH-306A; I, thin section EH-509; J, thin section EH-216b; Sonora and Baja California, Mexico.
- H - *Salpingoporella* sp., oblique section. Thin section EH-216A; Sonora, Mexico.



The limestone from this locality of the Sambosan Accretionary Complex (Shikoku Island, Japan) is broadly dated as Upper Triassic (Carnian-Rhaetian) (Peybernes et al. 2016b).

Genus *Salpingoporella* Pia in Trauth, 1918 emend.  
Carras et al., 2006

***Salpingoporella* sp.**

Pl. 10H

**Discussion**

One specimen of small dimension ( $D = 0.32$  mm;  $d = 0.21$  mm) identified in a sample from So-

nora (Mexico) has phloiophorous laterals arranged in euspondyle whorls, corresponding to characteristics of the genus *Salpingoporella*.

Family Sellenellaceae Korde, 1950, emend  
Bassoullet et al., 1979

Genus *Gyroporella* Gümbel, 1882

***Gyroporella* div. sp.**

Pl. 6I-K; Pl. 8G; Pl. 10E-G, I, J

**Discussion**

Several *Gyroporella* specimens have been

identified in samples coming from Far East Russia (Pl. 6I (Gy)-K), Japan (Pl. 8G) and from Mexico (Sonora, Pl. 10E-G, J, and Baja California Sur, Pl. 10I). They probably correspond to 2 or 3 different species. Some specimens (Pl. 6J, K; Pl. 8G; Pl. 10I) have laterals with a short tubular proximal part and a relatively large vesicular distal part, while other specimens (Pl. 10E-G, J) have slender and more numerous laterals, with a longer tubular proximal part and a small vesicular distal part. Due to the scarcity of the available material and the diagenetic alteration, a specific determination was not possible.

Genus *Macroporella* Pia, 1912 emend. Bassoullet et al., 1978

***Macroporella?* sp.**

Pl. 10B-D

**Discussion**

Different sections of a dasycladalean alga found in Sierra del Alamo (Sonora, Mexico) present phoiophorous laterals which apparently are not set in verticils (whorls) but are arranged randomly and very close of each other. This tight arrangement causes a mutual pressure of the laterals at their distal part, and hence the polygonal outline (Pl. 10C, D). The strong recrystallisation prevents a good observation of the laterals morphology.

**Dimensions (in mm):**

D = 0.500-0.740

d = 0.200-0.400

p = 0.030-0.050

A dasycladalean alga with a close morphology was described by Flügel & Mu (1982) as *Salpingoporella? tibetica*. The euspondyle arrangement of the laterals of this last species is not very convincing, and it could also belong to the genus *Macroporella*. However, its general dimensions are three times the dimensions of the Mexican species.

Family Polyphysaceae Kützing, 1843

Genus *Chypeina* Michelin (1845) emend. Bassoullet et al., 1978

***Clypeina* cf. *besici* Pantić, 1965 ex Granier & Deloffre, 1994**

Pl. 8H, I

**Discussion**

Two specimens found in the thin section JC-231a from Shikoku Island, Japan belong most probably to *Chypeina besici* Pantić.

**Dimensions (in mm):**

D = 0.760-0.850

d = 0.200-0.400

w = 14

Forma-genus *Patruliuspora* Barattolo, Ionesi & Țibuleac, 2019

***Patruliuspora pacifica* Bucur, Del Piero & Peyrotty n. sp.**

Pl. 11A-O

**Origin of the name:** From the occurrence of the alga in limestone located on both sides (North America and Far East Russia) of the Pacific Ocean.

**Holotype:** specimen in Pl. 11D, thin section WH-259 [MHNG-GEPI-2020-0024].

**Partypes:** Pl. 11A-C, E-N, thin sections WH-232b [MHNG-GEPI-2020-0017], WH-235a [MHNG-GEPI-2020-0021], WH-235b [MHNG-GEPI-2020-0022], WH-259 [MHNG-GEPI-2020-0024], WH-260 [MHNG-GEPI-2020-0025], GP-206C [MHNG-GEPI-2020-0004], GP-206C-2 [MHNG-GEPI-2020-0005].

**Type locality:** Lime Peak, Yukon (Canada).

**Type level:** late Norian.

**Material and repository:** More than 120 specimens identified in 15 thin sections, stored in the Museum d'Histoire Naturelle de Genève under the numbers MHNG-GEPI-2020-0004, 0005, 0006, 0007, 0016-0026.

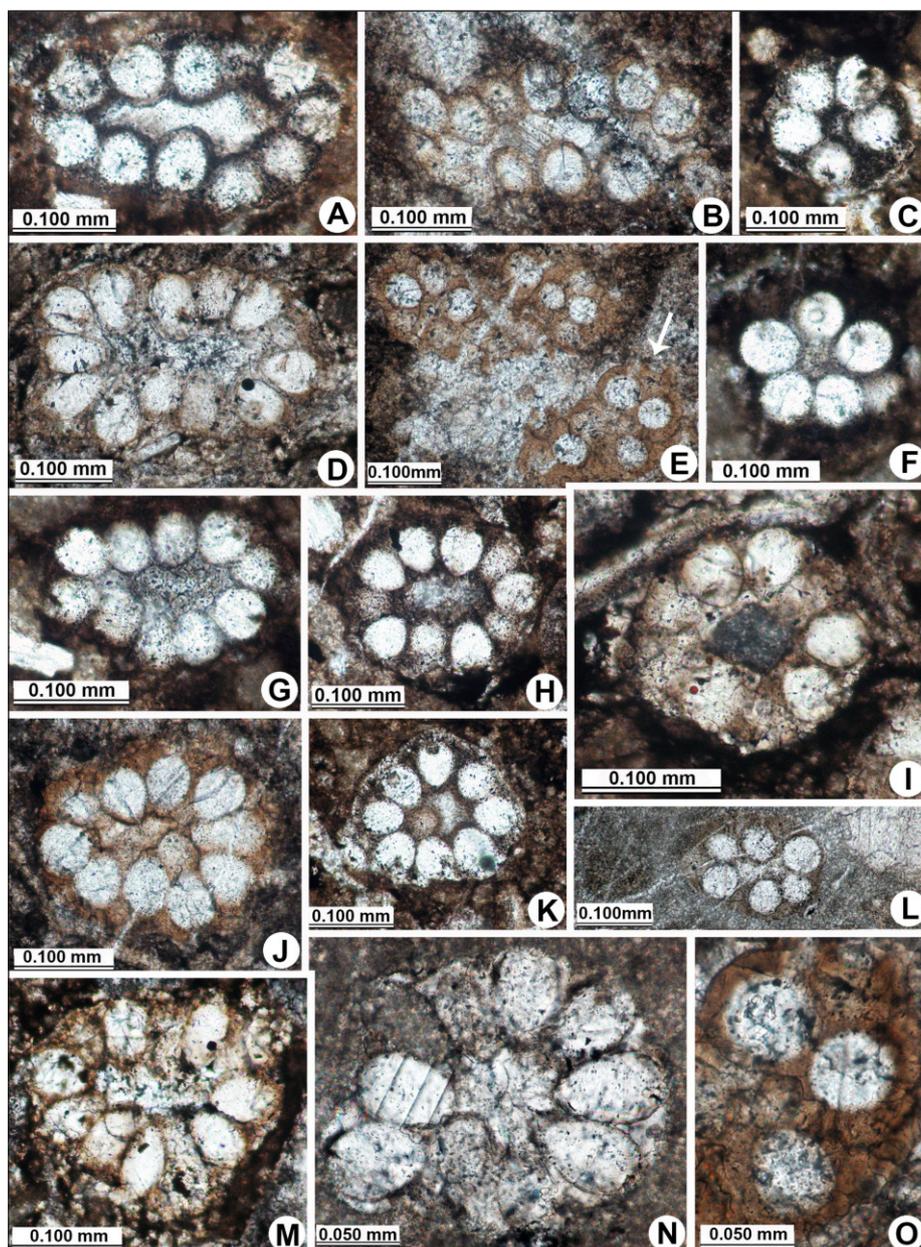
**Diagnosis:** Cyst aggregates (gametophores) of ovoid shape containing small ovoid to spherical cysts (gametangia), arranged more or less on the margins of the aggregates; consequently, the internal part of the aggregate is generally devoid of cysts.

**Description**

The gametophores have an ovoid slightly elongated form (Pl. 11A, B, D, G). The gametangia are also ovoid (Pl. 11D, G-J, N), sometimes ovoid-elongated (Pl. 11M), rarely close to a spheroidal shape (Pl. 11E, F). The gametangia are arranged in the marginal zone of the gametophore; consequently, the central part of the gametophore is frequently devoid of cysts as illustrated by longitudinal and oblique (Pl. 11A, G, H) as well as transverse (P. 11I, K, N) sections. The gametangia have a relatively thick calcified wall. In some specimens (e.g., Pl. 11E, O) the cyst wall is very thick, representing about 15-20% from cyst diameter, and the calcite has a brown color. In other cases (e.g., the Russian specimens, Pl. 11N) the cyst wall is much thinner.

## PLATE 11

A-O - *Patruliusspora pacifica* Bucur, Del Piero & Peyrotti n. sp. A, B, D, G, J) longitudinal and longitudinal-oblique sections of gametophores; E) Several gametophores in transverse or transverse-oblique sections; H, L, M) transverse-oblique sections of gametophores; F, E (arrow) showing the thick wall of gametangia. A, thin section WH-233b; B, E, O, thin section WH-235a; C, F, G, thin section WH-232b; D, M, thin section WH-259; H, K, thin section WH-232a; I, thin section WH-260; J, thin section WH-235b; Yukon, Canada. L, thin section GP-206C-2; N, thin section GP-206C; Dalnegorsk, Far East Russia. D - holotype; A-C, E-N, paratypes.

**Dimensions (in mm):**

Gametophores (aggregates) length = 0.240-0.420 (mean = 0.325)

Gametophores diameter = 0.15-0.350 (0.190)

Gametangia (cysts) diameter = 0.035-0.060/0.055-0.080 (0.051/0.065)

Thickness of the cyst wall = 0.010-0.025

Number of gametangia in a gametophore = about 25-50

**Comparisons:** Only one species of *Patruliusspora* has been known so far from the Triassic of Tethys, *P. carpatica* (Mišik, 1987). The two species, *P. pacifica* n. sp and *P. carpatica* are similar. Dif-

ferences are related to the shape of gametangia (predominantly ovoid, sometimes ovoid-elongated in *P. pacifica*, and spheric in *P. carpatica*), as well as to the arrangement of cysts within the aggregates (filling the whole space in *P. carpatica*; mainly arranged on the margins of the aggregate in *P. pacifica* n. sp.). Moreover, the holotype of *Patruliusspora carpatica* (as *Halicoryne carpatica* in Misik, 1987) was designated the fig. 2, pl. II, which contains several specimens (not a single specimen). Consequently, the Carpathian species is a nomen nudum (cf. Art. 8.1, 8.5 of the International Code of Nomenclature for algae, fungi, and plants, Turland et al. 2018) (see also Granier & Deloffre 1994 p. 67 and Granier & Grgasović 2000, p. 81). No *Patruliusspora*

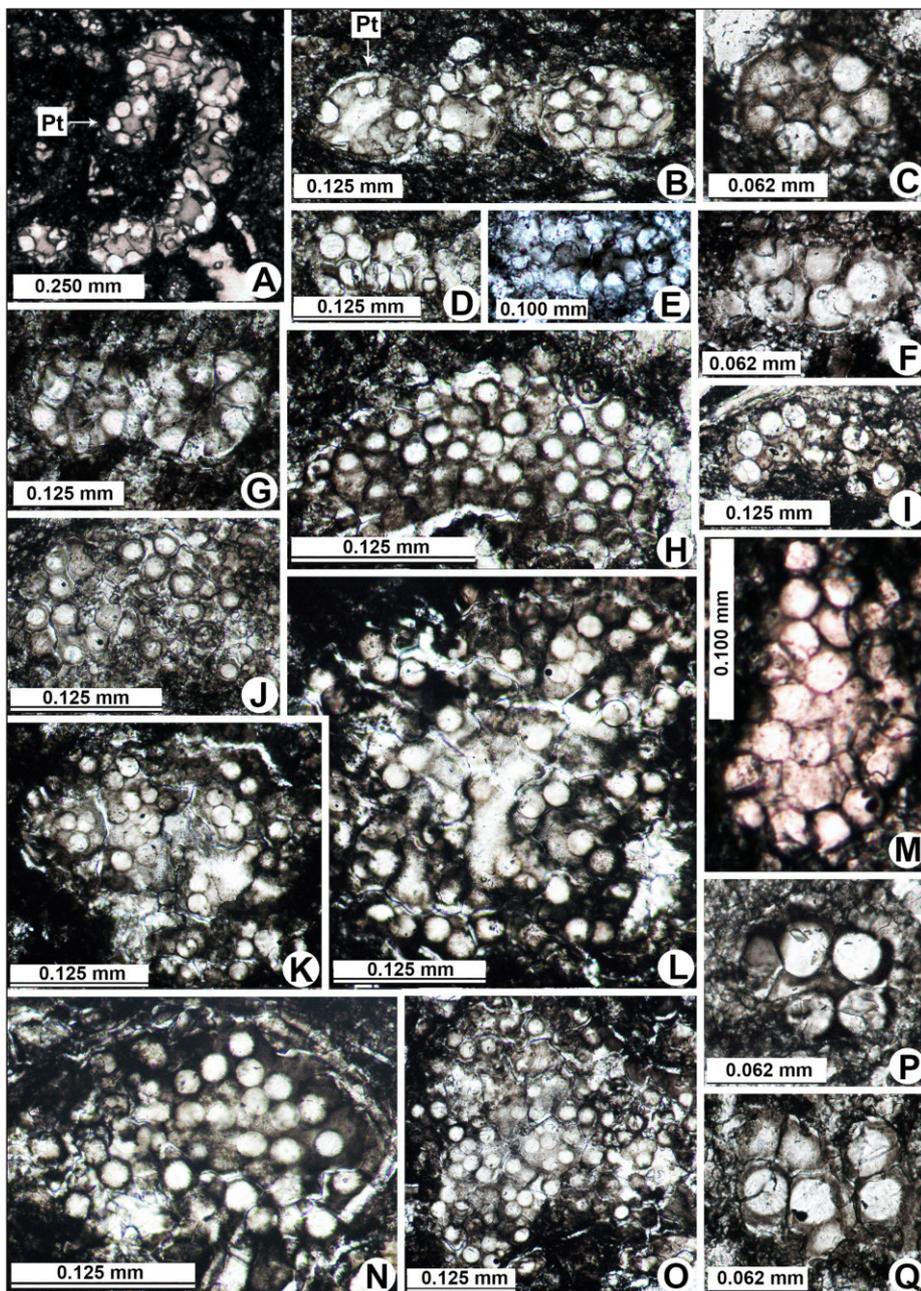


PLATE 12

A-Q - *Patruiliuspora oregonica* Bucur & Rigaud n. sp. A, B, G) several gametophores arranged in a chain-like succession. C-E, F, I) gametophores in longitudinal oblique (C, I), longitudinal (E), or tangential (D, F) sections. H, J-O) clusters of gametophores or free gametangia; P, Q) gametophores in tangential section containing gametangia with a relatively thick wall. A, thin section MQ-41-10; B, J, thin section BMQ-48R-2; C, D, F, H, I, O, Q, thin section MQ-48R-2; E, thin section MQAC-17b; G, thin section MQ-36; K, N, thin section BMQ-48; L, thin section MQ-48; M, thin section MQVHC-41; O, thin section MQ-48-3; Oregon, U.S.A. C - holotype; A(Pt) and B(Pt) - paratypes.

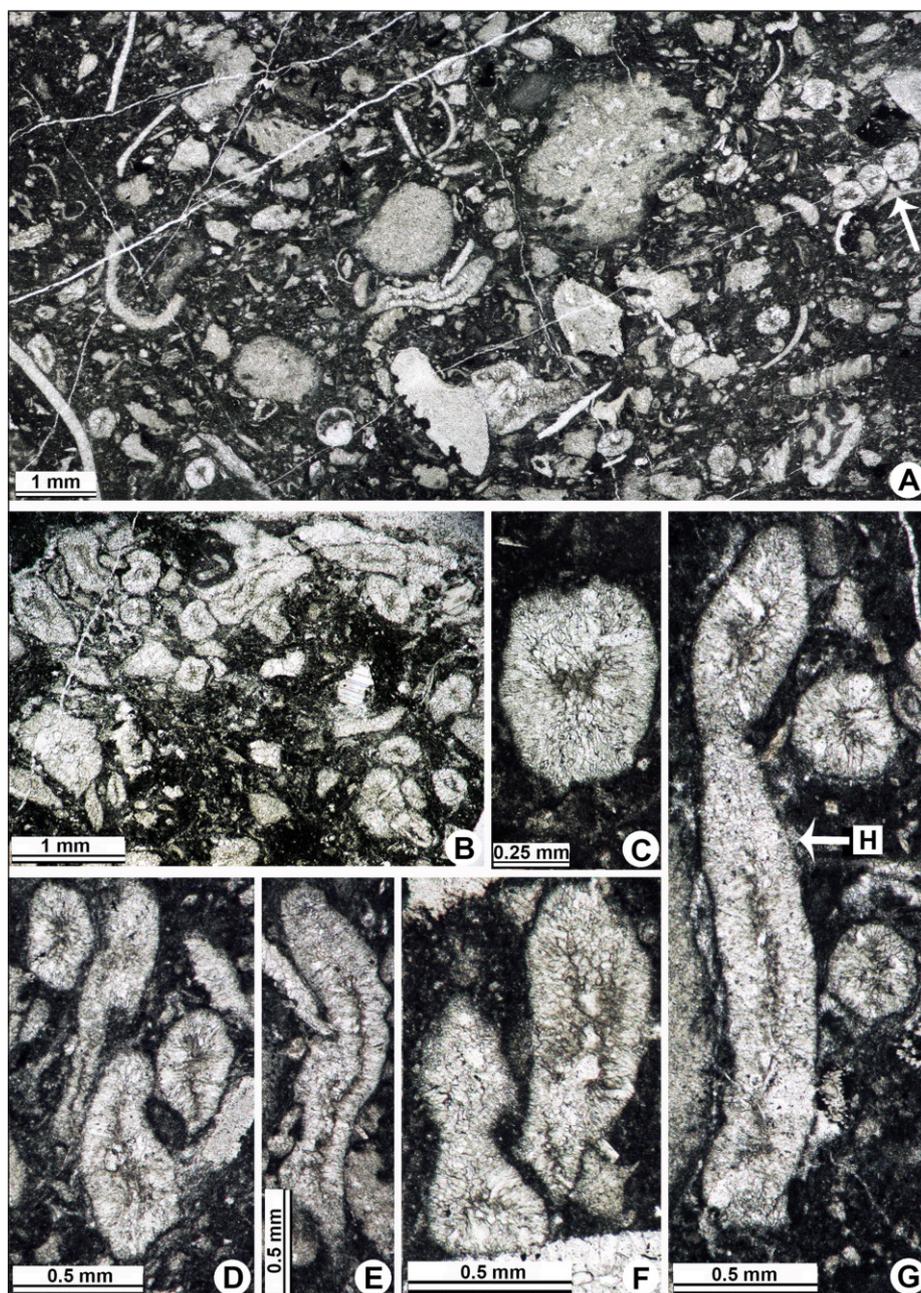
species is reported from Jurassic or Cretaceous. However, Schlagintweit & Sanders described from the Upper Cretaceous of the Northern Calcareous Alps *Terquemella? microsphaera*, a small species with a brownish appearance which probably belongs to the genus *Patruiliuspora*. It differs from *P. pacifica* n. sp. by the smaller number of gametangia and their smaller dimensions. Only one species of *Patruiliuspora* is known from the Miocene (*Patruiliuspora morelleti*). This last species differs from *P. pacifica* by its spherical gametangia and much larger dimensions. For comparisons with *Patruiliuspora oregonica* Bucur & Rigaud n. p. see description of the next species.

## Discussion

Cysts aggregates identified in geological deposits of different ages have been assigned to recent Polyphysaceae or Acetabulariaceae (e.g., *Halicoryne morelleti* Pokorny and *Halicoryne carpatica* Mišik) (Pokorny 1948; Mišik 1987). Granier & Berthou (2002) noted that such fragments, which do not preserve all characteristics of the whole algae, should be more conveniently assigned to a formagenus. Following this point of view, Barattolo et al. (2019) created the genus *Patruiliuspora* for species previously assigned to the genus *Halicoryne* (e.g. Mišik 1987) and subsequently to the genus *Ioanella*

## PLATE 13

A-G - *Collarecodium?* *nezpercae* Bucur & Rigaud n. sp. A, B) Microfacies; wackestone-packstone with several specimens of *Collarecodium?* *nezpercae*, and fragments of molluscs, echinoderms and bryozoans; C) transverse, slightly oblique section; D) several specimens in oblique and transverse-oblique sections; E) longitudinal-oblique section; F) oblique sections with a probably indication of dichotomous branching (lower left); G) longitudinal, slightly oblique, and transverse sections. A, C, G, thin section LQ-27; B, thin section LQ-24; Ihaho, U.S.A. G(H) - holotype; C-F - paratypes.



(Granier & Berthou 2002). Their main argument is that even if such rests come most probably from Polyphysaceae we do not know if the original alga bearing these gametopores had only one corona or two coronae and hence it is impossible to specify the natural generic assignment. Consequently, the gametophores found in the limestone from the Pacific region are assigned to the genus *Patruluspora*.

**Micropalaeontological assemblage:** *Patruluspora pacifica* n. sp. is found in association with abundant small-sized molluscs (bivalves and gastropods), brachiopods, echinoderms, calcimicrobes (*Cayeuxia* sp.), microproblematica (*Baccanella floriformis*) abundant foraminifers and rare corals, sponges

and ostracodes. The foraminifers include abundant involutinidae: *Parvalamella*, *Aulosina*, *Aulotortus*, *Triasina*, common trocholinidae: *Frentzenella*, *Licispirella*, common robertinida: *Robertonella*, *Cassianopapillaria*, *Trochosiphonia*, *Falsoreinboldella*, common mesoendothyridae: *Wernlina* and rare nodosariidae.

**Palaeoenvironment:** *Patruluspora pacifica* n. sp. is found in muddy, organic-rich limestone (mudstone to rudstone textures). These facies were deposited in back-reef and shallow lagoon environments in association with small sponge/coral debris and megalodontid bioherms. Sometimes in these muddy facies *Patruluspora pacifica* n. sp. is one of the most abundant bioclastic component.

***Patrulijspora oregonica* Bucur & Rigaud n. sp.**

Pl. 12A-Q

**Origin of the name:** from Oregon (USA) where the samples with the new species are coming from.

**Holotype:** The specimen in Pl. 12C, thin section MQ-48R-2 [MHNG-GEPI-2020-0062].

**Paratypes:** the specimens in Pl. 12A, thin section MQ-41-10 [MHNG-GEPI-2020-0055] (Pt), and B, thin section BMQ-48R2 [MHNG-GEPI-2020-0042] (Pt).

**Type locality:** Black Marble Quarry, Wallowa terrane, Oregon (USA), GPS coordinates: 45° 22' 23.27"N; 117° 21' 16.40"W.

**Type level:** Lower Norian.

**Material and repository:** more than 30 specimens identified in 10 thin sections stored in the Museum d'Histoire Naturelle de Genève with the numbers MHNG-GEPI-2020-0041, 0042, 0046, 0052, 0055, 0058, 0059, 0062, 0066, 0067.

**Diagnosis:** Spherical to ovoid aggregates (gametophores) of very small cysts (gametangia). The gametophores are attached to each other. Gametangia are usually arranged on the margins of the gametophores. Frequently they appear as clusters of free cysts, or groups of cysts, or as free cysts dispersed in the sediment.

**Description**

The gametophores have a slightly ovoid or spherical shape (Pl. 12A, C, E, G) with gametangia arranged on the marginal part leaving a free space in the middle. Gametangia are small (0.020 to 0.044 mm), spherical, rarely slightly ovoid and have a discrete wall of 3 to 10 microns in thickness. The gametophores seem to be attached to each other forming small chains (Pl. 12A, B, G), but frequently the gametangia are found as free elements in the sediments or as clusters of free cysts or groups of cysts.

**Dimensions (in mm):**

Gametophores (aggregates) length = 0.080-0.200 (mean = 0.138)

Gametophores diameter = 0.054-0.125 (0.096)

Gametangia (cysts) diameter = 0.020-0.045(0.0325)

Thickness of the cyst wall = 0.003-0.010

**Comparisons:** By its very small gametangia, *Patrulijspora oregonica* n. sp. differs from both *Patrulijspora carpatica* Misik and *Patrulijspora pacifica* n. sp., the two species with close similarities. Also, the chain-like arrangement of the gametophores makes a difference.

**Micropalaeontological assemblage:** *Patrulijspora oregonica* n. sp. is found in association with abundant molluscs (gastropods, bivalves), foraminifers, brachiopods, bryozoans, sponges, corals and ostracodes.

The foraminifers include various Involutinidae: *Aulosina*, *Aulotortus*, *Parvalamella*, Trocholinidae: *Frentzenella*, *Licispirella*, *Trocholina*, *Wallowaconus*, abundant Robertinida: *Robertonella*, *Cassianopapillaria*, *Falsoreinboldella*, *Trochosiphonia*, and common Mesoendothyridae: *Wernlina*, Polymorphinidae: *Eoguttulina* and nodosariidae, as well as rare miliolids and ophthalmidiids (see Rigaud 2012; Rigaud et al. 2010, 2012, 2013a-b, 2015 a-b, 2016).

**Palaeoenvironment:** organic-rich muddy limestone (involutinids-rich mudstone to packstone), shallow and restricted, periodically hypersaline lagoonal facies.

**Order Bryopsidales Schaffner, 1922**

?Family Udoteaceae Agardh, 1887

Genus *Collarecodium* Brandner & Resch, 1980***Collarecodium? nezpercae* Bucur & Rigaud n. sp.**

Pl. 4K-M, Pl. 13A-G

**Origin of the name:** for the Nez Perce Native Americans from Nez Perce Indian Reserve located in Lapwai. The Mission Creek Quarry is located inside this Reserve.

**Holotype:** the specimen in Pl. 13G left part (H), thin section LQ27 [MHNG-GEPI-2020-0031].

**Paratypes:** the specimens in Pl. 4L-K; Pl. 13C-F, thin section LQ 27 [MHNG-GEPI-2020-0031] and Pl. 4M, thin section LQ24 [MHNG-GEPI-2020-0030].

**Type locality:** Mission Creek Quarry (Idaho, USA), GPS coordinates 46°17'34.37"N; 116°42'02.69"W.

**Type level:** Norian.

**Material and repository:** tens of specimens found in 4 thin sections (LQ-24, LQ-27, Idaho, and MQ-33R3, MQ-43, Oregon, USA) stored in the Museum d'Histoire Naturelle de Genève, under the numbers MHNG-GEPI-2020-0030, 0031, 0048 and 0057.

**Diagnosis:** Slender cylindrical thallus, ramified dichotomic or even trichotomic. Weak calcification of the internal filaments (siphons). Medullary filaments, parallel to the thallus axis, bent outwards and end in a cortex made of very fines filaments.

**Dimensions (in mm)**

Length of branches (maximum observed) = 2.370

External diameter of branches = 0.250-0.500 (mean = 0.346)

Diameter of medullary filaments = 0.015-0.025

**Description**

The alga was found mainly as several fragments inside a bioclastic wackestone (Pl. 13A). They

represent branches of a cylindrical thallus presenting dichotomous (Pl. 12D, F, G) or even trichotomous (Pl. 4K, Pl. 13A- arrow) branching. The middle part of the branches is darker in color and seems to preserve better the shape of the filaments (Pl. 13G, holotype). The largest part of the thallus is replaced by sparitic crystals, which seem to mimic the path of the filaments. They are larger in the middle part, and become thinner towards the exterior. The very small, elongated crystals in the marginal part correspond most probably to the cortex of the alga. Rare specimens (Fig. 4) found in a sample from Black Marble Quarry (Oregon) show a very strong recrystallization, but the sparitic crystals delimitate very well a large medullary zone, and a thin cortical zone.

**Comparisons:** The type species of the genus *Collarecodium*, *C. oenipontanum*, was described by Brandner & Resch (1980) from lower Carnian limestone of the Northern Calcareous Alps. The thallus of this species presents constrictions accompanied by protrusions in a form of a collar. This characteristic, and the general dimensions (much smaller in *Collarecodium? nezpercae* n. sp.) make the difference between *C. oenipontanum* and the new species. Senowbari-Daryan & Zamparelli (2005) described a second species, *Collarecodium cornuformis*, from Ladinian reef limestone of Dolomites (Italy). It has a peculiar horn-like or antler-like ramification, but does not have the characteristic constrictions with collars of the type species. Dimensions are closer to our new species (even generally a little bit larger), but the type of ramification, the well-defined medullary and cortical zones, and the type of calcification differentiate this species from *Collarecodium? nezpercae* n. sp.

### Discussion

In creating the genus *Collarecodium* Brandner & Resch (1980) introduced in the generic diagnosis all the features of the new species *C. oenipontanum*, including the constrictions and the related collar-like protrusions (sculptures). Senowbari-Daryan & Zamparelli (2005) did not find the annulation and the collar-like sculptures in their new species *C. cornuformis*, but still assigned the species to the genus *Collarecodium*. The same authors (Senowbari-Daryan & Zamparelli 2005, pl. 1, fig. 1-3) illustrated specimens of strongly recrystallized *Collarecodium oenipontanum* showing ramification but no traces of fi-

laments. Such strong recrystallized specimens have been illustrated also by Brandner & Resch (1980, pl. 2, fig. 5). Moreover, the specimens illustrated in pl. 1, fig. 3, 4 (Brandner & Resch 1980) show a thin darker zone in the central part of the branches, just like in *Collarecodium? nezpercae* n. sp. However, we cannot find bush-like “colonies” in the American material. Together with the lack of constrictions and collars, this was an argument to assign with doubt the new described species to the genus *Collarecodium*.

**Micropalaeontological assemblage:** *Collarecodium? nezpercae* n. sp. is associated with abundant echinoids, porostromates, molluscs (gastropods, bivalves), less abundant brachiopods, red algae, coprolites, and robertinid foraminifers (*Cassianopillaria*, *Praereinholdella*) and rare other benthic foraminifers (e.g., *Parvalamella*, *Wernlina*) (Rigaud 2012; Rigaud et al. 2012, 2015a).

**Palaeoenvironment:** alga/porostromate/echinoid-rich wackestone-floatstone/rudstone levels in an overall muddy, lagoonal succession with more or less abundant corals, molluscs, echinoderms and sponges.

Family Gymnocodiaceae Elliott, 1955

Genus *Permocalculus* Elliott, 1955

### *Permocalculus* sp.

Fig. 5; Pl. 6I (Pm)

Several specimens of *Permocalculus* were found in a sample from Dalnegorsk (Far East Russia). The oblique sections of the thallus show a highly recrystallized skeleton pierced by thin pores in the marginal part. Ovoid to ovoid-acuminate small bodies are visible in some specimens in a subcortical position. Elliott (1955) has interpreted such structures as possible reproductive organs.

### Dimensions (in mm):

External diameter: 2.580-3.680

Thickness of the calcareous wall: 0.600-1.310

Diameter of the cortical pores: proximal = 0.030-0.043; distal = 0.045-0.065

### Discussion

Gymnocodiaceans, including the two genera *Gymnocodium* and *Permocalculus*, were long time regarded as red algae (Pia 1937; Elliott 1956; Mu

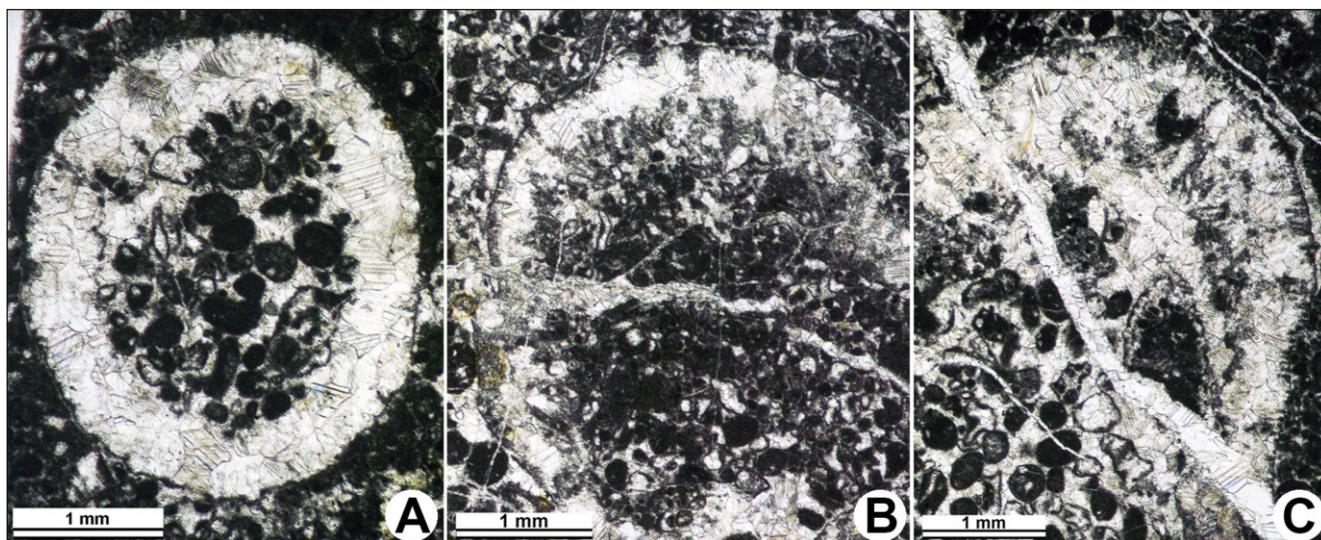


Fig. 5 - A-C - *Permolaculus* sp., specimens in oblique section. Sample GP-152 (Dalnegorsk, Far East Russia).

1991). Several species have been separated based on the external morphology and, mostly, on the diameter and shape of the cortical filaments as well as the shape and position of the “reproductive structures”. Discussing the taxonomic position of gymnocodiaceans, Bucur (1994) considered that there are no arguments to include this group into red algae (no cross partitions within the filaments, and internal structure similar to that of other bryopsidaleans) and that gymnocodiaceans should be included among green algae together with udoteaceans and halimedaceans (see also Radoičić 2004).

downwards and upwards on the margins). This part corresponds to the ventral core (or hypothallus) in Senowbari-Daryan et al. (2002). In the upper part of the core the filaments run perpendicular to the substrate. In this part, rare transverse partitions are visible in the filaments delimitating small cells (Pl. 14C, arrow). The peripheral thallus (perithallus) is very thin (two or three rows of very small cells; Pl. 14A, arrows). Prominent struts like in the type specimens have not been observed, but some bulbous irregularities in the lower part of the ventral core are present (e.g., Pl. 14A, B).

Phylum **RHODOPHYTA** Wettstein, 1901  
 Class **FLORIDEOPHYCEAE** Cronquist, 1960  
 ?Order **Corallinales** Silva & Johanson, 1986  
 Genus *Norithamnium* Senowbari-Daryan, Keupp,  
 Abate & Vartis-Matarangas, 2002

*Norithamnium madoniensis* Senowbari-Daryan,  
 Keupp, Abate & Vartis-Matarangas, 2002  
 Pl. 14A-C

2002 *Norithamnium madoniensis* nov. sp., Senowbari-Daryan et al., p.202, figs. 1-3, pl. I, figs. 1-6; pl. II, figs. 1-9

### Description

Superimposed crusts of slender, irregular thalli randomly cut (Pl. 14A). The individual crusts consist of a lower thicker part made up of small rectangular cells arranged in a “water jet” manner (parallel to the substrate in the middle, and getting

### Dimensions (mm):

Length of the thallus: between 4 and 10  
 Ventral core (hypothallus) = 0.250-0.500  
 Perithallus = 0.030-0.050  
 Cell diameter = 0.010-0.030

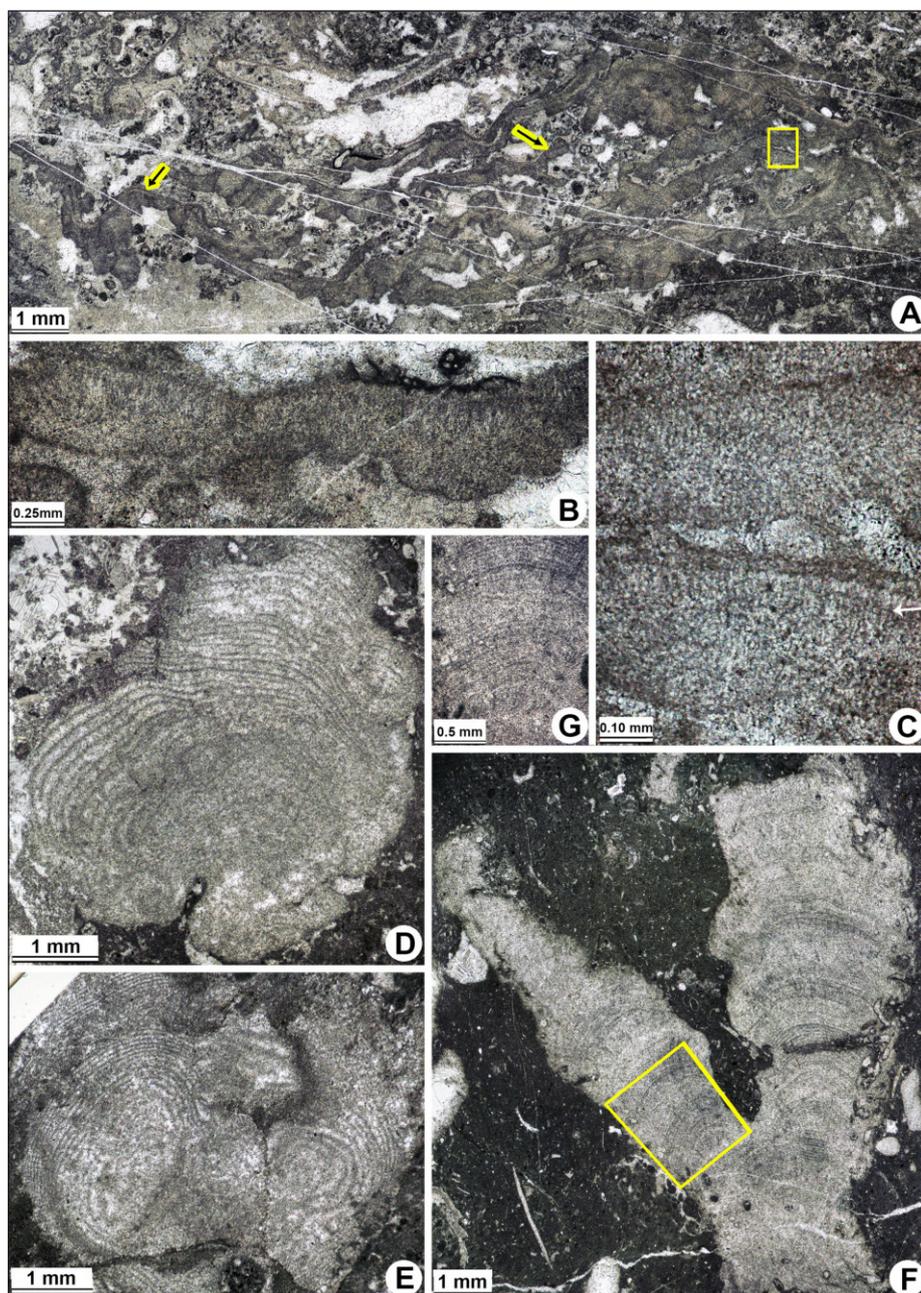
### Discussion

*Norithamnium madoniensis* described by Senowbari-Daryan et al. (2002) from Norian-Rhetian reef limestones of Sicily, Greece, and Austrian Alps, was assigned to Corallinales by comparison with the Recent coralline alga *Synarthrophyton schielianum* Woerkerling & Foster, 1989. The similarity consists mostly in the aspect of the thin (lamellar) thallus and the presence of ventral struts which have an anatomy like that of the lamellae. However, Senowbari-Daryan et al. (2002) did neither find evident partitions separating cells inside the filaments of *Norithamnium*, nor conceptacles. Consequently,

## PLATE 14

A-C - *Norithamnium madoniensis* Senowbari-Daryan, Keupp, Abate & Vartis-Matarangas. A - several specimens growing as superimposed crusts on the substrate. The rectangle shows the location of the close-up view in C; arrows point on the thin peripheral thallus; B - longitudinal-oblique section showing some bulbous irregularities in the lower part, probably equivalent of struts-like elements; C - close-up view of the specimen in A (rectangle) showing some transverse partitions within the filaments (arrow). Thin section CP-259b; Sambosan, Shikoku Island, Japan.

D-G - "*Parachaetetes*" sp. D, E - Nodular-lobate specimens similar with "*Parachaetetes*" *triassinus* or "*Parachaetetes*" *cassianus*; F - branched specimen similar with "*Parachaetetes*" *maslovi*; G - close-up view of the specimen in F (rectangle). D, thin section FA-48B; E, thin section FA-210; F, G, thin section FA-50-2a; California, U.S.A.



this suprageneric attribution remain uncertain (Senowbari-Daryan et al. 2002, p. 204). These authors exclude also the close affinity of *Norithamnium* with the encrusting red algae of the family Peyssonneliaceae Denizot (Denizot 1968), even if the structural organization of *Norithamnium* is more similar to some peyssonneliacean algae (e.g., genus *Peyssonnelia* Decaisne, 1841) than to Corallinales. Their argument is that all modern peyssonneliacean taxa are aragonitic and the microcrystalline preservation of *Norithamnium* skeletons proves their primary calcitic mineralogy (Senowbari-Daryan et al. 2002, p. 204). The morphology of *Norithamnium madoniensis* is indeed similar to some peyssonneliacean morphology

(not only *Peyssonnelia*, but also *Polystrata* and *Ethelia* with a "plumose" ventral core; e.g., Pfender 1936; Massieux & Denizot 1964). The present-day mineralogy of these algae is aragonitic, as noted by Senowbari-Daryan et al. (2002) but the fossil *Peyssonnelia antiqua* (Johnson, 1964) shows a micritic cell wall. This inconsistency was elucidated by Bassi et al. (2005) which consider the assignment of *Peyssonnelia antiqua* to peyssonneliaceans as inappropriate; they also consider *P. antiqua* as a younger synonyme of *Karpathia spherocellulosa* Maslov 1962, and assign this alga to Mastophoroideae (Corallinales).

**Stratigraphic range:** Norian-? Rhaetian reef limestone from Sicily, Greece and Northern Cal-

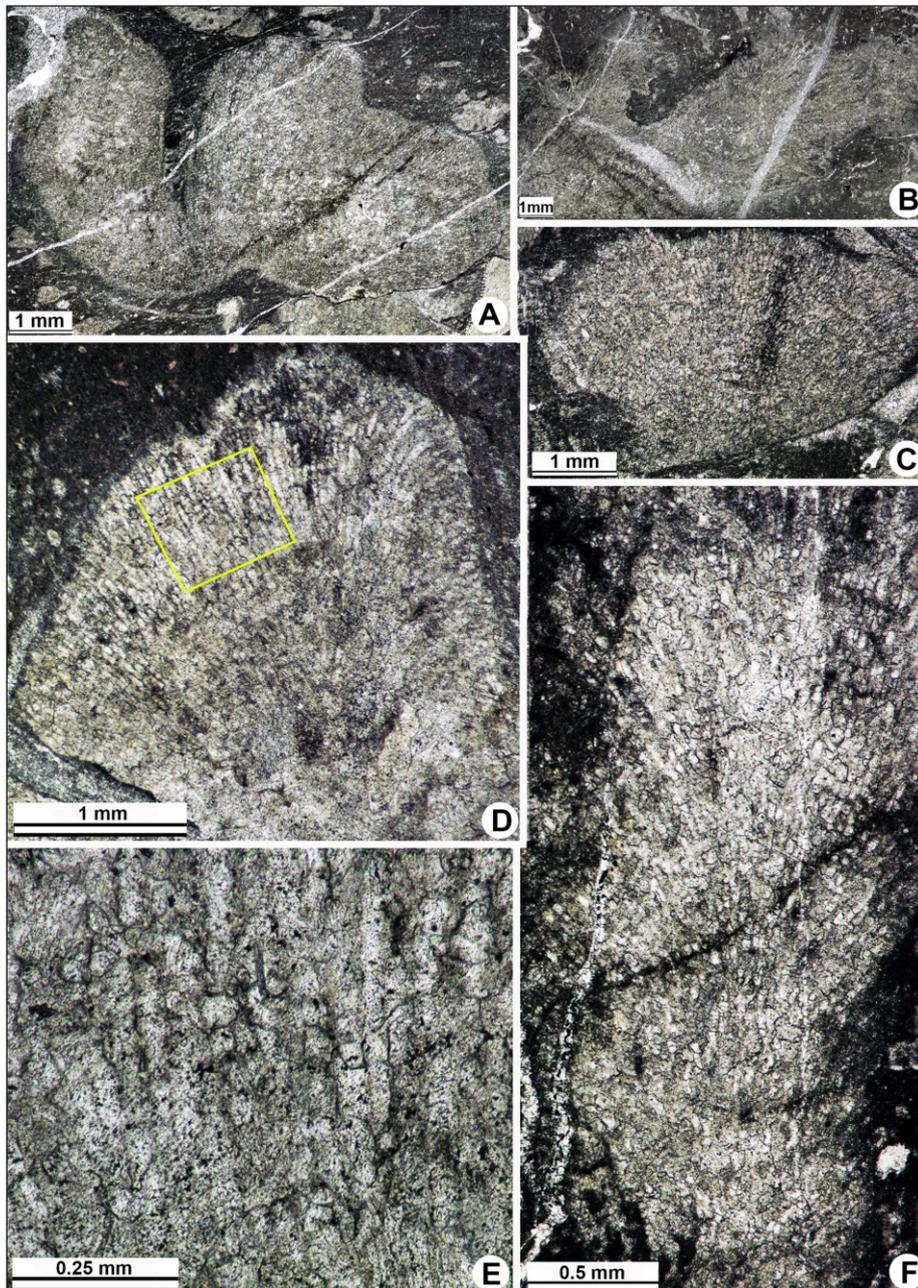


PLATE 15

A-F - "*Solenopora*" sp. Nodular-lobate (A-E) and branched (F) specimens; E - close-up view of the specimen in D (rectangle). A, thin section LQ-39D; B, D, E, thin section LQ-39A; C, thin section LQ-5; F, thin section LQ-27; Idaho, U.S.A.

careous Alps (Gosaukamm, Austria) (Senowbari-Daryan et al. 2002). The specimens described and illustrated in this paper are coming from Upper Triassic limestone of Sambosan type locality, Shikoku Island (Japan).

?Order **Rhodogorgonales** Fredericq, Norris & Puschel in Fredericq & Norris, 1995  
Family **Elianellaceae** Granier in Granier & Dias-Britto, 2016

?Genus "*Parachaetetes*" (Deninger, 1906)

?Genus "*Solenopora*" Dybowski, 1879

### "*Parachaetetes*" sp.

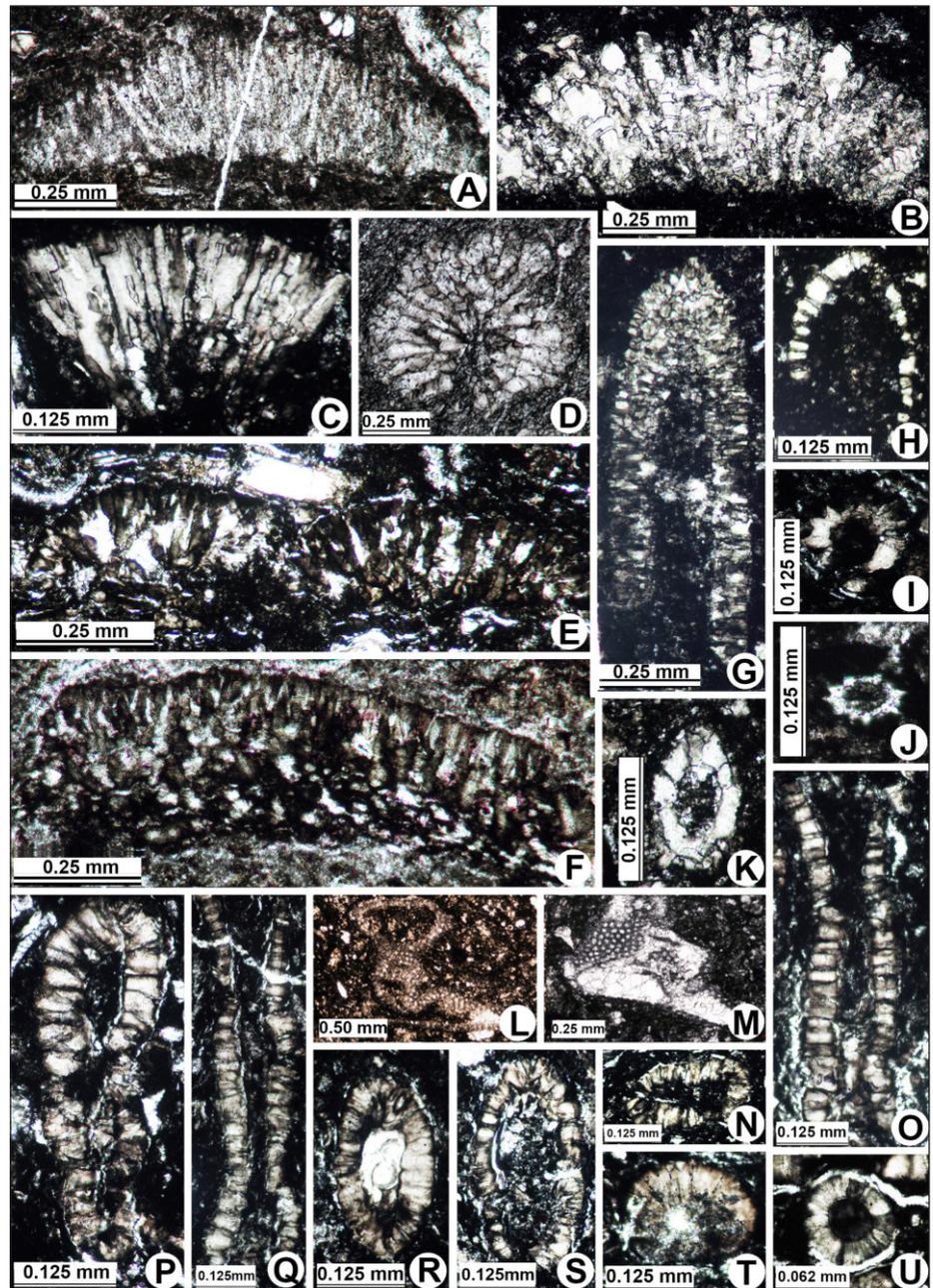
Pl. 14D-G

#### Description

Nodular lobate and branched thalli found in several samples coming from California can be assigned to the so-called "solenoporacean" red algae. The specimens in Pl. 14D and E are similar with "*Parachaetetes*" *triassinus* Vinassa de Regny or with "*Parachaetetes*" *cassianus* Flügel (Vinassa de Regny 1915; Flügel 1961). The strong diagenesis obliterates the internal structures, and the wall of the radial filaments as well as the cells, are impossible to

## PLATE 16

- A-D - Rivulariacean-like cyanobacteria. A, thin section MQ-33R-3; B, thin section MQ-16; C, thin section MQ-41; D, thin section MQ-7D; Oregon, U.S.A.
- E, F - Udoteacean green algae. E, thin section BMQ-48; F, thin section MQ-33R-3-2; Oregon, U.S.A.
- G - K - Dasycladalean green algae in longitudinal-oblique (G, H), oblique (K) and transverse (I, J) sections. G, thin section MQ-16D; H, thin section MQ-41D; I, J, thin section MQ-48-3; K, thin section MQ-41; Oregon, U.S.A.
- L, M - *Thaumatoporella* sp. L, thin section MQ-34-9; M, thin section MQ-19-1; Oregon, U.S.A.
- N-U - Problematic microfossil with possible algal affinity in longitudinal (O, Q), longitudinal-oblique (P), oblique (R, S), transverse-oblique (N, T) and transverse (U) sections. N, thin section MQ-48; O, thin section MQ-48-4; P, thin section MQ-48D; Q, thin section MQ-48-2; R, S, thin section BMQ-48; T, U, thin section MQ-48-3; Oregon, U.S.A.



be distinguished. Only concentric dark micritic lines separated by slightly larger light sparitic intervals are visible.

The specimen in Pl. 14F is closer to "*Para-chaetetes*" *maslovi* Flügel (Flügel 1975). The concentric rows inside the branches have smaller dimensions, and the radial filaments are visible in some places (Pl. 14G).

*"Solenopora"* sp.

Pl. 15A-F

**Description**

Numerous specimens of nodular-lobate or

branched morphology (P. 15A-C) have been found in samples from Mission Creek Quarry in Idaho. The radial filaments inside the nodulus are well visible; they are delimited by thin micritic walls (Pl. 15D, F). Thin micritic transverse partitions delimitate cells inside the filaments. The thallus dimensions can reach more than 12 mm. The filaments have a diameter of 0.03-0.04 mm, and the cells can reach 0.07 mm in length.

**Discussion**

The palaeontology of this group of algae known in literature as solenoporaceans is very controversial. Riding (2004) showed that the type

species of the genus *Solenopora* Dybowski, 1879 is a chaetetid sponge and consequently the authentic solenoporaceans, restricted to the Lower Palaeozoic do not belong to the red algae. Riding (2004, p. 120) also noted that “*Parachaetetes* Deninger and *Pseudochaetetes* Haug are likely to be chaetetids”. Moreover, in examining the type collection of Maslov, Bassi et al. (2005) found that some species assigned by different authors to *Parachaetetes* (*Parachaetetes palaeozoicum* Maslov, and *P. johnsonii* Maslov) belong to the valid genus *Solenophyllum* Maslov (Maslov 1935). Bassi et al. (2005, p. 939) noted that: “*Parachaetetes* was described by Deninger (1906) as a Jurassic tabulate and the original drawing of the species show internal vertical projections within the tubes that can be interpreted as septa. Although the type of *Parachaetetes* seems to be lost, the original illustration suggests that Pia’s (1937) interpretation of *Parachaetetes* as an alga is inaccurate”. These statements create a great problem within this group of fossils, because many of the described genera and species belong to genuine algae. To solve part of this problem, Granier (in Granier & Dias Brito 2016) created the family Elianelleaceae including the “solenoporaceans” *Elianellella*, *Parachaetetes* and *Cordilites*, and tentatively assigned this family to the Order Rhodogorgonales. As mentioned above, *Parachaetetes* is most likely to be also a chaetetid. New generic names would be necessary for genuine algae assigned by different authors to *Solenopora* and *Parachaetetes*. However, this would be a strenuous work because many tens of species have been assigned to these two genera in the last 140 years, and all of them need to be revised.

## PALAEOBIOGEOGRAPHIC SIGNIFICANCE

Until recently, calcareous green algae were regarded as anomalously rare and poorly diversified in Panthalassa. Flügel et al. (1989) noted that in the Pacific realm (North America, but also Japan, Timor and New Guinea areas containing Triassic reef carbonates) the dasycladalean algae are inexplicably rare, and “the absence of algae in the western Pacific mirrors the general trend in Western North America, with the notable exception of northeastern Oregon” (Flügel et al. 1989, p. 380). However, as emphasized in the present paper, a more detailed research revealed the existence of a much richer algal assemblage in Panthalassa than previously thought.

Apart from Oregon, the dasycladalean calcareous algae were also found in Yukon, Idaho, Nevada, Mexico, Japan, and Far East Russia. Locally they are associated with udoteaceans (Oregon and Idaho, and Far East Russia) and with elianellacean (solenoporacean auct.) red algae. Dasycladaleans and udoteaceans, growing in very shallow waters, were found in more or less restricted lagoonal or back-reef environments, while elianellacean red algae are related to genuine reef facies where they frequently play a constructional role. Contrary to dasycladaleans, “solenoporaceans” were frequently reported, in several studies on Triassic reef limestone rocks of Panthalassa (e.g., Reid 1985; Stanley & Senowbari-Daryan 1986; Senowbari-Daryan et al. 2012), and Flügel (2002) emphasized their important role as reef builders.

Similarly to other fossil groups (corals, spongiomorphids, bivalves, gastropods, foraminifers, ostracodes, etc...) found in more or less far-travelled allochthonous Panthalassan terranes and in autochthonous deposits of America, calcareous algae assemblages from Panthalassa consists of both endemic (6 new species of green algae are described in the present paper) and common taxa (13 taxa, genera and species). These latter are frequently found in the Tethyan realm. A close connection with Tethys was assumed by Tollmann & Tollmann (1982) and Flügel et al. (1989). Flügel (2002) synthesized several hypotheses related to the coincidences of the taxonomic composition of benthic Triassic faunas identified in North and South America with Tethyan taxa. For the influence of palaeolatitude on reefs distribution in Panthalassa see also Martindale et al. (2015). Kristan-Tollmann (1988, 1990) and Peybernes (2016a) noted that the vast Panthalassan Ocean does not seem to be an efficient barrier to faunal dispersal during the Late Triassic, even for sessile organisms without planktonic stage. For instance, the reefal biota from the Sambosan Accretionary Complex (SAC), Japan [including benthic foraminifers showing a “...remarkable spread between Panthalassan Ocean from Carnian to Rhaetian” (Chablais 2010, p. 177)] display strong taxonomic affinities with their counterparts in Oman, indicating a biogeographic connection between the southern Tethys and western Panthalassa during the Late Triassic. Japanese reefs also show affinities with reef fauna from Stikinia (Yukon), indicating longitudinal migrations of reefal faunas during the

Norian (Peybernes 2016a). To explain that, the stepping stone hypothesis (Grigg & Hey 1992; Stanley 1994) is usually favored and palaeoecological conditions (latitude, temperature, salinity, water currents, specific nutrients and stable ecosystems) are regarded as the main factors explaining the presence or absence of Upper Triassic taxa in the Tethys and Panthalassa (see Chablais et al. 2010 for foraminifers). Yet, in Late Triassic times, the Tethys was only open to the east (i.e. on the Western Panthalassa; Fig. 6). The Hispanic corridor, a “central Atlantic” epeiric seaway linking the Tethys with Eastern Panthalassa associated with the break-up of the Pangea supercontinent, did not open before Sinemurian-Pliensbachian times (Smith 1983; Porter et al. 2013; Dera et al. 2015). Hence, the “stepping stone hypothesis” would only partially explain the cosmopolitan distribution of Upper Triassic calcareous algae. The distribution of marine calcareous algae during the Late Triassic is most likely less affected by the distribution of landmasses and volcanic islands than previously thought. An effective long-range dispersal mean is required to explain the wide distribution of some Upper Triassic calcareous algae.

Water masses, floating substrates and neritic animals are the few long-distance dispersal mechanisms, possibly mutual, that have been proposed or exemplified in the literature to explain the distribution of marine algal communities (e.g., Santelices 1990; Norton 1992). Long-range algal dispersal as spores, propagules, or re-suspended juveniles, which are typically observed in marine environments, is generally excluded as: i) there is no convincing evidence available (van den Hoek 1987) and ii) spore/propagule viability is low (Santelices 1990) and such dispersal mechanism would require better protective envelopes and greater resources (Norton 1992). Moreover, calcareous spores, propagules and juveniles, heavier, would rapidly settle on the substratum. Nevertheless, although most algae cannot float, they can be transported (especially as juveniles) by drifting wood and algae. These “floating islands” harbor a large number of attached benthic organisms that do not float naturally and can travel farther than their spores or propagules, and therefore, may serve as an efficient dispersal mechanism, especially after a major storm or tsunami event (e.g., Highsmith 1985; van den Hoek 1987; Jokieli 1990; Santelices 1990; Norton 1992; Carlton et al. 2017). This mechanism was proposed by Kristan-

Tollmann (1988) to explain the wide distribution of Triassic foraminifers. In modern environment, Hobday (2000) noticed that species richness on floating algae is independent of the distance from the shore, implying that drifting material may represent an efficient dispersal mechanism for a great variety of organisms. Neritic animals, which dispersal covers greater distances (Kinlan & Gaines 2003), may alternatively be responsible for the dispersal of calcareous algae, by either external or internal transport (e.g., Santelices 1990; Norton 1992; Vermeij et al. 2013). Algae have been found covering the shell or skin of several neritic organisms (e.g., turtles and fishes: see Santelices 1990 and references therein) and their spores may survive intestinal passage (digestion), an ability demonstrated in some modern marine and freshwater algae (Vermeij et al. 2013; Boedeltje et al. 2019). In the latter case, one may wonder whether the time during which a given spore will remain in the digestive system before re-emerging in faecal droppings is sufficient for long-distance dispersal. A food chain can be complex and its length would be difficult to estimate: a viable algal spore may ultimately be encased in a faecal dropping that does not belong to the animal that originally consumed it. Long-range dispersal surely exists and its mechanisms may not be exclusive but as noted by van den Hoek (1987), it is the exception as opposed to the rule. If long-range algal dispersal was highly effective, Tethyan and Panthalassan assemblages would display greater similarities.

In order to test those statements, data were located on the PANALESES plate tectonic model, the sole model - to date - that reconstruct the Panthalassic realm.

## THE PANALESES PLATE TECTONIC MODEL

The PANALESES model is a global plate tectonic model with maps being created (still under development) every 10 Ma from the Tonian (Neoproterozoic) to present (Vérard 2019a, b). The PANALESES model supersedes a former model created at the University of Lausanne (e.g., Stampfli & Borel 2002; Hochard 2008) and uses the same techniques and *savoir-faire*. The definition of synthetic isochrones, in particular, helps reconstructing not only continental areas, but also oceanic realms including those having disappeared with subduction proces-

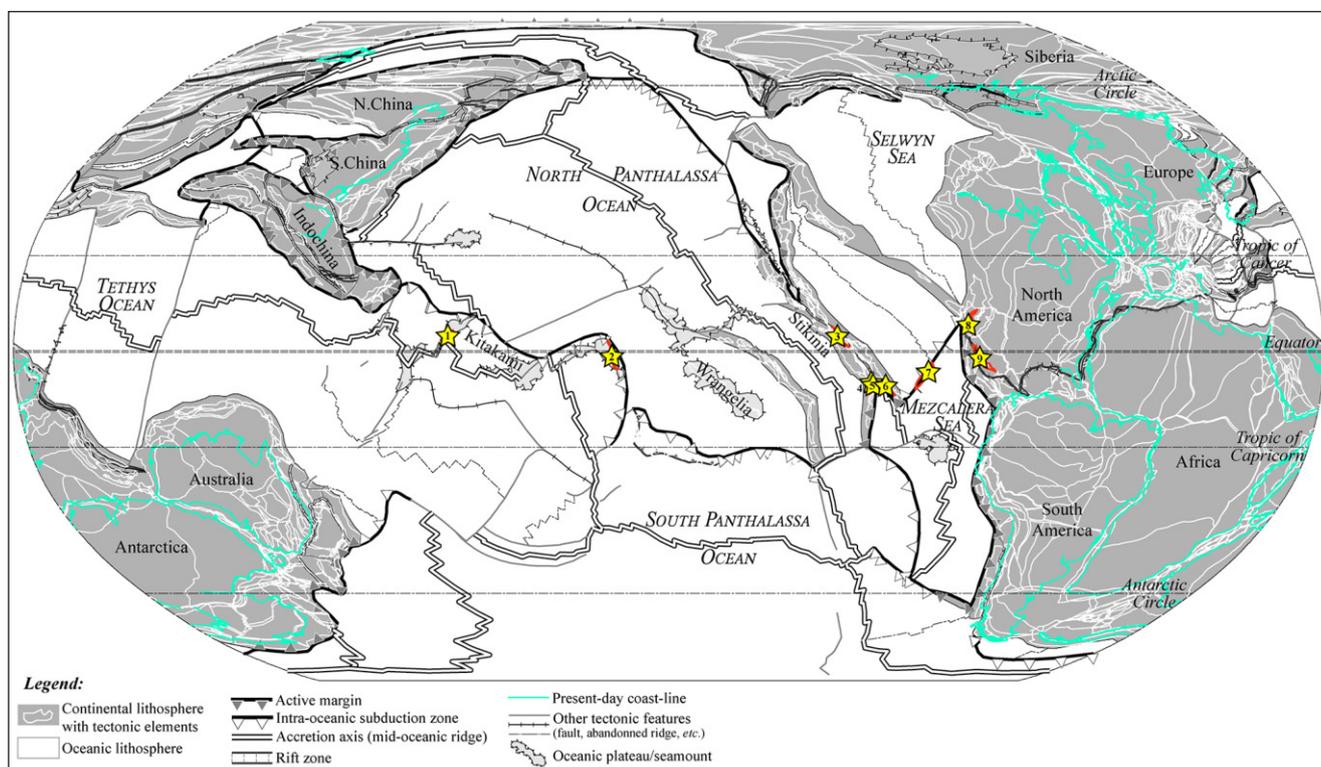


Fig. 6 - Global reconstruction at 220 Ma (Norian) after the PANALESES model (Vérard, 2019b); Robinson projection. Present-day coastlines (green) are shown for information only; the boundary between continental (grey) and oceanic (white) lithosphere correspond to the continent-ocean boundary and not to the palaeoshore-line. Paleo-position of the studied localities are numbered as per Figure 1 and Table 1, i.e., 1 - Dalnegorsk (far East Russia); 2 - Shikoku Island (Japan); 3 - Yukon (Canada); 4 - Idaho (USA); 5 - Oregon (USA); 6 - California (USA); 7 - Baja California Sur (Mexico); 8 - Nevada (USA); 9 - Sonora (Mexico).

ses. Entirely developed from scratch, the PANALESES model is based on a new architecture and is thought for further developments (Vérard 2019b).

The global reconstruction proposed at 220 Ma (Fig. 6) is the result of an iterative reconstruction process where tectonic plates (with closed plate boundaries and 100% of the earth surface covered) are moved according to geological data of broad-type plate geometry and plate kinematics, and to geodynamical scenario defined in three dimensions and time (see for instance example in fig. 2.5, 11-13 in Hochard 2008).

## THE RECONSTRUCTION AT 220 MA

At 220 Ma (Norian) (Fig. 6), Pangaea begins to break up and a rift zone forms between Gondwana and Laurasia (North America). The Tethys realm corresponds to the Neo-Tethys Ocean (*sensu* Stampfli & Kozur 2006). The palaeo-position of most continental areas have been discussed in many other publications (e.g., Stampfli & Borel 2002, 2004

for the Cimmerian blocks; Ferrari et al. 2008 for China and Indochina; Wilhem 2010 for China and Siberia; Flores 2010 for the northern, central and southern cordillera of the Americas; and Vérard & Stampfli 2013a, b for southern Gondwana). The reconstruction of the Panthalassic realm itself follows the work done by the group of the University of Lausanne, and published piecemeal (in particular in Flores 2010; Wilhem 2010; Chablais et al. 2011; Webb 2012; Vérard et al. 2013a-b).

Carbonate platforms, now found in the Taukha tectonic element (TE = tectonic element in Vérard 2019a; Dalnegorsk locality, star #1 in Fig. 6), developed in shallow water environment on volcanic edifices (seamounts and/or oceanic plateau) of the Kitakami plate. The Kitakami plate corresponds to the eastern end of Cimmerian plate. The location of the mid-oceanic ridge is therefore related to the motion of the Cimmerian blocks. The Kitakami plate kept on moving northward until the volcanic edifices were accreted to North China in the latest Jurassic to Early Cretaceous (Kemkin et al. 1997; Peyrotty et al. 2020).

The Sambosan limestone, belonging to Sambagawa-Chichibu TE, also deposited on seamounts (Sambosan localities, stars #2 in Fig. 6) and has a different history from the previous limestone of the Dalnergorsk locality (star #1). These seamounts probably drifted away only as the Pacific plate formed in the Jurassic, and were accreted to the Asian margin in the Late Jurassic–Early Cretaceous (Matsuoka 1992; Onoue & Sano 2007).

Carbonate deposits from Yukon (star #3 in Fig. 6), Idaho and Oregon (stars #4 and #5 in Fig. 6) and California (star #6 in Fig. 6) fall inside the North Cache Creek (Stikinia) TE, the Wallowa TE, and the North East Klamath TE, respectively. Those TEs are believed to be part of the Stikinia continental ribbon, which formerly detached the western margin of North America (Flores 2010). Note that the limestone from Baja California Sur (star #7 in Fig. 6) belong to the Vizcaíno TE, which is placed, in the Norian, onto an intra-oceanic volcanic arc that is associated with the subduction of the Mezcalera Sea (Centeno-García 2017; Heerwagen & Martini 2020 and references therein). All those TEs will eventually be amalgamated back to North America from the mid-Cretaceous on.

Data from Nevada (star #8 in Fig. 6) and from Sonora (star #9 in Fig. 6) belong to TEs (Golconda and Caborca, respectively) that are located on the main continent of North America. Their location is related to the early phase of rifting between Gondwana and Laurasia. This palaeo-position is in good agreement with the presence of siliciclastic component in the carbonate record (Lucas & Estep 1999; González-León 1997; Lucas et al. 1997; Heerwagen & Martini 2018 and references therein).

One of the striking results of the palaeogeographic reconstruction is the location of all localities at various longitudes throughout the Panthalassic Realm on the one hand and well within the inter-tropical zone, close to the equator, on the other hand. We note that the PANALESES model locates some tectonic elements further south than other models. Data from the Yukon record, in particular, are here located close to the equator, when other models locate it just north of the Tropic of Cancer (see for instance, fig. 11 in Peybernes et al. 2016a).

## CONCLUSION

1. Upper Triassic carbonate deposits from the Panthalassa Ocean, occurring today along the Circum-Pacific region, contain relatively rich and diversified calcareous algae assemblages consisting of dasycladaleans, bryopsidaleans and rhodophyceans.

Six of the identified species represent new, possibly endemic taxa and were described in detail in this paper. Some other taxa (identified at species or only at genus level) are also common within the Tethyan realm.

2. Although endemism existed, similarities between Panthalassan and Tethyan algal flora are remarkable and point to unexpectedly long-distance dispersal in Triassic seas. The palaeo-longitudinal dispersion in the Norian is estimated to be about 16'150 km (from the Dalnergorsk locality, star #1 in Fig. 6, to the Sonora locality, star #9 in Fig. 6). To explain strong similarities between Tethys and both Western and Eastern Panthalassa, a passive, indirect (e.g., on “floating islands”) long-distance dispersal, likely favored by high-energy events (major storms, tsunamis) is proposed. A mixing of similarity and endemism was also recorded by different authors for other benthic fossil groups.

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