A coral hotspot from a hot past: The EECO and post-EECO rich reef coral fauna from Friuli (Eocene, NE Italy)

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ABSTRACT

The early Paleogene "greenhouse" is the warmest geological period of the Cenozoic and a suitable source to unlock crucial information for better understanding how ecosystems such as coral reefs reacted to a climate much warmer than the present.

Herein, we analyse in detail the rich museum coral collections from Friuli region (NE Italy) focusing only on the so-called reef corals, mostly colonial, and on those localities for which the age constraints are well-defined. We grouped the localities into four time-intervals within the Ypresian-Lutetian and thus within EECO (Early Eocene Climatic Optimum) and post-EECO phase, in order to assess the main changes in the following traits: 1) richness and relative abundance at the generic and species level; 2) relative abundance of growth forms; 3) colony size.

By systematic revision we recognized a total of 37 genera and 103 species. During the EECO interval (late Ypresian or Cuisian), the diversity at both genus and species level was relatively low (21 genera, 37 species). An abrupt increase is then recorded in the post-EECO 1 interval (latest Ypresian), whereas a peak is reached in the earliest Lutetian (post-EECO 2) (35 genera, 90 species). These results undoubtedly show that a coral hotspot occurred in the region during the late Ypresian-early Lutetian time and highlight that corals of Friuli reacted positively immediately after the warming event of the EECO.

This coral hotspot was the most diverse at global scale during the Ypresian and formed in a deltaic depositional setting, most probably in mesophotic conditions as suggested by the dominant growth forms, where rapid sediment accumulation, enhanced nutrient delivery and stressful climatic conditions reduced frame-building capacity.

We finally document that corals were resilient to climate stressors and recovered before reefs which, in contrast, required much more time to achieve their buildup potential.

1. Introduction

The current anthropogenic increase of atmospheric greenhouse gas concentrations is rapidly changing Earth's climate, pushing it toward a warmer state for which there is no historical precedent. In this world of warming temperatures, rising sea levels, and changes in oceanographic conditions and water quality, coral reefs are one of the ecosystems most threatened and for which a global severe decline or a total demise is expected at atmospheric CO_2 levels of 560 ppm that are predicted by the end of the 21st century (Hoegh-Guldberg et al., 2007; Silverman et al., 2009).

Although a perfect analogue does not exist for this kind of extremely

rapid perturbation, the geological record is the only observational source where crucial information can be unlocked for better understanding how the climate system operates and how ecosystems such as coral reefs react to a climate much warmer than the present (Dee et al., 2019; Tierney et al., 2020).

Navigating back in the geological record, the late Paleocene-early Eocene interval (~ 59 to 48 Ma) represents the most recent time window with extremely warm global temperatures that coincided with CO_2 levels well over 1000 ppm; it is also the final phase of the last "greenhouse" climate state that started in the middle Cretaceous (Zachos et al., 2001, 2008; Scotese et al., 2021). In particular, rapid carbon injections into the ocean and atmosphere, with a magnitude similar to that

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expected for the future, triggered abrupt increases in global temperatures indicated by a series of rapid, high-temperature peaks known as hyperthermal events. These events include the Paleocene-Eocene Thermal Maximum (PETM, ~55 Ma), but the most prolonged warm interval is represented by the Early Eocene Climatic Optimum (EECO, ~ 53–49 Ma) (Zachos et al., 2001; Luciani et al., 2016), when mean sea surface temperature reached about 27 °C (Inglis et al., 2020).

This warm period caused changes in hydrological cycles, ocean acidification, increases in continental weathering, and strongly influenced the shallow-water marine calcifying organisms, triggering turnovers in Larger Benthic Foraminifera (LBF) assemblages (Hottinger, 2001; Drobne et al., 2011; Whidden and Jones, 2012; Benedetti and Papazzoni, 2022) and the demise of coral reefs (Scheibner and Speijer, 2007, 2008; Kiessling and Simpson, 2011; Zamagni et al., 2012). As concerns LBF, Drobne et al. (2011) underlined that temperature rise, favouring stable oligotrophic conditions, led to diversification of alveolinids, followed by an abrupt decrease in number of species after the EECO. Similarly, Benedetti and Papazzoni (2022) suggested that, among rotaliids, the large K-strategists (with reproductive dimorphism) increased their generic diversity at the base of EECO, followed by an increase in specific diversity as well. The richness and diversity of both r- and K-strategists declined right after the EECO. Whidden and Jones (2012), investigating the diversity patterns of the major groups, such as nummulitids, alveolinids and orthophragmines, concluded that temperature was the main factor leading to change in frequency of first occurrences and total number of species, rather than oligotrophy and eustatic sea level rise. As regards coral reefs, their response to the late Paleocene–early Eocene greenhouse seems to be different if we look separately at reef-building capacity and reef volume as opposed to the diversity and composition of the zooxanthellate scleractinian coral fauna (the so-called reef corals). A coral reef gap is documented in this period (Kiessling and Baron-Szabo, 2004; Scheibner and Speijer, 2008; Kiessling and Simpson, 2011; Zamagni et al., 2012) and is interpreted as related to rising temperatures and extreme environmental conditions that greatly affected reef coral development and probably favoured the expansion of marginal settings where corals had a limited frame-building capacity (Scheibner and Speijer, 2007; Zamagni et al., 2012). This collapse of coral reefs, however, did not coincide with marked coral extinctions at either the genus or species level (Zamagni et al., 2012). Weiss and Martindale (2019), in analyses of the Paleobiology Database (PBDB), recently documented an increase in genus and species richness throughout the late Paleocene and early Eocene and suggested that the reef coral fauna of this period was constituted by a suite of resilient corals with specific traits, such as flexible photosymbiosis and feeding strategy, together with growth in siliciclastic depositional settings.

Most previous studies assessing coral diversity during the late Paleocene-early Eocene are based on data extracted directly from the literature and compiled in a database, whereas very few are papers dealing with data derived from detailed taxonomic analysis of corals sampled in the field or investigated in museum collections (Turnšek and Drobne, 1998; Schuster, 1998; Vescogni et al., 2016).

Herein, we revise and analyse in detail the extremely rich coral collections from Friuli region (NE Italy) (Fig. 1), a region that has provided a significant amount of palaeontological data on the early Paleogene since the seminal works by Taramelli (1870), d'Achiardi (1875), Marinoni (1877), Marinelli (1902) and Dainelli (1915). These authors collected and described hundreds of taxa in their precursor studies on the geology and paleontology of northeastern Italy. This coral fauna was described first by d'Achiardi (1875) followed by Dainelli (1915), but it was later almost forgotten and so far never revised according to the recent changes in scleractinian taxonomy. In addition to taxonomic analysis, we provide a detailed biostratigraphic analysis (this paper, Benedetti et al., 2022) placing the fauna within the Ypresian-Lutetian time interval and thus within EECO and post-EECO phase. With regard to shallow benthic zonation (see also below), the Ypresian is routinely considered subdivided in Ilerdian (early Ypresian) and Cuisian (late Ypresian), which can be usually well-differentiated in terms of faunal turnover and different evolutionary steps in lineages belonging to nummulitids and alveolinids. Because the Ilerdian and Cuisian are non-standard, regional stages, Pomerol (1981) suggested avoiding their use, as was also remarked by Speijer et al. (2020), but they are still useful for age constraints of the early Eocene biozones (Shallow Benthic Zones: SBZ) of Serra-Kiel et al. (1998). We further specify that early/lower Cuisian corresponds to SBZ10, middle Cuisian to SBZ11 and late/upper Cuisian to SBZ12.

Despite the scarcity of fossil coral outcrops in the region, the vast amount of data from carefully curated museum occurrence records (i.e. Museo di Storia Naturale, Geologia e Paleontologia University of Florence; Museo Friulano di Storia Naturale, Udine) can be considered a reliable source for quantitatively estimating relative diversity and abundance as recently demonstrated by Gotelli et al. (2021), and thus is valuable for 1) documenting this Eocene coral hotspot; 2) assessing the impact of EECO event on coral diversity; and 3) providing additional data to interpret the original depositional environment where this rich coral community thrived.
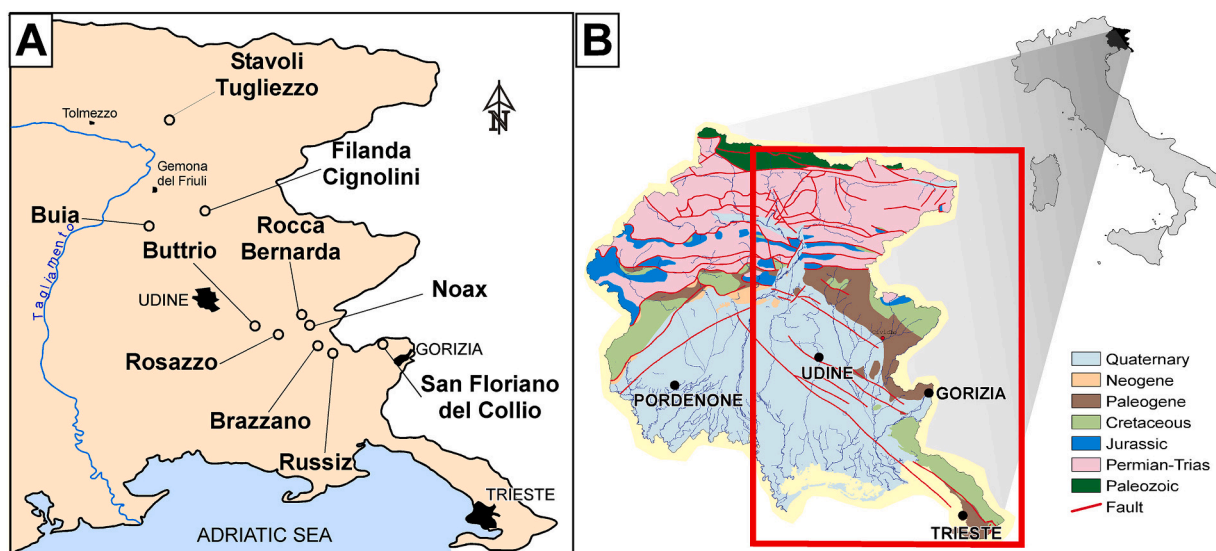

Fig. 1. A. Location of the selected coral-bearing investigated localities in Friuli Region. B. Simplified geological map of the area (Carulli, 2006).
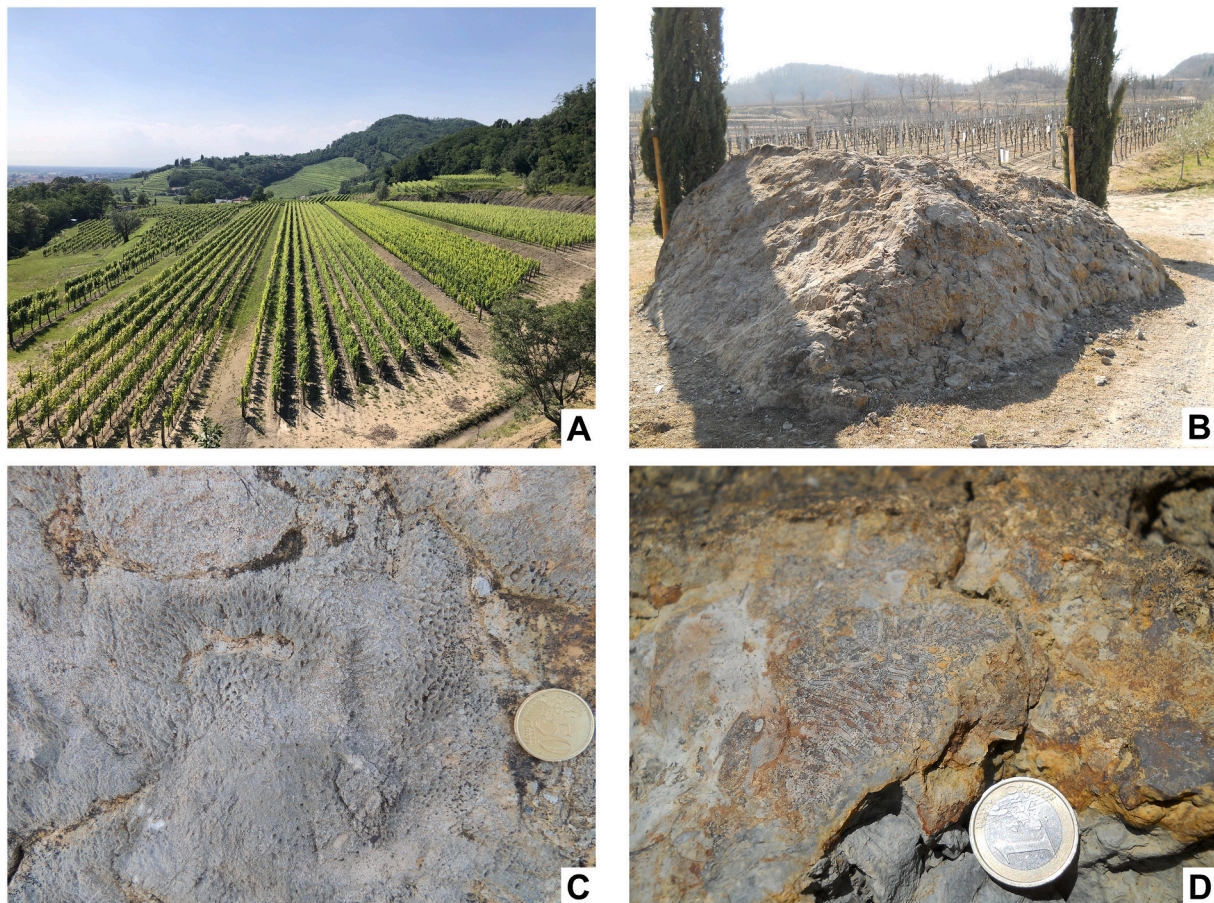
2. Geological setting

The Friuli-Venezia Giulia Region (hereafter Friuli) is part of the northeastern sector of the Italian peninsula and its very complex geology spans from the Palaeozoic metamorphic basement to the Recent alluvial deposits (Carulli, 1987, 2006) (Fig. 1b). The structural setting of Friuli derives from a complex overlapping of different tectonic phases. During the Mesozoic, the Friuli Carbonate Platform was active until the Middle Jurassic (i.e., Dogger) and controlled by extensional tectonics due mainly to normal NW-SE faults (Castellarin and Vai, 1982; Tunis and Venturini, 1992). Since the Late Cretaceous up to the middle Eocene, the Friuli Carbonate Platform and the surrounding Julian High evolved into a complex foredeep system under the effect of the SW migration of the front of the Dinaric Thrust Belt, connecting the Dinarides with the Alps (Doglioni and Bosellini, 1987).

The Cenozoic is then represented mostly by flysch-type deposits of different stratigraphic age, with the exception of limestone rocks outcropping mainly in the Carso region. Terrigenous to mixed carbonate-siliciclastic sedimentary successions are widespread along the southern sectors of Alps and Prealps reliefs and in the eastern Friuli plain. The Friuli Basin (or Friuli Paleogene Basin sensu Placer et al., 2010) was mainly characterized by filling from dismantling of a shallow-water carbonate platform producing calciclastic megabeds to siliciclastic turbidites up to deltaic sandstones and conglomerates (Ogata et al., 2014).

The easternmost Friuli, also known as Collio, is a region characterized by several tectonic disturbances consisting of NW-SE trending thrusts, faults and folds resulting in intense deformation and repetition of fossiliferous beds (e.g., Tunis and Pirini Radrizzani, 1987; Venturini and Tunis, 1989, 1992a). Most of the scleractinian corals stored in the museum collections come from this area and in particular from the upper Ypresian-lower Lutetian Flysch di Cormons Formation (Martinis, 1962), which has been routinely interpreted as deposited in a prodelta setting where patch reefs formed in the deltaic environments during a transgressive phase (Venturini and Tunis, 1992b). The Flysch di Cormons Formation consists of an alternation of fossiliferous marls and sandstones mainly characterized by the abundance of larger foraminiferal tests such as the nummulitids *Nummulites* and *Assilina*, with subordinate alveolinids. Locally, there are fossiliferous lenses yielding solitary and colonial corals (Dainelli, 1915; Maddaleni, 1997), molluscs, echinoids (Maddaleni and Tunis, 1993), and bryozoans. The age of the upper part of Flysch di Cormons Fm, as above, is constrained to the late Cuisian-early Lutetian (Piccoli and Proto Decima, 1969; Benedetti et al., 2022). The coral-bearing deposits near Russiz, together with nummulitic breccias, interbedded to arenaceous levels and microconglomerates with siliciclastic material of fluvial origin, were interpreted as derived from patch reefs in a deltaic environment (Venturini and Tunis, 1992b).

Some Paleogene deposits with LBF are also cropping out in the Stavoli Tugliezzo area, close to the town of Carnia, in central Friuli. Here some limited outcrops of Eocene rocks occur at Monte Forcella, Monte Zovet, and Stavoli Tugliezzo, as part of a transgressive cycle over Triassic rocks (Carulli et al., 1982, 2010). There are conglomerates at the base, made by clasts of Triassic limestones and dolostones, soon followed by limestones and marly limestones. The latter contain LBF (*Alveolina*, *Assilina*, *Nummulites*, etc.), sometimes accompanied by corals as already indicated by Marinoni (1877). The Eocene of Stavoli

Fig. 2. The recent aspect of the coral-bearing sedimentary successions cropping out in the easternmost Friuli. A. parallel rows of grapevines cover the lower to middle Eocene deposits belonging to the Flysch di Cormons Fm. B. Coral-bearing block cropping out among grapevines. Coral colonies recognized on the surface of the block: *Siderofungia* (C) and *Astreopora* (D).

Tugliezzo area is the northernmost cropping out in the Southern Alps.

3. Material and methods

The rich Eocene coral fauna from Friuli, in particular from the Collio area, is basically known from museum collections because the corals occur loosely embedded in the marly sediments of the Flysch di Cormons Formation that forms the substrate of the famous Collio vineyards (Fig. 2A). They have been studied by relatively few palaeontologists or donated to museums by amateur collectors. True outcrops where corals can be studied in the field are absent, and today the increasing exploitation of the land for cultivation makes it difficult to find any coral. Only occasionally, an isolated rock block with corals indicates the original presence of in situ coral colonies (Fig. 2B-D).

3.1. Coral collections and previous studies

The rich Eocene coral fauna from the Friuli region has been studied first by d'Achiardi (1875), with the identification of 126 species, and subsequently by Dainelli (1915) in his comprehensive geological and palaeontological monograph "L'Eocene Friulano" with the description of 154 species. In both monographs, most of the taxa belong to scleractinian corals, but some hydrozoans are also present. Unfortunately, the d'Achiardi collection has been lost and thus is not currently available. The Dainelli collection, on the other hand, is hosted at the Museo di Storia Naturale, Geologia e Paleontologia of University of Florence, and consists of about 757 coral specimens (colonial and solitary).

Apart from these historical collections, the coral fauna of Friuli can also be examined at the Museo Friulano di Storia Naturale, Udine, in which corals are deposited from many localities, including those sampled by Dainelli, and donated over the years to the museum by amateurs and specialists. This collection consists of >1034 specimens (colonial and solitary). More recently, some corals from Friuli have been included in the PhD dissertation of Barta-Calmus (1973), and 28 species from Russiz locality have been described by Maddaleni (1997) and are also deposited in the museum in Udine.

Repository abbreviations: MFSN: Museo Friulano di Storia Naturale, Udine; MSN-Unifi: Museo di Storia Naturale, Geologia e Paleontologia of the University of Florence.

3.2. The study of the coral collections

We combined digital catalogues of both museums and created a single new database, which served as the basis for our revision and analysis (Table S1, supplementary material). This integrated compilation consists of a total of 1791 occurrences representing the coral pool of the Friuli region. Scleractinian colonial corals are dominant (69.9%), followed by solitary scleractinian corals (16.4%), unidentified corals (8.6%) and non-scleractinian corals (5.1%) (Fig. 3A).

For our study of the coral collections, which comprise a large number of specimens, we decided to concentrate on the so-called reef corals, mostly colonial and presumably zooxanthellate, for two main reasons: 1) they archive more information about shallow-water tropical conditions of the period; and 2) their identification, at least at the genus level, can be updated using more recent systematic revisions and thus be compared with other faunas.

As regards the Dainelli collection in Florence, we (Bosellini and Budd) visited the museum several times and examined and photographed all the colonial corals. We did the same thing in Udine but also it was possible to borrow a considerable number of specimens so that we could study them more in detail at the Dipartimento di Scienze Chimiche e Geologiche of the University of Modena and Reggio Emilia.

The original name assigned to each specimen was confirmed or revised at the generic level, taking into account the systematics based on recent molecular analysis and phylogenetic relationships between traditional families (Fukami et al., 2004, 2008), together with macro-morphological characters used in recent systematic revisions (Budd and Stolarski, 2009; Budd et al., 2012): colony shape, colony organization, budding, corallite, septa, internal lobes, columella, dissepiments, wall, coenosteum, corallite diameter, valley width, distance between corallite centers, corallite spacing, number of septa. Updates also considered the World Register of Marine Species (WoRMS). Revision of species names was based on comparison of the literature on the Paleogene coral fauna from northern Italy and nearby areas, ranging from classic monographs to more recent revisions.

Our study of the reef coral fauna also involved the characterization of the colony growth form and size. We categorized the growth form of each specimen as branching, phaceloid, encrusting, flabellate, fungiform, massive, platy and tabular, following the definitions given in Veron (2000, vol. 1, p. 56). These specimens included solitary and colonial scleractinians as well as non-scleractinians (hydrozoans, helioporids) and unidentified specimens in our database. Their relative
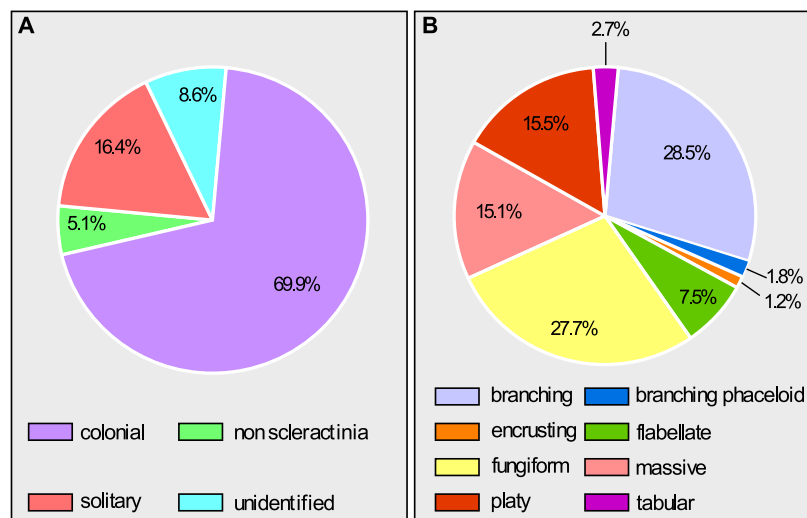

Fig. 3. Composition of the entire coral fauna of the Friuli region after the revision of the museum collections. A. Relative abundance of colonial and solitary scleractinian corals, non scleractinian (i.e. hydrozoans), and coral specimens poorly preserved and unidentified. B. Relative abundance of different growth forms of colonial and solitary (flabellate) scleractinian corals identified at the Museo Friulano di Storia Naturale, Udine.

abundance is illustrated in Fig. 3B.

Quantitative analysis has been applied only to the colonial corals of the Udine collection, because of the greater quantity of specimens than those of the Florence collection and the possibility to obtain a part of them on loan. A growth form has been assigned to each specimen and the size of the colony has been measured including the maximum width and the maximum height (in cm).

To assess the paleogeographic distribution and diversity of coral assemblages during the Ypresian, we used data from the Paleobiology Database (PBDB), freely available online, and we also referred to our PalEoCoral dataset, as yet under construction, on the scleractinian corals from the Paleocene-Eocene of the Neotethys (i.e. the peri-Mediterranean region). From these sources, and for the purpose of the present paper, we extracted only data about revised colonial coral genera.

3.3. Biostratigraphic methods

The original catalogues of both Florence and Udine museums provided specific information about the locality of each collected specimen, with also an indication of the possible stratigraphic age (series and stage) according to the knowledge of the collector or to some stratigraphic studies in the area. We also became aware that with time, since d'Achiardi (1875) and Dainelli (1915) first studies, the same locality has been called by different names. Thus, in order to assign a correct locality and age to each specimen it was necessary to: 1) make a survey of the area and, with the use of detailed maps, assign a single name to the localities that occurred at the same place; 2) revise the stratigraphic age of each locality according to the most recent biozonation schemes.

The geological age of the material stored in the investigated museum collections has been determined by studying accompanying larger foraminiferal taxa. LBF are shallow-water dwelling single-celled organisms with good stratigraphic potential due to their rapid evolution, especially Eocene nummulitids, alveolinids and orthophragmines (e.g., Hottinger, 1960; Drobne, 1977; Schaub, 1981; Less, 1987). A total of 20 Shallow Benthic Zones (SBZ) are routinely identified from the Paleocene-Eocene interval of the western Neotethys (Serra-Kiel et al., 1998) based on the concomitant occurrence of phylogenetically unrelated shallow-water foraminifera (Pignatti and Papazzoni, 2017). Some intervals and boundaries between contiguous biozones have been recently recalibrated by means of integrated analysis, such as the Paleocene-earliest Eocene (Scheibner and Speijer, 2009; Serra-Kiel et al., 2020; Papazzoni et al. (2022)), the Ypresian-Lutetian (Rodríguez-Pintó et al., 2012, 2013; Mochales et al., 2012; Costa et al., 2013; Silva-Casal et al., 2021) and Bartonian-Priabonian intervals (Luciani et al., 2020; Agnini et al., 2021).

To constrain the stratigraphic attribution of the investigated material from museum collections, we often had to resort to literature data. When possible, we collected new data for the accompanying LBF specimens deposited in the Dainelli collection (Fornaciari et al., 2016) and a revision is still in progress. We also collected and investigated new samples taken as accurately as possible from the localities from which the corals have been historically found.

We then assigned each investigated location to a biozone within the SBZ scheme according to the occurrence of markers, such as especially short-ranging species of *Nummulites*, *Assilina* or *Alveolina*, or to the total faunal assemblage.

The investigated time interval spans from late Ypresian (i.e., Cuisian) to early Lutetian.

3.4. Selected localities

To avoid misinterpretations due to wrong age assignment, we decided to focus our attention only on those localities for which the age constraints are well-defined as described above. We grouped the localities into four time-intervals to assess the main changes in coral abundances, diversity and the distribution of growth forms (Table 1):

Table 1

The selected investigated localities listed according to their stratigraphic age and SBZ (Shallow Benthic zones) and to assigned time-interval. The number of coral specimens analysed in the collections for each locality is also indicated.

Selected locality	n° occurrence	SBZ	Stratigraphic attribution	Interval
Buia	61	10	Lower Cuisian	EECO
San Floriano del Collio	3	10	Lower-middle Cuisian	EECO
Buttrio	37	11	Middle Cuisian	EECO
Filanda Cignolini	22	12	Upper Cuisian	post-EECO 1
Noax	249	12	Upper Cuisian	post-EECO 1
Rosazzo	14	12	Upper Cuisian	post-EECO 1
Rocca Bernarda	314	12/13 boundary	Basal Lutetian	post-EECO 2
Russiz Superiore	824	12/13 boundary	Basal Lutetian	post-EECO 2
Stavoli Tugliezzo	74	13	Lutetian	post-EECO 3

- EECO interval. This group includes the following localities: Buia (lower Cuisian: SBZ10), Buttrio (middle Cuisian: SBZ11), San Floriano del Collio (lower-middle Cuisian: SBZ10–11).
- post-EECO 1 interval. This group includes those localities unambiguously assigned to the lower middle part of SBZ12, corresponding to upper Cuisian: Noax, Filanda Cignolini and Rosazzo. While the latter localities are characterized by very few occurrences, Noax can be easily compared with the other localities in terms of number of specimens stored in the museum collections.
- post-EECO 2 interval. It is represented by the two localities for which the biostratigraphic analysis of the samples recently reinvestigated (Benedetti et al., 2022) suggests an age very close to the SBZ12/13 boundary, corresponding to the lowermost Lutetian: Rocca Bernarda and Russiz.
- Post-EECO 3 interval. It is documented by the clearly lower Lutetian assemblage of Stavoli Tugliezzo.

3.5. Quantitative and statistical analysis

For the investigated intervals, we performed different analyses and provided a suite of data useful to characterize the changes of the coral fauna during and after the EECO event.

We calculated the frequency and relative abundance of species and genera recognized after our systematic revision of the collections. We also obtained normalized data evaluated per million year per each shallow water biozone.

We compared the growth forms of 961 well-preserved specimens among the four time-intervals (EECO, post EECO-1, post EECO-2, post EECO-3) in the Udine collections. The material consisted of 10 specimens from EECO, 119 specimens from post EECO-1, 827 specimens from post EECO-2, and 5 specimens from post EECO-3. We calculated frequencies using cross-tabulation in SPSS Statistics 27.

In order to correct for the sample size we also used a rarefaction analysis and calculated diversity indices by PAST (v.3.0) – Paleontological Statistics data analysis package (Hammer et al., 2001; Hammer and Harper, 2006): (1) the Shannon (Shannon and Weaver, 1963) and Chao-1 (Chao, 1984) indices, which estimate the diversity from abundance data; (2) Margalef's richness index (Margalef, 1951), which compensates for the effects of sample size by dividing the number of taxa in a sample by the natural log of the number of occurrences (Gamito, 2010); and (3) finally Pielou's equitability index (Pielou, 1977), which provides the degree of homogeneity of distribution of specimens within species.

4. Results

4.1. The revised stratigraphy of coral localities

Most of the coral-bearing sites are from the easternmost Friuli and especially from the Collio area and they can be easily assigned to the coarse sandstones to siltstones of the Flysch di Cormons. This Formation, currently interpreted as derived from deltaic sedimentary processes (Venturini and Tunis, 1992b), is characterized by a huge bioclastic content composed mainly by LBF (alveolinids and nummulitids), molluscs, echinoderms and corals. A big, massive boulder with a rich coral assemblage is well-documented among grapevines rows close to Russiz (coord. N 45° 57′ 40.3″; E 13° 30′ 20.5″, alt. 85 m (Fig. 2). We recently assigned this boulder to SBZ12 p.p. of Serra-Kiel et al. (1998), i.e., upper Cuisian-lowermost Lutetian according to the larger foraminiferal assemblages constituted by *Assilina cuvillieri, A. maior punctulata, Nummulites friulanus, N. tauricus, N. praelorioli, N. campesinus, N. manfredi* and *N. praediscorbinus* (Benedetti et al., 2022).

As concerns the investigated collections, the stratigraphically lowest sample is that labelled as Buia, here referred to SBZ10 (lower Cuisian) on the basis of our ongoing revision of Dainelli's collection. We recognized *Assilina marinelli, Nummulites rotularius, N.* cf. *planulatus* and *N. subdistans* from the analysis of specimens stored in the Museo di Storia Naturale, Geologia e Paleontologia of the University of Florence. Similarly, the locality San Floriano del Collio can be referred to SBZ10–11 (lower to middle Cuisian) because of the occurrence of *Alveolina fornasinii, A. canavarii, Assilina marinellii, Nummuites pavloveci, N. pratti* and *N.* cf. *planulatus*.

Buttrio is a well-known locality that yielded middle Cuisian taxa generally referred to the *Alveolina dainellii* zone (Hottinger, 1960; Schaub, 1981; p. 65, fig. 63, point 1) fully consistent with SBZ11 (Papazzoni et al., 2017).

We refer the Rosazzo locality to SBZ12 (upper Cuisian-lowermost Lutetian) because it is the type locality of *Alveolina violae* Checchia-Rispoli, 1905, marker of the *A. violae* zone sensu Hottinger (1960) and *Nummulites friulanus* Schaub, 1962 as indicated by Schaub (1981; p. 65, fig. 63, point 5). Noax is very close to Rosazzo and is assigned also to SBZ12 according to our own data. We collected a sample (NOAXII in Benedetti et al., 2022) characterized by the occurrence of a rich fauna composed mainly of *Alveolina violae, Assilina cuvillieri, Nummulites friulanus, N. tauricus. N. praelorioli, N.* aff. *Lehneri* and *N.* cf. *campesinus*. We here assign also the locality Filanda Cignolini, an historical textile factory near Tarcento, known as Cascamificio di Buflons, to SBZ12 on the basis of the occurrence in the assemblage of *Alveolina violae* (Dainelli, 1915).

We consider the localities Rocca Bernarda and Russiz superiore as very close to the SBZ12/13 boundary, according to our investigation of samples taken as accurately as possible. In his monograph, Dainelli (1915) reported *Alveolina violae, Assilina granulosa* (=*A. maior*) and *Nummulites laevigatus* (=? *N. quasilaevigatus*); similarly, Schaub (1981; p. 65, fig. 63, point 2) reported an upper Cuisian assemblage. We collected samples that commonly show transitional forms between the typical Cuisian and the Lutetian forms, such as *Assilina* cf. *cuvillieri, A.* cf. *maior, Nummulites* cf. *friulanus* at Rocca Bernarda (CASMIC1, 3, 4) and Russiz (RSZIII, IVC, VI); the occurrence of *Blackites inflatus* in the nannofossil assemblages indicates a basal Lutetian (i.e., CNE8 zone of Agnini et al., 2014) age assignment (Benedetti et al., 2022).

Ongoing analysis of samples from Stavoli Tugliezzo allows us to refer the locality to the lower Lutetian SBZ13 based on the presence of *Assilina spira abrardi, A. suteri, A. tenuimarginata,* and *Nummulites verneuili*.

According to the museum labels, corals were collected also from other localities for which the age attribution is unfortunately not certain. Brazzano could be possibly referred to SBZ11–12 according to literature data (Cimerman et al., 1974), but Dainelli (1915) reported LBF taxa actually marking different ages: *N. atacicus* (SBZ8), *N. irregularis* (SBZ10–11) and *A. violae* (SBZ12). Brazzano (Case Limbard) is cited by Venturini and Tunis (1992a) as a lower Lutetian locality but data from LBF are not unambiguous because of the description of *A. violae, Nummulites obtusus* (=*N. tauricus*) in assemblage with *N. laevigatus*. Similarly, data from unpublished revision of the Dainelli's collection are not sufficient to discriminate the age of Brazzano (Villa Macorig) with again a mixture of different age LBF. Also, for other sites, from which a few corals occur, we cannot provide an accurate age assignment because of the absence of direct observations and unclear attributions of the accompanying LBF from the stored material in the museum collections. For example, Dainelli (1915) suggested for Attimis an older age in respect to Rosazzo, but the ongoing revision prevents constraining the few LF within the biozonal scheme of Serra-Kiel et al. (1998). Similarly, the *Assilina* and *Nummulites* specimens stored in the museum of Florence are not sufficient to determine a correct age of the localities Col dei Soldi (?SBZ12 with *Assilina maior* or ?SBZ13 with *A. spira abrardi*), Oleis (? SBZ13 with *N. laevigatus* or ?SBZ12 with *N. quasilaevigatus*), Meduno (? SBZ12–13), Tarcento (?SBZ-11), Rio Cideis (?SBZ13, possibly with *A. spira abrardi*) and Fiume Stella (?SBZ13, possibly with *N. laevigatus*).

4.2. EECO and post-EECO coral traits

The analysis and revision of all the specimens belonging to the whole collection depicts an overall high diversity for reef colonial corals. At the genus level, 37 revised genera have been recognized, with those more frequent represented by *Astreopora, Astrocoenia, Cyathoseris, Montastrea, Pachygyra, Placosmilia,* and *Stylophora* (Fig. 4). It is important to underline that the abundance of *Stylophora* in the collection could be overestimated due to the dominance of fragments rather than entire branching colonies.

At the species level, a total of 103 species has been identified (Table S2, supplementary material). Despite biases most probably related to a different degree of sampling in the numerous localities, we believe that the large amount of specimens collected during more than one century can be considered significantly representative of the period of time that we divided in four intervals (EECO, post-EECO1, post-EECO 2, post-EECO 3) by an accurate biostratigraphic study (Table 1).

Traits that we have examined within the four time-intervals are: 1) richness and relative abundance at the generic and species level; 2) relative abundance of growth forms; 3) colony size.

Coral richness and relative abundance. The composition of the coral fauna at the generic level in the four time-intervals is represented in Fig. 5, where richness and frequency are indicated, together with the total number of species for each interval. The complete list of species is provided in Table S2 (supplementary material).

The EECO interval has 21 coral genera and 37 species. Dominant genera are: *Astrocoenia* (11,8%), *Cyathoseris* (7,4%), *Montastraea* (7,4%), *Pachygyra* (5,9%), *Paraleptoria* (5,9%), *Stylocoenia* (8,8%) and *Stylophora* (17,6%).

The post-EECO 1 interval has 24 genera and 61 species. Dominant genera are: *Astrocoenia* (17,0%), *Pachygyra* (10,5%), *Placosmilia* (18,7%), *Stylophora* (8,2%).

The post-EECO 2 interval has 35 genera and 90 species. Dominant genera are: *Astreopora* (8,3%), *Astrocoenia* (11,3%), *Caulastraea* (3.4%), *Cyathoseris* (5,6%), *Montastraea* (7,9%), *Pachygyr*a (9,8%), *Placosmilia* (5,0%), *Siderofungia* (4.4%), *Stylophora* (5,6%).

The post-EECO 3 interval has 15 genera and 21 species. Dominant genera are: *Astreopora* (22,2%), *Astrocoenia* (17,8%), *Placosmilia* (15,6%).

A gradual increase of both genera and species richness can be recognized from the EECO interval to post-EECO 2 interval, whereas a decrease is clearly visible in the post-EECO 3 interval. Despite differences in the number of specimens, the four intervals show a total of 11 dominant genera, of which 7 are also those more frequent for the whole collection (Fig. 4). The most common species of these dominant genera are illustrated in Fig. 6. *Caulastraea, Euphyllia, Paraleptoria* and *Stylocoenia* are dominant in only one interval, all the others are dominant at
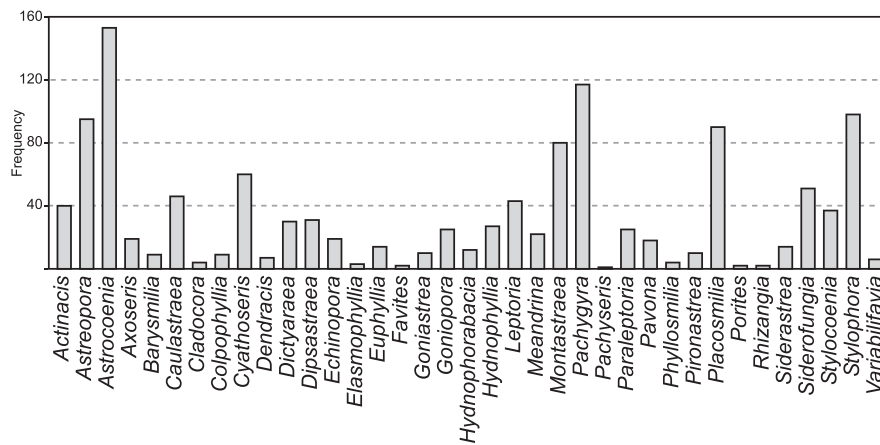
Fig. 4. Frequency of colonial scleractinian genera within the museum collections.
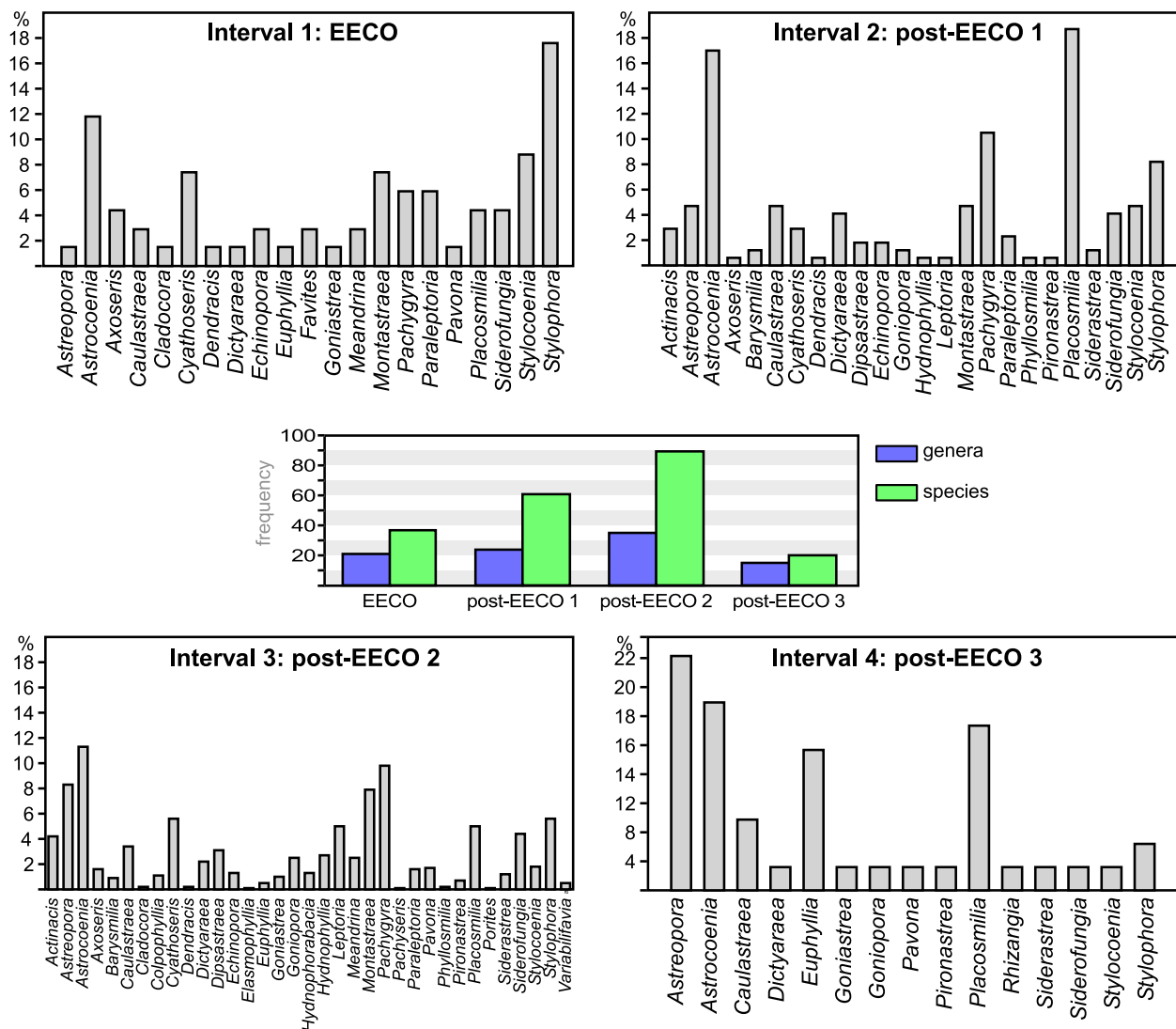

Fig. 5. Relative abundance of colonial scleractinian genera in the four time-intervals (EECO, post EECO-1, post EECO-2, post EECO-3). The total number of colonial scleractinian genera and species for each time interval is also represented in the central plot.

least in two intervals with *Astrocoenia* being the only genus that appears to dominate all four intervals. It is also important to underline that all the dominant genera occur in this collection from the EECO interval.

Coral colony growth forms. Colonial corals in the collection are undoubtedly dominant as they represent almost the 70% of all the specimens (Fig. 3A). As regards the total of growth forms exhibited by the
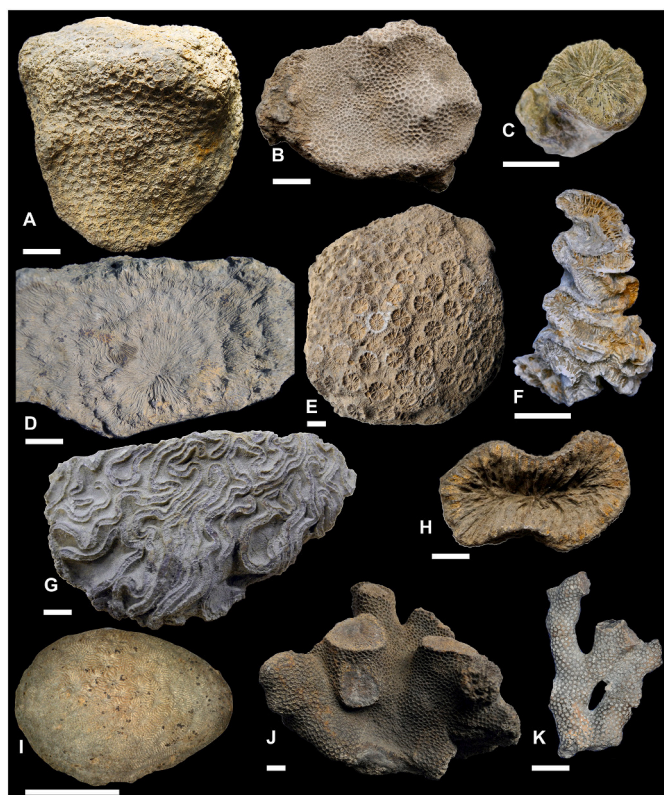
Fig. 6. Dominant coral genera with their most representative species. A. *Astreopora* (*A. annulata*, MSN-Unifi IGF100557). B. *Astrocoenia* (*A. parvistellata*, MSFN 20007). C. *Caulastraea* (*C. granulosa*, MSFN 20007). D. *Cyathoseris* (*C. raristella*, MFSN 26112). E. *Montastraea* (*M. alpina*, MSN-Unifi IGF100703). F. *Pachygyra* (*P. savii*, MFSN 21499). G. *Paraleptoria* (*P. flexuosissima*, MFSN 12972). H. *Placosmilia* (*P. multisinuosa*, MSN-Unifi IGF100655). I. *Siderofungia* (*S. eocenica*, MFSN 21511). J. *Stylocoenia* (*S. taurinensis*, MSN-Unifi IGF100670). K. *Stylophora* (*S. pulcherrima*, MFSN 21524). Scale bar: 1 cm.

colonial corals, branching (28.5%) and fungiform (27.7%) habits are those more frequent and almost equally represented. These are followed by platy (15.5%) and massive (15.1%), and by a minor occurrence of flabellate, tabular, branching phaceloid and encrusting growth forms (Fig. 3B).

The distribution and relative abundance of growth forms in the selected localities, that represent the four time-intervals, is represented in Fig. 7. In general, the two most common growth forms of the whole collection, branching and fungiform, are also those mostly represented in the selected time intervals except for the post-EECO 3 interval where fungiform corals are totally absent.

The results show that the proportions of growth forms are the same in EECO vs post-EECO 1 (Phi = 0.182, p = .637); but they are different in post-EECO 1 vs post-EECO 2 (Phi = 0.225, p < .001), and in post-EECO 2 vs post-EECO 3 (Phi = 0.181, p < .001). Branching corals dominate the EECO interval and gradually decrease toward the post-EECO 3 interval. Flabellate forms were more frequent in EECO and in post-EECO 1 than at other times. Massive and platy forms became relatively more frequent in post-EECO 2, and tabular forms along with massive and platy forms were more frequent in post-EECO 3.

Coral colony size. We measured maximum width and maximum height on 953 specimens (10 EECO, 119 post-EECO 1, 819 post-EECO 2, 5 post-EECO 3) in the Udine museum (Fig. 8). The dataset included both scleractinians and non-scleractinians. Although the colonies are relatively small in general, Kruskal Wallis and Median tests indicate that significant differences do exist for maximum width (Kruskal Wallis H = 73.789, df = 3, p < .001; Median = 4.2, chi-square = 42.873, df = 3, p ≤0.001), and maximum height (Kruskal Wallis H = 28.234, df = 3, p < .001; Median = 2.7, chi-square = 20.022, df = 3, p ≤0.001). Tukey HSD tests for both variables show that specimens in post-EECO 2 differ from the EECO, post-EECO 1, and post-EECO 3, and that EECO, post-EECO 1, and post-EECO 3 do not differ. Specimens in post-EECO 2 are larger (Fig. 8).

5. Discussion

The revision of the museum collections undoubtedly highlights that a coral hotspot occurred in the Friuli region during the late Ypresian-early Lutetian time interval. The diversity of the Friuli coral fauna is in fact exceptional, especially in the post-EECO 2 interval, being the oldest high diversity assemblage ever reported after the K-Pg extinction event.

The combination with a high-resolution biostratigraphy also provides the unique opportunity to subdivide the coral occurrences into shorter time intervals and thus analyse the changes in the reef coral fauna from the interval corresponding to the final part of the Early Eocene Climatic Optimum to the immediately following phases. Our findings allow us to assess which are the most resilient coral taxa and growth forms and, despite the absence of in situ outcrops, to infer the possible original palaeoenvironmental conditions of the Friuli coral hotspot.
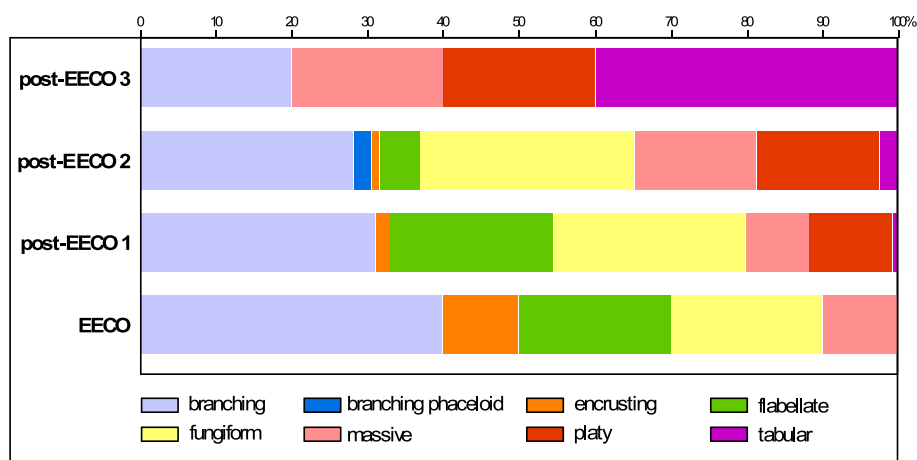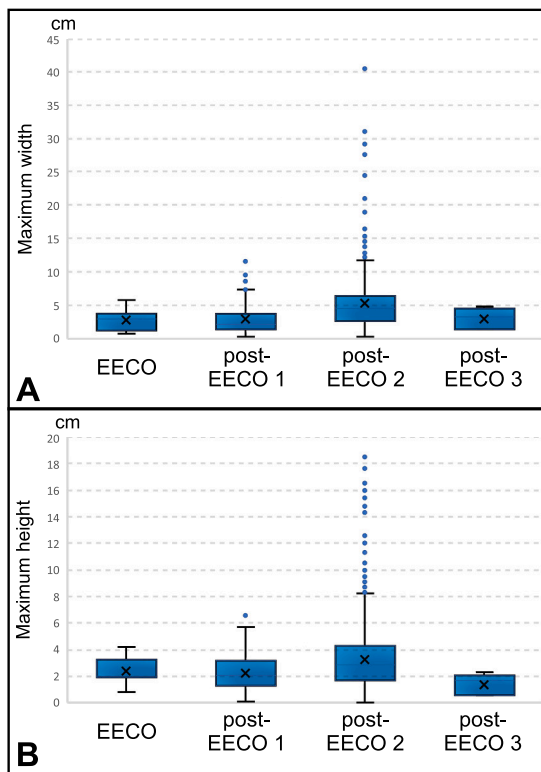

Fig. 7. Percentages of coral growth forms in the four investigated time-intervals (EECO, post EECO-1, post EECO-2, post EECO-3).
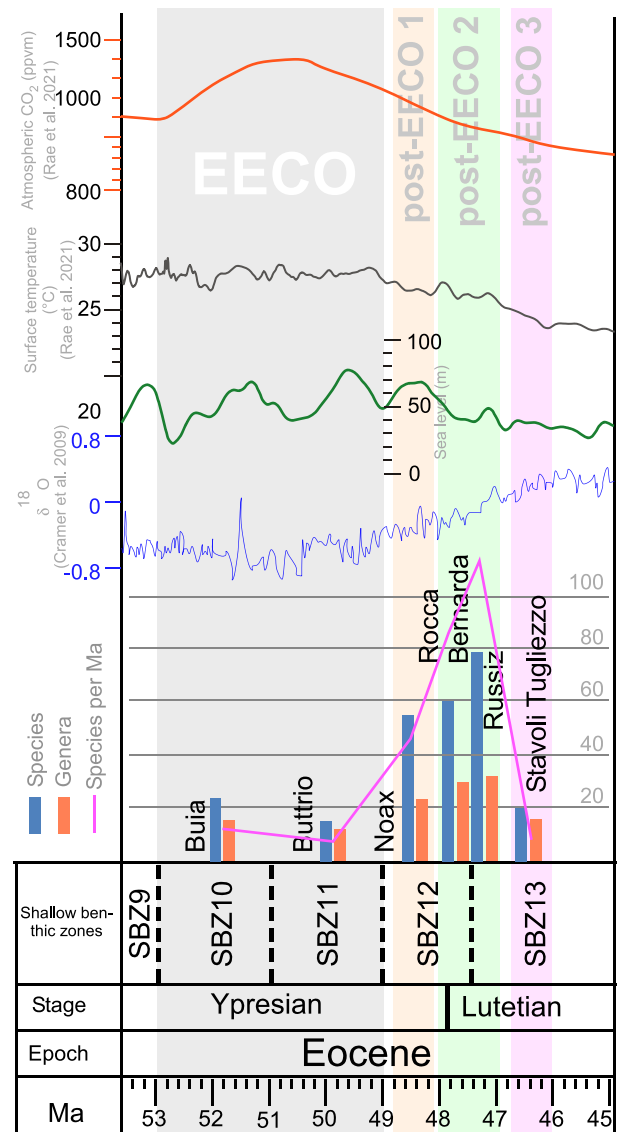
Fig. 8. Box and whisker plots comparing: A) specimen width, and B) specimen height among the four investigated time-intervals. Boxes enclose 50% of the measurements, lines within each box are medians, whiskers above and below each box are maximums and minimums, and points above whiskers are outliers. Specimens in post-EECO 2 are larger than in EECO, post-EECO 1, and post-EECO 3.

5.1. The coral hotspot: changes in diversity and composition

In order to better understand how the Friuli reef coral fauna reacted to the extreme warming phase of the EECO, we statistically analysed diversity data trying to compensate the effects of samples size as previously explained in the Methods section, and compared the observed trends with the most recent curves that reconstruct Sea Surface Temperature (SST) and atmospheric pCO_2 values during the Ypresian-Lutetian time interval (Figs. 9, 10). Our data suggest that during the EECO interval, when estimated surface temperature varied between 26 and 29 °C, the diversity at both genus and species level (Fig. 9), and according to the Chao-1 and Shannon indexes (Fig. 10), was relatively low. An abrupt increase in diversity of the investigated collections is then recorded in the post-EECO 1 interval, whereas a peak is reached in the earliest Lutetian (post-EECO 2), as suggested also by the increasing richness (Margalef index) and diversity (Shannon) (Figs. 9, 10). Despite there being no significant change in number of taxa after rarefaction analysis (Fig. 10), there is a drop in both diversity and richness recorded at Stavoli Tugliezzo (post-EECO 3 interval), roughly corresponding to the decrease of SST and atmospheric pCO_2. Future investigations of larger datasets will be necessary to clarify whether the values of post-EECO 3 interval represent Lutetian coral biodiversity, or if it is more likely an artefact due to the reduced sample size.

Our analysis clearly shows that the reef corals of Friuli reacted positively immediately after the warming event of the EECO, increasing in both richness and in colony size especially in the early Lutetian (post-EECO 2 interval). However, despite the increase in species richness and diversity recorded by our analyses (Fig. 10), the fluctuation of Chao-1 index and the almost constant decline in equitability not many taxa became dominant. We can thus determine which are the dominant/

Fig. 9. Changes in the number of colonial coral genera and species in the selected localities during the four investigated time-intervals and their relationship with the fluctuations of major paleoclimatic proxies (atmospheric pCO_2, seawater temperature, sea level, $\delta^{18}O$) (Cramer et al., 2009; Rae et al., 2021).

resilient genera that have sustained the Friuli coral hotspot according to the two main following criteria: 1) genera occurring in the EECO interval and in most of the post EECO-intervals, except post-EECO 3 that is represented in general by few specimens; 2) genera that are dominant in the EECO interval, and/or at least in one of post-EECO intervals. These criteria, together with the stratigraphic range of all the investigated genera, are illustrated in Fig. 11 and are met by the following genera: *Astreopora*, *Astrocoenia*, *Caulastraea*, *Cyathoseris*, *Montastraea*, *Pachygyra*, *Paraleptoria*, *Placosmilia*, *Siderofungia*, *Stylocoenia*, *Stylophora* (see also Fig. 6). Although a detailed analysis of the morphological traits of the coral taxa that proliferate after the EECO warming event is beyond the scope of this paper, and is still part of an ongoing project, we can observe that dominant coral genera do not possess any common traits. Degree of corallite integration, size of corallites and other characters are quite different among these corals and further analyses will be performed adding data from other coeval localities to determine if a particular suite of morphological traits can actually predict resilience vs extinction risk (Raja et al., 2021). Furthermore, of the 11 dominant
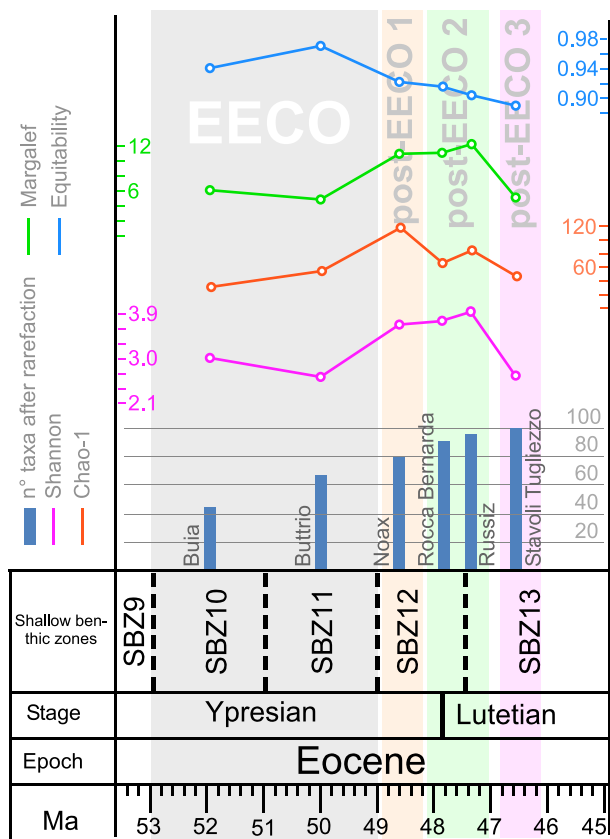
Fig. 10. Changes of diversity, richness and equitability indexes in the selected localities during the four investigated time-intervals.

genera, eight occurred during the Cretaceous and survived the K-Pg extinction event and most of the dominant genera extended into the Miocene epoch, with only *Pachygyra* restricted to the Eocene. Four of the dominant genera and 18 of the total of 37 genera are still extant, supporting the hypothesis that the central Neotethys was probably the "cradle" of the coral fauna, which developed and diversified subsequently, especially during the Oligocene, also in both the Caribbean and Indo-Pacific provinces.

If we compare our data for genus richness with those available from our PalEoCoral database and from the PBDB database and we place them in the palaeogeographic map of the early Eocene (Fig. 12), we can actually see that, during the Ypresian, colonial scleractinian corals were actually concentrated in the central Neotethys (Kühn, 1966; Košir, 1997; Vecsei and Moussavian, 1997; Baron-Szabo, 2004; Turnšek and Košir, 2004; Kleeman, 2009; Zamagni et al., 2012; Accordi et al., 2014; Giusberti et al., 2014; Vescogni et al., 2016; Bosellini et al., 2020) and subordinately from western (Eichenseer and Luterbacher, 1992; Ferratges et al., 2021) southern (Schuster, 1998) and easternmost (Nuttall, 1932; Carbone et al., 1993; Bernecker, 2005; Jauhri et al., 2006) parts of the Neotethyan realm. Only a few genera have been reported from isolated localities of New Zealand (Campbell et al., 1993), North (Durham, 1942; Squires and Goedert, 1994; Vaughan, 1941; Toulmin, 1977) and Central (Frost and Langenheim, 1974; Budd, 2000) America, and Africa (Herbig, 1986; Trappe, 1991). All detailed localities are listed in Table S3 (supplementary material). By comparison with the available literature and database, this fauna represents the oldest high diversity assemblage ever reported after the K-Pg extinction event with values, especially during the post-EECO 2 interval, also higher than those of the Oligocene when luxuriant coral reefs emerged at the global scale (Budd, 2000; Bosellini et al., 2021).

5.2. New insights about the original palaeoenvironment of Friuli corals

Do the collections help to better understand the original palaeoenvironmental conditions of the Friuli coral hotspot? What is known so far about these corals, and especially about those found in the Collio area, refers to a few publications that infer the occurrence of patch reefs developed in a deltaic depositional system (Venturini and Tunis, 1992a, 1992b; Maddaleni, 1997). During the early Eocene in fact, the hills between Rosazzo and Cormons constituted a large deltaic system subject to terrigenous supply from the emerged Julian Prealps located to the north (Tunis and Pirini Radrizzani, 1987). Unfortunately, the absence of in situ coral outcrops prevent us from making any detailed palaeoecological reconstruction; however, some traits recognized from the study of the coral collections can be useful in providing some additional information to the general reconstruction of a deltaic depositional setting.

Coral colonies embedded within relatively loose marly-arenaceous sediments have been collected intact and are quite well preserved. Apart from the fine fragments of branching colonies, corals are in fact rarely broken, and other taphonomic signatures such as abrasion, bioerosion and encrustation are limited. These features suggest that corals were poorly transported and most probably rapidly buried by sediments (Perry and Smithers, 2006; Silvestri et al., 2011). An environment characterized by a relative rapid sediment accumulation and most probably turbid waters is also suggested by the dominant types of coral growth forms. If we exclude the flabellate growth form that includes solitary corals, coral colonies are mainly dominated by branching and fungiform growth forms that are both considered a good strategy to cope with sediment accumulation in mixed carbonate-siliciclastic settings. Branching corals are known to be the most effective with respect to sediment clearance by passive removal, whereas the fungiform habit prevents the coral from being directly in contact with the soft sediment (Sanders and Baron-Szabo, 2005 and references therein). The occurrence of a consistent number of platy colonies may also suggest a reduced light availability that could be related to turbidity or to deeper waters (Rosen et al., 2000; Kołodziej and Bucur, 2020). These aspects, together with the occurrence of several planktic foraminifera in the loose sediment of the coral localities, may suggest a mesophotic coral ecosystem (Lesser et al., 2009; Morsilli et al., 2012; Kahng et al., 2019) that, due to the deltaic sedimentation, was also affected by river runoff, sediment accumulation and nutrient delivery. It is important to underline that the term "mesophotic reef" is usually associated with coral assemblages from relatively deeper settings (30 m to 150 m) but is also used for modern shallow-water turbid environments (Morgan et al., 2016, 2017).

Did this depositional setting change during the four investigated time intervals? Without facies analysis it is difficult to answer this question, however we do not see significant changes in the taphonomic signatures of the corals and especially in the LBF assemblages which are useful palaeobathymetric and palaeoenvironmental indicators (e.g. Hottinger, 1997; Beavington-Penney and Racey, 2004). It is thus possible, although still speculative, that the depositional setting remained quite stable and that changes in coral richness and size may be more associated to ameliorating climatic conditions. The occurrence of both megalospheric and microspheric generations in *Nummulites* and *Assilina* proves a reduced or absent transport of the shallow-water biota and, together with the presence of *Alveolina* and the absence or rarity of discocyclinids (see Beavington-Penney and Racey, 2004), it calls for depth consistent with mesophotic conditions.

What about the possible presence of a real coral reef? Although it is impossible to verify the occurrence of any reef structure, the reduced coral size with an average width and height in the range of centimeters could suggest a relatively weak capacity to calcify and/or a low longevity and a high faunal turnover as consequences of enhanced nutrient delivery and unstable conditions characteristic of the deltaic environment. Similar traits have been underlined by Zamagni et al. (2012) describing the nature of earliest Eocene coral assemblages and

genera	Cretaceous	Paleocene	Investigated intervals - corals from Friuli				Oligocene	Miocene	Recent
			EECO	post-EECO1	post-EECO2	post-EECO3			
Actinacis	x	x		▒	▒		x		
Astreopora	x	x	▒	▒	■	■	x	x	x
Astrocoenia	x	x	■	▒	■	▒	x	x	
Axoseris			▒						
Barysmilia	x	x					x		
Caulastraea		?	▒	▒	■		x	x	x
Cladocora	x	x	▒				x	x	x
Colpophyllia	?		▒				x	x	x
Cyathoseris	x	x	■	▒	■		x	x	
Dendracis		x	▒				x	x	
Dictyaraea	?		▒				x	x	
Dipsastraea			▒		▒		x	x	x
Echinopora			▒			▒	x	x	x
Elasmophyllia	x	x	▒						
Euphyllia		x	▒		▒		x	x	x
Favites	?		▒				x	x	x
Goniastrea	x	x	▒		▒		x	x	x
Goniopora	x	x		▒	▒		x	x	x
Hydnophorabacia					▒				
Hydnophyllia							x	x	
Leptoria	x	x	▒		▒		x	x	x
Meandrina		x	▒				x	x	x
Montastraea	x	x	■	■	■		x	x	x
Pachygyra	x	x	■	■	■	■			
Pachyseris					▒		x	x	x
Paraleptoria			■				x		
Pavona		x	▒		▒		x	x	x
Phyllosmilia	x	x							
Pironastrea		x	▒				x	x	
Placosmilia	x	x	▒	■	■	■	x	x	
Porites		?					x	x	x
Rhizangia	x	x				▒	x	x	
Siderastrea	x	x	▒	▒	▒		x	x	x
Siderofungia	x	x	▒		■		x		
Stylocoenia		x	■	▒			x	x	
Stylophora	x	x	■	■	■	■	x	x	x
Variabilifavia					▒		x		

Fig. 11. The stratigraphic range of all the recognized reef coral genera. Their occurrence in the four investigated time-intervals is illustrated, with the black pattern showing when they are dominant. Dominant genera are in red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

their poor frame-building capacity, which characterized the so-called coral reef gap of this period (Kiessling and Baron-Szabo, 2004; Kiessling and Simpson, 2011). All coral localities of this age in fact do not show large and well-developed reefs, but mostly small coral patches (Vescogni et al., 2016) and mounds dominated by algae (Bernecker, 2005; Eichenseer and Luterbacher, 1992; Ferratges et al., 2021; Košir, 1997) or encrusting foraminifera (Plaziat and Perrin, 1992). In general, their coral richness is not high but moderately low with the highest number of z-coral genera so far recorded at Monte Postale (Veneto, N Italy) where some isolated coral patches bordered a small pure carbonate platform (Vescogni et al., 2016; Bosellini et al., 2020). Large coral reef buildups reappeared in the Bartonian (Perrin, 2000; Pomar et al., 2017).

If we assume that the Friuli deltaic paleoenvironment, associated with the stressful climatic conditions, most probably did not favour the formation of a massive reef structure, we provide another consistent proof that the response to climate related stressors of reef-building

corals may be different from that of reefs. The complex relationship between reef development and reef coral diversity has been in fact documented during the Cenozoic, with examples of both coupling (Bosellini et al., 2021) and decoupling (Kiessling and Baron-Szabo, 2004; Johnson et al., 2008; Zamagni et al., 2012; Perrin and Bosellini, 2013) and highlight once more that high temperature in synergy with high CO_2 values is detrimental for coral reef construction but not necessarily for the survival of reef corals.

6. Conclusions

The early Paleogene "greenhouse" has been extensively investigated by the scientific community in order assess the response of reef corals and coral reefs to climate related stressors. Most of these studies, elaborated at a regional and global scale using data extracted from the literature and from public database (mainly the PBDB), did not document a coral extinction, but underlined the scarcity and the limited
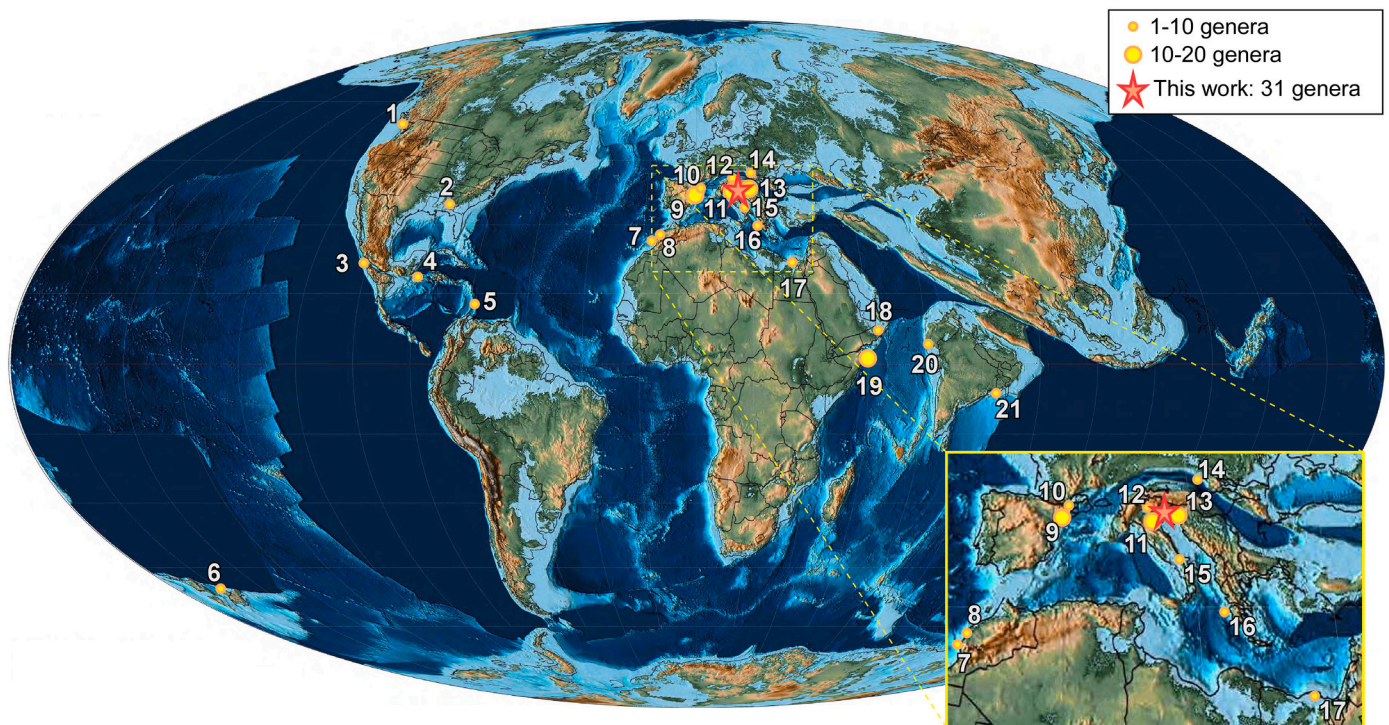
Fig. 12. Palaeogeographic distribution of colonial coral genera during the Ypresian, with a closeup of the central Neotethys region. Numbers indicate localities listed in Table S2 (supplementary material). Palaeogegraphic map after Scotese (2014).

development of bioconstructions and thus the so-called coral reef gap that lasted until the end of the Lutetian.

With this research about the Eocene reef corals from Friuli we characterize a coral fauna that, being studied only by authors at the end of the 19th century and beginning of the 20th, is not included in the above cited recent revisions and database, and we provide the first analysis of the response of reef corals to a warming event by an accurate specimen-based systematic revision of museum collections associated with a detailed biostratigraphic calibration. The main outputs are the following:

- We document a striking coral hotspot of zooxanthellate scleractinian corals during the late Cuisian and early Lutetian, immediately after the Early Eocene Climatic Optimum (EECO) that occurred between 53 and 49 Ma.
- The so-called reef corals (i.e. mainly colonial z-corals), contrarily to coral reefs, reacted positively immediately after the EECO suggesting that reef coral diversity may recover earlier than coral reef building.
- The coral taxa that dominated and sustained this coral hotspot have quite different morphological traits but are all characterized by having a relatively long stratigraphic record.
- This coral hotspot of Friuli, located in the central part of the Neotethys, was the most diverse at the global scale during the Ypresian and the oldest high diversity assemblage ever reported after the K-Pg extinction event.
- The deltaic paleoenvironment, most probably mesophotic, associated to the stressful climatic conditions, did not favour the formation of a massive reef structure, but harboured a rich pool of taxa as sort of refuge waiting for more suitable conditions for rapid growth and reef-building capacity that subsequently characterized the coral reef assemblages of the upper Eocene and Oligocene of the Southern Alps.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2022.111284.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All data are reported in the article

Acknowledgments

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