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Exceptional development of dissepimental coenosteum in the new Eocene scleractinian coral genus *Nancygyra* (Ypresian, Monte Postale, NE Italy)

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KEY WORDS - Aphroid colony, dissepiments, Euphylliidae, coral diversity, EECO, lower Eocene.

ABSTRACT - In colonial corals, the polyps are interconnected with a common tissue called coenosarc. Polyps and coenosarc secrete distinct skeletal structures: corallites and coenosteum, respectively. Ratio of corallite to coenosteum development may vary resulting in two extreme architectural patterns of coral colonies: corallite-dominated (e.g., cerioid) and coenosteum-dominated (e.g., aphroid) colonies. A large suite of examples of these patterns can be identified among extant and fossil corals, including Paleozoic rugosan corals. Herein we describe the new early Eocene colonial scleractinian coral genus Nancygyra *that forms exceptional coenosteum-dominated colonies. The colonies were found in Ypresian limestones at Monte Postale (Lessini Mountains, Veneto, NE Italy), very close to the Pesciara di Bolca Fossil-Lagerstätte, where coralgal buildups have been recently recognised and described. The corallum is massive and consists of corallites of variable size (typically few millimeters in lesser calicular diameter) dispersed and protruding from a very extensive and dense dissepimental coenosteum. The coenosteum forms ca. 60-80% of the corallum volume and is made of vesicular convex dissepiments. The new coral is tentatively assigned to Euphylliidae (known in the fossil record since the Paleocene) whose modern representatives develop similar extensive coenosteum with sticking-out corallites (*Galaxea*) and form coralla with well-developed walls and thickened axial margins of septa (*Euphyllia*). Among stratigraphically older scleractinian corals, similar extent of dissepimental coenosteum development is shown by some Mesozoic amphiastreids and rhipidogyriids.*

INTRODUCTION

In colonial corals, the polyps are interconnected with a common tissue called coenosarc. In certain types of colonies, e.g., plocoid or aphroid colonies, the coenosarc is particularly developed. Polyps and distinct skeletal coenosarc secrete different structures: corallites and coenosteum, respectively (Fig. 1). The coenosteum, also known as peritheca or coenenchyme, is the skeleton between corallites and in "robust" corals (as defined in Fukami et al., 2008) its structure can be costate, vesicular, spinose, or solid. If the coenosteum is narrow and regular, it may form a "double wall" (Budd & Stolarski, 2011; Budd & Bosellini, 2016). Coenosteum is most frequently composed of dissepiments and tabulae (e.g., in zooxanthellate *Galaxea*), rarely as massive thickening deposits (e.g., in azooxanthellate *Lophelia*). Ratio of corallite to coenosteum development may vary resulting in two extreme architectural patterns of coral colonies: corallite-dominated (e.g., in cerioid colonies) and coenosteum-dominated (e.g., in aphroid colonies). A large suite of examples of these patterns can be identified among extant and fossil corals, including Paleozoic rugosan corals (Fig. 2).

During a recent research on the early Eocene (Ypresian) coral buildups of the Monte Postale (Lessini Mountains, Veneto, NE Italy) (Vescogni et al., 2016), sampling of corals revealed the occurrence of a new colonial scleractinian coral that forms exceptional coenosteum-dominated colonies. The discovery of this coral, that we aim herein to describe and interpret, may provide new information on the composition of the still poorly known early Eocene reef coral fauna, developed during a time-window containing few coral reefs (Scheibner & Speijer, 2008; Zamagni et al., 2012) when Cenozoic Earth surface temperature reached its warmest state (EECO) (Zachos et al., 2001, 2008).

GEOLOGICAL BACKGROUND

The Monte Postale site is located in the Lessini Mountains (Veneto region, NE Italy), very close to the Pesciara di Bolca Fossil-Lagerstätte (Fig. 3a). The Lessini Mountains are characterised by a complex geological setting derived from the evolution of the Trento Platform, a large, shallow-water carbonate platform that during the Early Jurassic was one of the main structural components of the Southern Alps (Fig. 4). Since the Middle Jurassic, this platform suffered a progressive drowning, and starting from the Paleogene the Alpine collision led to a block-faulting of the area, with several blocks that were uplifted to a different degree (Bosellini et al., 1981; Winterer & Bosellini, 1981). In the early Eocene some of these blocks reached the photic zone and started to act as centers of carbonate production, eventually coalescing together to form the Lessini Shelf (Fig. 4) (Bosellini, 1989).

The Eocene limestones are grouped into an informal unit indicated as "Calcari Nummulitici" (nummulitic limestones) that includes a wide spectrum of carbonate

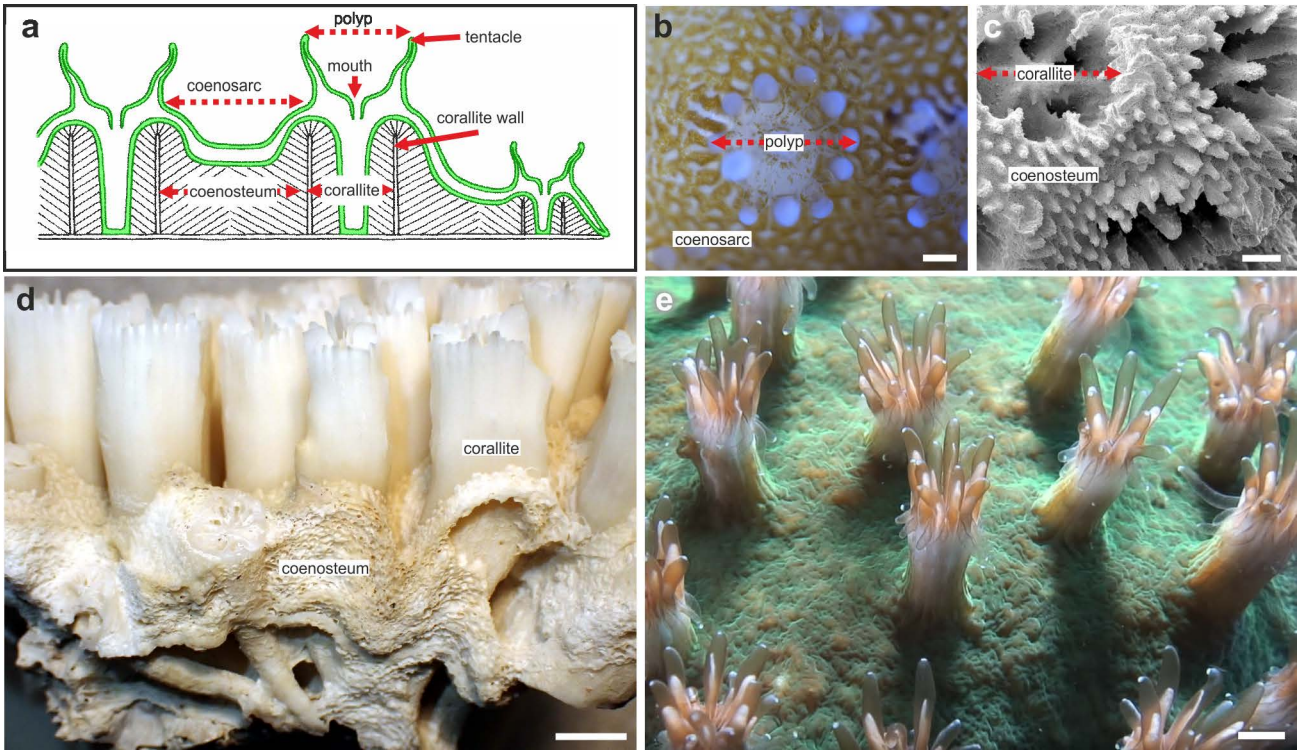

Fig. 1 - (color online) Coenosteum. a) Model of longitudinally sectioned colonial coral with main skeletal and soft tissue structures: polyps are interconnected with a common tissue called coenosarc. Polyps secrete corallite skeleton whereas coenosarc secretes coenosteum. b-c) Tissue cover and corresponding skeleton showing corallite and coenosteum in zooxanthellate scleractinian *Stylophora pistillata* Esper, 1797. d) Plocoid colony of zooxanthellate *Galaxea fascicularis* (Linnaeus, 1767) with well-developed vesicular coenosteum (specimen broken longitudinally) and corallites sticking-out of surface of the colony. e) Polyp-tissue relationship in plocoid colony of zooxanthellate *Galaxea paucisepta* Claereboudt, 1990: tissue with expanded polyps and greenish coenosarc (courtesy Bruce Carlson, CC BY, specimen from Solomon Islands, Morovo Lagoon near Wickham Island: https://www.youtube.com/watch?v=-WdMunCwN6o). c: SEM micrograph. Scale bars: b-c: 250 µm, d: 5 mm; e: 2 mm.

facies: larger foraminifera, coral and molluscs limestones, coralline algae breccias, marly limestones with freshwater fossils (Bosellini et al., 1967; Carraro et al., 1969; De Zanche et al., 1977). In the Monte Postale area the "Calcari Nummulitici" are mainly represented by shallow-water carbonates. In this zone the occurrence of isolated blocks of coral limestone has been firstly reported by Barbieri & Medizza (1969), while Trevisani (2015) mentioned the presence of in situ larger foraminifera-calcareous algal buildups. Vescogni et al. (2016) provided the first detailed description and facies analysis of the Monte Postale coralgal bioconstructions and Papazzoni et al. (2017), by the integration of larger foraminifera and calcareous nannofossils biostratigraphy, dated these limestones as late Ypresian (SB11 Zone of Serra-Kiel et al., 1998). During the early Oligocene, the Lessini Shelf became a rimmed platform, with the presence of a well-preserved reef tract along its southwestern margin (Frost, 1981; Bosellini & Trevisani, 1992; Bosellini et al., 2020). Upper Oligocene to lower Miocene sediments are represented by sandstone and limestone successions, followed by a few meters of Burdigalian marly clays that constitute the last marine deposits in the Lessini area (Bosellini et al., 1967; Bassi et al., 2007, 2008; Bassi & Nebelsick, 2010).

The upper Ypresian Monte Postale coralgal buildups (Vescogni et al., 2016) display a maximum thickness of five meters, forming a discontinuous rim along the northern side of the Monte Postale, arranged as a northward-convex arc about 20-30 m wide and 200 m in length (Fig. 3b). The coralgal boundstone facies is dominated by a scleractinian association of 17 genera and by solenoporaceans algae (Fig. 5). In particular, three main growth forms characterise the coral fauna, with no evident zonation in their distribution: platy colonies dominate the assemblage (*Actinacis*, *Siderofungia*), usually associated with small, massive growth forms (*Actinacis*, *Paraleptoria*, *Goniopora*) and to a minor amount with branching colonies (ramose and phaceloid: *Stylophora*, *Acropora*, *Cladocora*, *Caulastraea*). Scleractinians and solenoporaceans algae grew in close association with a well-developed encrusting structure, mainly composed of calcareous algae and encrusting foraminifera, sometimes forming up to 80 cm thick polygenic, laminar bindstones. Within the coralgal buildups bioclastic deposits are also abundant, mainly represented by *Alveolina* grainstones and by rudstones derived from the breakage of the reef-building organisms. Sediment textures and presence of abundant dasycladacean algae and *Alveolina* indicate for the Monte Postale coralgal buildups a high-energy, shallow-water depositional environment.

MATERIAL AND METHODS

Coral colonies investigated in this paper were collected in the field and formerly indicated as

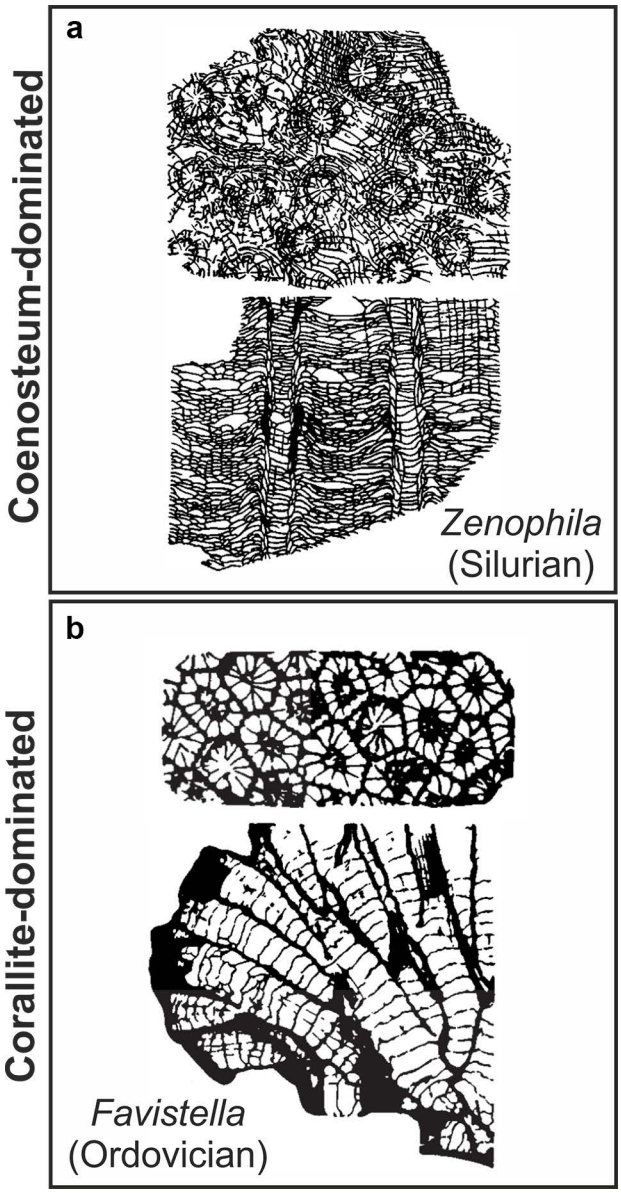

Fig. 2 - Coenosteum-dominated (a) vs corallite-dominated (b) coral colonies. Here exemplified by two rugose corals (Silurian *Zenophila* and Ordovician *Favistella*).

"undetermined corals" in Vescogni et al. (2016). These are five massive colonies that have been cut for polished slabs and thin sections. Polished sections parallel to corallite growth have been used to trace transects and calculate the coenosteum/corallite ratio (Fig. 6). Thin sections have been prepared to describe morphological characters and check preservation of microstructural details.

The thin-sections were first examined with a Nikon Eclipse 80i transmitted light microscope fitted with a DS-5Mc cooled camera head, next with hot cathode microscope HC1-LM at the Institute of Paleobiology, Polish Academy of Sciences. The following parameters of cathodoluminescence microscope were used: electron energy of 14 keV and a beam current density of 0.1 µA mm^{-2}. The observed orange to red luminescence was characteristic of secondary calcite with high Mn^{2+} concentrations (the main activator of luminescence in carbonates) (Marshall, 1988). Calcitic mineralogy of the sectioned coralla was further confirmed by immersion for ten minutes in Feigls's solution: no black staining was observed which is typical of aragonite (Friedman, 1959).

Studied specimens are housed at the Department of Chemical and Geological Sciences, University of Modena and Reggio Emilia (Italy).

Repository abbreviations

IPUM: Inventario Paleontologia Università di Modena, Italy.

SYSTEMATIC PALEONTOLOGY

Order Scleractinia Bourne, 1900
Family Euphylliidae Alloiteau, 1952

Genus *Nancygyra* n. gen. Bosellini & Stolarski
Type species *Nancygyra dissepimentata* n. gen. n. sp.

Etymology - It is our pleasure to name this genus after the scleractinian coral specialist Professor Dr. Ann (Nancy) Budd.

Diagnosis - Massive aphroid colony with corallites protruding from an extensive and dense dissepimental coenosteum as in *Galaxea*. Budding intracalicular. It differs from *Galaxea* in developing two first orders of septa with thickened (rhopaloid) axial margin.

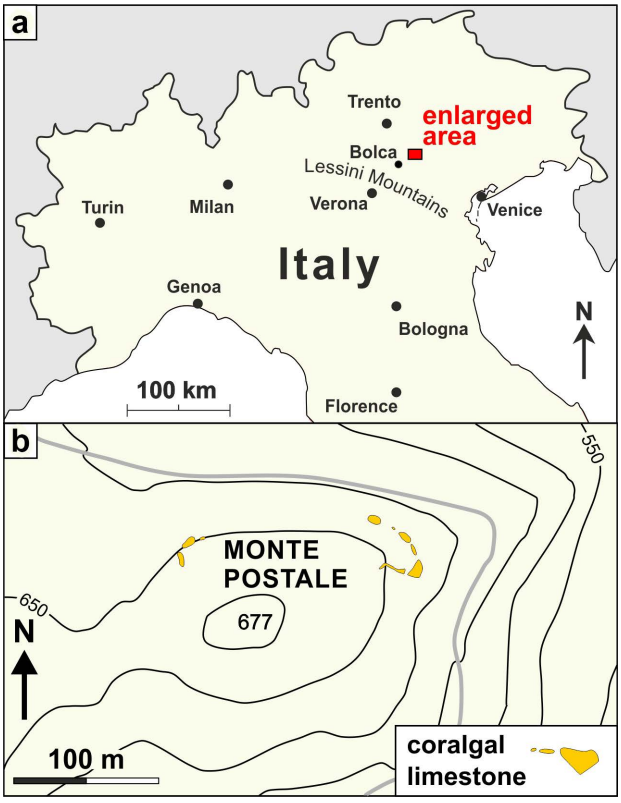

Fig. 3 - (color online) Location map. Map of the study area (a) with close-up of the Monte Postale area and location of the coral outcrops (b).

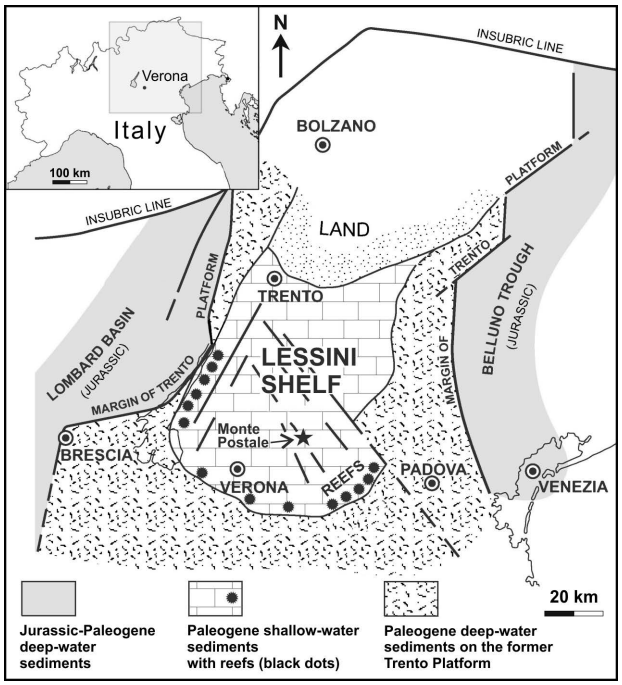

Fig. 4 - Paleogeographic reconstruction of the Lessini Shelf during the Paleogene (modified from Bosellini, 1989).

Composition - Type species only.

Nancygyra dissepimentata n. sp. Bosellini & Stolarski (Figs 6-7)

Etymology - After the abundant dissepiments that characterise the coenosteum.

Type locality - Lower Eocene (upper Ypresian, 48.5-51 Ma) of the Monte Postale (Lessini Mountains, Verona, NE Italy).

Holotype - IPUM 28983.

Paratypes - IPUM 28984, IPUM 28985, IPUM 28986, IPUM 28987.

Diagnosis - As for the genus.

Material - Five colonies (IPUM 28983, IPUM 28984, IPUM 28985, IPUM 28986, IPUM 28987).

Diagnosis - As for the genus.

Description - Massive aphroid (neighboring corallites united by dissepiments only) colonies with monocentric intracalicular budding. Corallites mostly elliptical in outline, sometimes circular, with diameter ranging from 3 to 4 mm in smaller corallites and from 4 to 6 mm in larger ones (Figs 6-7). Unequal septa arranged in three, typically incomplete orders with septa of first two cycles with thickened (rhopaloid) inner margin. Columella absent. Wall well defined and thick.

Corallites protrude 7 to 10 mm from an extensive concave dense coenosteum made by vesicular convex dissepiments. These are quite irregularly arranged and spaced around sparse corallites. The coenosteum represents approximately the 50% of the colony structure.

The skeleton is entirely recrystallised to sparry calcite (Fig. 7a-c, f). The possible traces of original intra-skeletal microstructural boundaries were found inside the thick corallite wall (Fig. 7f). Similar sparry calcite is developed in the region originally occupied by the coral skeleton and in intracalicular space. These calcite crystals show zoned bright to dully red cathodoluminescence (Fig. 7g, regions marked "1"). Original skeletal boundaries show less bright luminescence (Fig. 7g, regions marked "2") whereas secondary deposits (cements) that form around the skeletal boundaries (Fig. 7g, regions marked "3") are non-luminescent.

DISCUSSION

Nancygyra n. gen. forms aphroid, lightweight coralla with a vesicular coenosteum similar to *Galaxea* but with corallites having more massive skeletal structures (thicker corallite wall, thickened axial margins of two first orders of septa). According to modern phylogenetic analyses (Luzon et al., 2007; Fukami et al., 2008; Kitahara et al., 2016), *Galaxea* forms a clade (family Euphyllidae) within the Complexa super-clade that groups *Euphyllia*, *Fimbriaphyllia*, and *Ctenella*. The oldest representatives of *Galaxea* date to the Miocene of the Indo-Pacific region (Wells, 1964; Bromfield, 2013; Santodomingo et al., 2016) but euphylliids have an early Cenozoic fossil record as *Euphyllia* is known from the Paleocene of Costa Rica (Aguilar & Denyer, 2001). Consequently, the Eocene occurrence of the herein proposed euphylliid *Nancygyra* n. gen. is consistent with the Cenozoic diversification of this group. Deciphering of phylogenetic position of euphyllids within Mesozoic groups of scleractinians is difficult due to different taxonomic values ascribed to different characters among the Mesozoic/Cenozoic taxa and/or possible loss in the evolution of euphylliids of some characters of their Mesozoic ancestors. Moreover, a complete recrystallisation of the skeleton of *Nancygyra* n. gen., highlighted by development of successive generations of differently cathodoluminescent mineral deposits, and lack of early ontogeny data of this coral hamper more in-depth skeleton-based phylogenetic

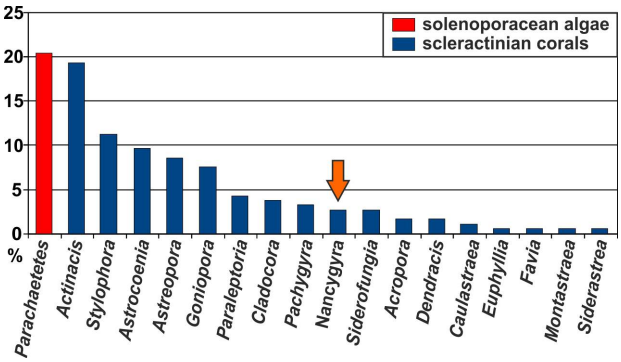

Fig. 5 - (color online) Relative abundance of scleractinian corals and solenoporacean algae genera in the Monte Postale buildups (modified from Vescogni et al., 2016).

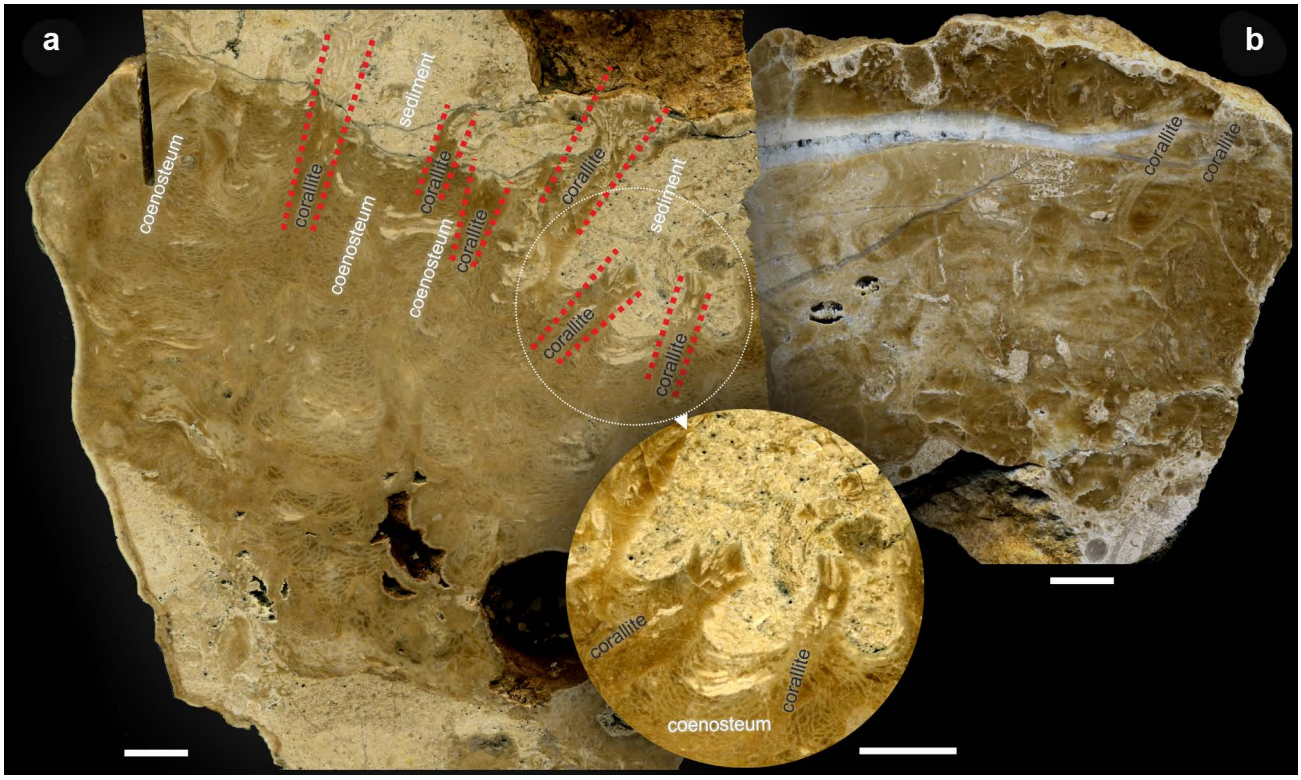

Fig. 6 - (color online) Macroscopic characters. Polished slabs of two colonies (a: holotype IPUM 28983; b: paratype IPUM 28985). Section of the larger specimen (a) shows particularly well the relationship between corallites and vesicular coenosteum, with corallites sticking-out of the natural surface of the colony (covered with sediment); see also slightly enlarged region with enhanced contrast (circle). Scale bars: 1 cm.

analyses. Nonetheless, the similar extent of dissepimental coenosteum development and corallite architecture that exists in *Nancygyra* n. gen. and some rhipidogyrids and amphiastraeids (Kołodziej, 2003) indicates possible further research targets.

The appearance of this new peculiar genus occurred near the end of the hyperthermal event named EECO (Early Eocene Climatic Optimum), when Cenozoic global temperatures reached their maximum under high atmospheric pCO_2 concentrations (Zachos et al., 2001, 2008) and coral reefs underwent a marked decline (Kiessling & Baron-Szabo, 2004; Scheibner & Speijer, 2008; Zamagni et al., 2012). This reef gap, however, did not correspond to a decrease in coral richness. The Eocene of the west Tethyan region has been considered a true hotspot of tropical marine biodiversity (Renema et al., 2008) and an increase in coral richness has been documented from the late Paleocene to the early Eocene (Kiessling & Baron-Szabo, 2004; Weiss & Martindale, 2018). Recent database analysis also underlined that coloniality was favoured during this period of habitat restriction, with heat stress limiting corals to shallow waters because of the shoaling lysocline (Weiss & Martindale, 2018).

Experimental studies show that dissepiments are rapid growing skeletal elements (Brahmi et al., 2012). Formation of light, dissepiment-dominated coralla may therefore be an efficient strategy to compete for space in the warm and shallow-water reef environment represented at Monte Postale. Noteworthy, some modern examples of dissepiment-dominated coralla (e.g., *Symphyllia*) may show buoyancy due to gas trapped interstitially between the dissepiments and may be capable of floating (possible dispersal) after storm events (DeVantier, 1992). Analogous dispersal capability by floating of *Nancygyra* n. gen. seems however unlikely due to the occurrence of this taxon being limited to type locality.

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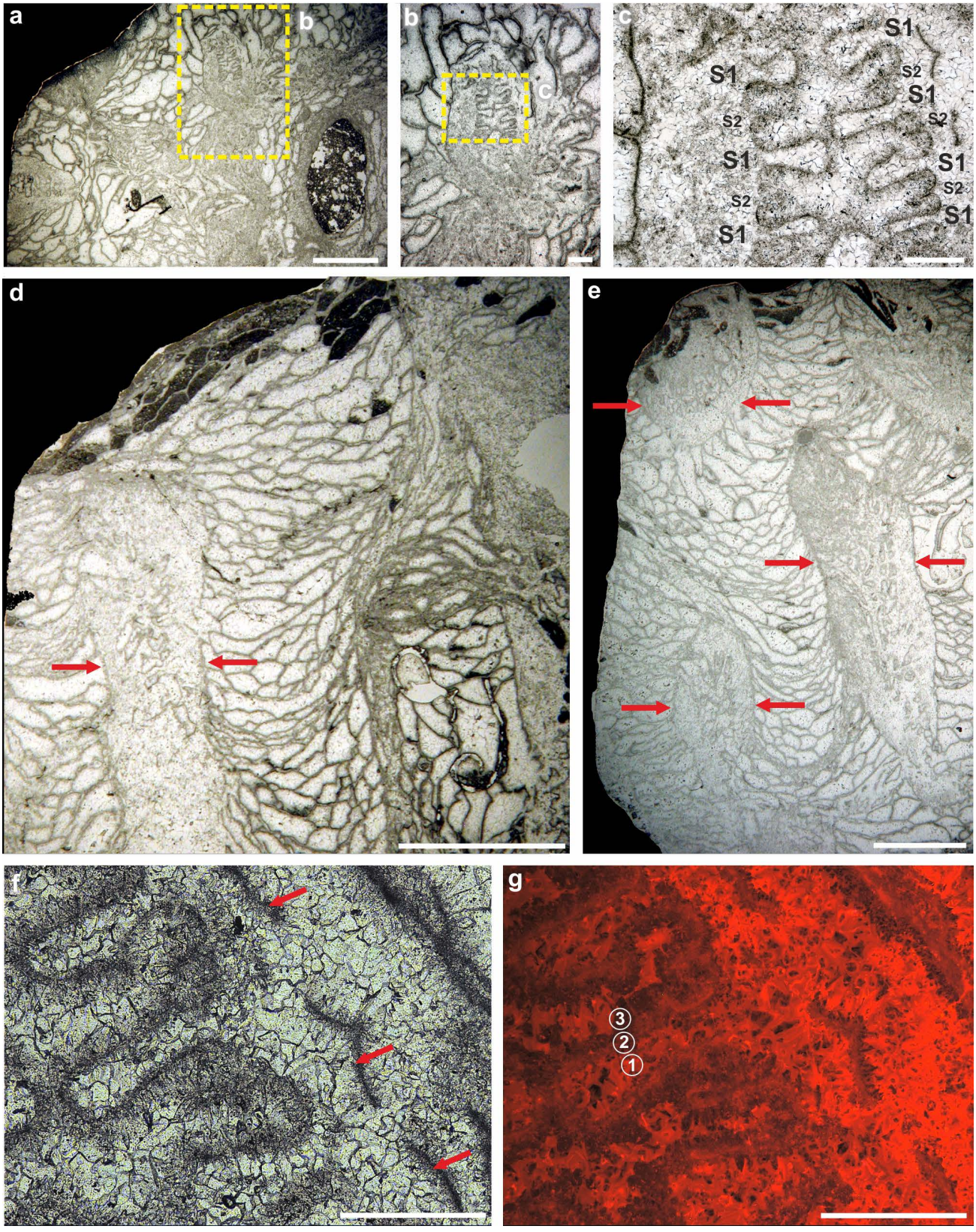

Fig. 7 - (color online) Macro and microstructural characters (paratype IPUM 28984): structural and preservational details. Transverse (approximately) (a-c) and longitudinal (d-e) thin-sections of colony fragments. Corallites sectioned transversely (a-c) show elliptical outline, thick wall and septa of first two cycles with thickened (rhopaloid) inner margins. Longitudinal sections (d-e) show thick-walled corallites embedded in vesicular coenosteum. The skeleton of all coralla is entirely recrystallized (f) with possible traces of original intra-skeletal microstructural boundaries (red arrows). Diagenetic alteration of the skeleton is highlighted by bright-red cathodoluminescence (corresponding g image). The distinct luminescence signals (1-3) correspond to region originally occupied by the coral skeleton (1) and the subsequent generations of secondary deposits (2-3) infilling the calicular space. Scale bars: a, d-e: 5 mm; b: 1 mm; c, f-g: 500 µm.

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