



A new *Fossil-Lagerstätte* from the Lower Eocene of Lessini Mountains (northern Italy): A multidisciplinary approach



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ABSTRACT

Hemipelagic dark limestones within calciturbiditic deposits at Monte Solane in the western Lessini Mountains of northern Italy yield a fish fauna dominated by stomiiforms. A minor component of the fossil assemblage is represented by a macroalgal non-calcareous flora associated with rarer terrestrial components including few angiosperm leaves and seeds. Micropaleontological (foraminifera, dinoflagellate cysts), sedimentological and geochemical proxies (TEX₈₆) indicate a deposition of the fossil-bearing bed in a hypoxic to possibly anoxic, warm, restricted basin. High-precision dating based on rich foraminiferal and calcareous nannoplankton content allows ascribing the site to the upper part of the Ypresian (Lower Eocene). The site is slightly older than the Ypresian worldwide-famous shallow-water Bolca *Konservat-Lagerstätte* located in the same region. Convergent paleoenvironmental clues based on both microfossils and ichthyofauna indicate that the sediments were deposited in the upper bathyal zone, probably between 300 and 600 m. Solane is therefore one of the rare and precious Eocene *Lagerstätte* to have fossilized in a deep marine setting. The site contains the oldest Cenozoic record of an ichthyofauna dominated by meso-bathypelagic taxa.

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1. Introduction

The Paleogene of Veneto region of northeastern Italy has been known since centuries for its richly fossiliferous shallow-water sediments outcropping in the central-western part of the region. Specifically, the Eocene *Konservat-Lagerstätte* of the worldwide-famous “Pesciara di Bolca” (Lessini Mountains) attracted the interest of the scholars since the Renaissance time (Mattioli, 1555) for its extraordinarily well-preserved fish fauna (Sorbini, 1972; Tang, 2002; Papazzoni and Trevisani, 2006). In the last two centuries the attention of the scientists has been merely focused, with few exceptions, on the spectacular macrofaunal and macrofloral content of Paleogene deposits of the Veneto region, whereas the geological, sedimentological and stratigraphical aspects were largely neglected. In addition, the general

interest for the area gradually decreased at the end of the 20th century. Only in recent years, some sites as the iconic Pesciara of Bolca regained interest and were object of “modern” paleoenvironmental and stratigraphical reappraisals (Papazzoni and Trevisani, 2006; Schwark et al., 2009). Within the framework of this stimulating “Third Millennium” re-birth of the researches in Veneto region, a new Paleogene *Fossil-Lagerstätte* was recently discovered in the western Lessini Mountains (Zorzin et al., 2011). The present paper describes a fossil assemblage of marine fishes and macroflora recovered, for the first time in the region, within Eocene open marine sediments outcropping in Monte Solane area (Verona province; Fig. 1). The aim is to present a detailed description of the deposit and discuss its paleoenvironment and age through an integrated macro-micropaleontological and geochemical investigation. This study has been carried out within the framework of a project aimed to investigate the possible relationships between *Fossil-Lagerstätten* and climatic disruptions in the Paleogene sedimentary record of northeastern Italy.

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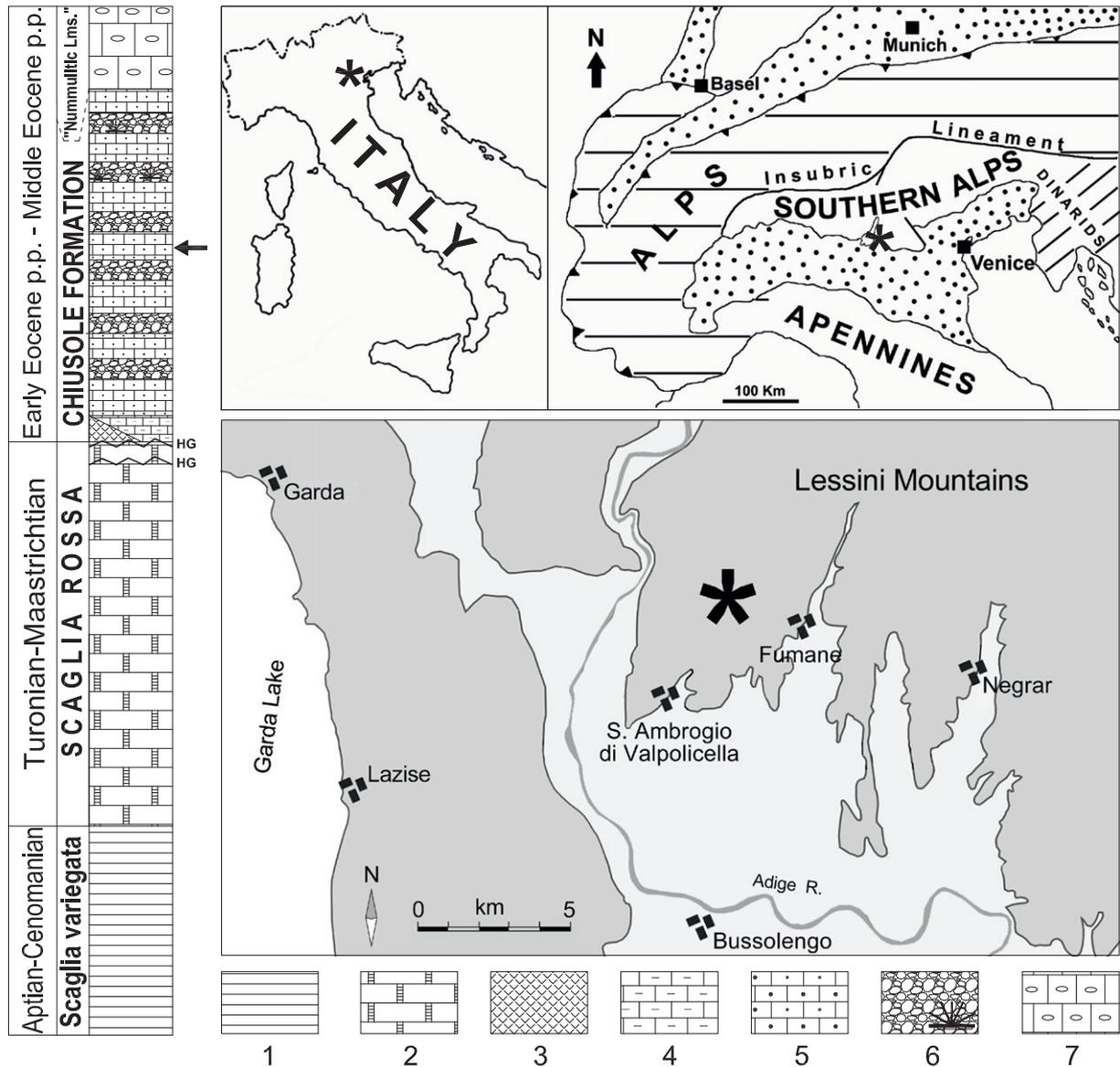


Fig. 1. Location map of the Solane site and simplified lithostratigraphic scheme of the western Lessini Mountains. Legend: 1. Gray cherty limestones and gray, green and red marls (Scaglia Variegata Alpina; thickness unknown); 2. Reddish and pinkish well bedded limestones and marly limestones with red and brown chert nodules and beds (Scaglia Rossa formation; ca. 70–80 m); 3. Volcanic deposits; 4. Whitish chalky marls and marly limestones (up to 10 m thick); 5. Whitish and light brown calcarenitic and subordinated calciruditic limestones with rare intervals of limestones and marly limestones. Presence of sporadic chert nodules; 6. Metric or submetric banks of coarse biocalcrites; 7. Coarse-grained nummulitic limestones. Lithostratigraphic units not in scale. HG = hard grounds. The asterisks indicate the location of the site. The arrow indicates the stratigraphical position of the fossiliferous interval outcropping at Solane.

2. Geographical and geological context

The Monte Solane site outcrops in the western Lessini Mountains (Verona province, northeastern Italy), ca. 27 km SW of the Bolca Lagerstätte and 116 km W of Venice (Fig. 1). The Lessini Mountains are a sector of the Southern Alps of the northern Italy (Fig. 1), a south-verging thrust and fold belt (Doglioni and Bosellini, 1987) resulting from the polyphasic deformation of the southern passive continental margin of the Tethys (Adria promontory; Channell et al., 1979; Winterer and Bosellini, 1981). During Paleogene times, the Lessinian area was a portion of the “Lessini Shelf” (Bosellini, 1989), a paleogeographic element superimposed to the Trento Platform, a Jurassic structural and paleogeographic domain of the Adria promontory. This platform drowned completely since the Middle Jurassic and was draped by pelagic sediments, thus becoming the Trento Plateau, an articulated structural high characterized by reduced sedimentation (e.g. Winterer and Bosellini, 1981). The Trento Plateau reacted rigidly during the Alpine

collision and was segmented by uplifted blocks that acted, since the Early Eocene, as centers of initiation of shallow-water carbonates (e.g. Torbole Limestone), which coalesced to form the Lessini Shelf (Bosellini, 1989; Luciani, 1989; Rasser and Harzhauser, 2008). This platform shed abundant biodebris into the surrounding depressed areas, as testified by slope deposits (e.g. Malcesine Limestone) that graded into the basal sediments of the Chiusole Formation (Luciani, 1989).

2.1. Lithostratigraphy of the western Lessini Mountains

In the western Lessini Mountains the concluding phase of Mesozoic pelagic sedimentation is represented by alternations of gray limestones and marls of the Scaglia Variegata Alpina (Aptian-Cenomanian), followed by pinkish and reddish cherty limestones, marly limestones and marls of the Scaglia Rossa (Turonian-Maastrichtian) Formation (Fig. 1). The Scaglia Rossa (ca. 70–80 m thick) is frequently capped at the top by two hardgrounds associated with major stratigraphic gaps.

The first gap includes part of the Santonian, the Campanian and the Early Maastrichtian. The second gap includes most of the Late Maastrichtian, the Paleocene and part of the Early Eocene (Malaroda, 1962; Massari and Medizza, 1973; De Zanche et al., 1977). Above the second hardground, a package of Lower Eocene whitish chalky marls and marly limestones may occur (De Zanche et al., 1977), sometimes overlying volcanic deposits. In the Fumane area, few km east of Solane (Fig. 1), the presence of ca. 10 m of Upper Paleocene (Thanetian) light brown and whitish marly limestones overlying the Scaglia Rossa (Garavello and Ungaro, 1996) has been documented. Such lithologies, which laterally strongly vary in thickness, grade into irregularly bedded marly calcarenitic limestones and biocalcirudites, associated with sparse chert nodules and subordinated hemipelagic marls and marly limestones (Fig. 1). The entire complex (>80 m thick), informally named “Pietra Gallina” (Sarti, 1980) or, improperly, “Calcare di Spilecco” (Ungaro, 2001), is here referred to as the Chiusole Formation sensu Luciani (1989). It testifies deep-sea sedimentation in basinal to slope setting during the Early Eocene, increasingly influenced by the production of biodebris of the growing/prograding Lessinian Shelf. The presence of coarse conglomerates and olistoliths intercalated within the Chiusole Formation, widely described in Val d’Avesa (east of Monte Solane), indicates earthquakes associated with penecontemporaneous volcanism (Sarti, 1980). The Chiusole Formation is crowned by thick beds of coarse-grained nummulitic limestones, indicative of shallow-water sedimentation, known in the regional literature with different names (“Nummulitic Limestones” or “Pietra d’Avesa”) and traditionally ascribed to the Middle Eocene (Carraro et al., 1969; De Zanche et al., 1977; Sarti, 1980; Ungaro, 2001).

2.2. The Monte Solane section: lithostratigraphy and lithology

The Solane section (Fig. 1) outcrops on a hill (“Monte Solane”) located on the southern portion of the Monte Pastello ridge (western Lessini Mountains). The section is exposed along a small valley cutting the northwestern slope of the Monte Solane, and the stratigraphical succession is almost entirely represented by the Chiusole Formation. The lower portion of this formation is faulted, in direct contact with the Cretaceous Scaglia Variegata. The section starts above the fault with fine-grained whitish or light brown cherty calcarenites, sometimes grading into dark marly limestones, in which metrical banks of coarse foraminiferal-rich biocalcirudites are intercalated. The total thickness of Chiusole Formation at Solane probably exceeds 80 m and its uppermost portion mostly consists of alternations of fine whitish calcarenitic limestones and coarse nummulitic biocalciruditic limestones containing micritic clasts and sparse silicified colonial corals (e.g. *Astrocoenia bistellata* and *A. lobatorotundata*).

2.2.1. The fossiliferous interval

The Lagerstätte interval is located in the middle–upper portion of the Chiusole Formation and is exposed at ca. 605 m AMSL, N of the top of the Solane hill (655 m AMSL), where the bedding strike is ca. N 80° with a dip angle of 10°. The measured and sampled section object of this paper spans an interval of ca. 17 m across the fossiliferous bed and is represented in Fig. 2. Field observations integrated with thin section analyses allow subdividing the section into 6 main lithozones/lithological intervals:

Lithozone I. The lower part of the section represents a 2.7 m-thick package of fine-grained light brown irregularly bedded calcarenitic limestones with a cherty brownish bed at +1.2 m (Fig. 2). The microfacies (Fig. 3A) mainly consists of bioclastic packstones dominated by densely packed planktic and small benthic foraminifera associated with fragments of larger foraminifera and echinoderms and other unidentifiable bioclasts. In the upper part of the interval 3 thin marly layers (≤ 2 cm thick) occur and have been sampled for calcareous nannoplankton and foraminiferal analyses.

Lithozone II. It consists of >4 m thick of normally-graded calciruditic bank that overlies with lower erosional contact the calcarenitic interval of lithozone I. The clasts at the base of the calciruditic bank are locally silicified and mainly represented by larger foraminifera (nummulitids, orthophragminids and rare alveolinids), calcareous algae, echinoderms, bivalves and slabs of planktic foraminiferal limestones (Fig. 3B). The top of the calciruditic bed does not crop out (Fig. 2).

Lithozone III. Above 1.45 m of covered interval, a package of coarse calcarenitic limestones (ca. 1.2 m thick) has been observed (Fig. 2). It grades into fine-grained cherty wackestone/packstones (1.7 m-thick interval; Fig. 2), of which the grains are planktic foraminifera and, subordinately, fragments of larger foraminifera, echinoderms and other unidentifiable bioclasts. The contact with the overlying lithozone is gradual.

Lithozone IV. This lithozone consists of 80–85 cm of grayish and brown, irregularly laminated, marly limestones and marls with frequent millimetric bioclastic turbidites. The microfacies (Fig. 3C) is mainly represented by planktic foraminiferal-dominated wackestones and packstones containing elongate and thin phosphatic remains (fish scales?). Sporadic vegetal debris occurs in the upper half of the lithozone.

Lithozone V. At ca. +12.2 m from the base of the section, the marly interval grades into a package of laminated dark-brown and gray hard limestones (ca. 30 cm thick). Small pyrite nodules occur just below the base of the level, subdivided into 3 beds 10 cm thick. It corresponds to the fish and plant-bearing interval (Fig. 2). Some bioturbations, filled by bioclasts, obliquely cut the beds. The microfacies is a planktic foraminiferal wackestone rich in phosphatic remains and spotted by small opaque grains, likely iron sulfides (Fig. 3D). Planktic foraminifera are much smaller than those observed within lithozone 4 (Fig. 3C). No evidence for microbial mat development on the sea floor (e.g. uneven, wavy lamination with thicker, light-colored laminae; see Papazzoni and Trevisani, 2006) was observed in the thin sections from this laminated limestone. The lithozone V is truncated at the top by a 6 cm-thick foraminiferal biocalcirudite.

Lithozone VI. This lithozone, overlying the fish-bearing bed, is mainly represented by brownish marly limestones containing millimetric bioclastic turbidites (interval from ca. 12.5 to 13.5 m). In such interval, very similar to the mid-upper part of lithozone IV, are intercalated three biocalcirudites of different thicknesses (Fig. 2). The lower biocalcirudite is ca. 6 cm thin and truncates the underlying lithozone V. The middle biocalcirudite is ca. 40 cm thick, shows a lower erosional contact and is normally graded. The upper biocalciruditic bed is 10–12 cm thick. The lower and upper biocalcirudites contain clasts of Cretaceous Scaglia Rossa. At the base of the lithozone vegetal debris are common.

Above lithozone VI a poorly outcropping interval (>2.5 m) of light brown fine-grained calcarenitic limestones capped at ca. 16.2 m by a biocalciruditic bank containing chert nodules (Fig. 2) has been observed. Such lithologies are virtually identical to lithozones I and II.

3. Material and methods

The Solane site was discovered in the 2000s by a private collector, Mr. Luigi Ambrosi (Zorzin et al., 2011). After this initial discovery, fieldwork activity and sampling for macro-micropaleontological and geochemical analyses were officially carried out by Padova and Modena Universities and Museo Civico di Storia Naturale di Verona, between 2011 and 2013. Most of the efforts were concentrated on a 17 m-thick interval containing the fossiliferous bed described above (Fig. 2; Appendix A). Some samples of marls, limestones and larger foraminiferal-bearing calcirudites were collected at the base of the Chiusole Formation ca. 60 m below the fish bed for supplementary micropaleontological

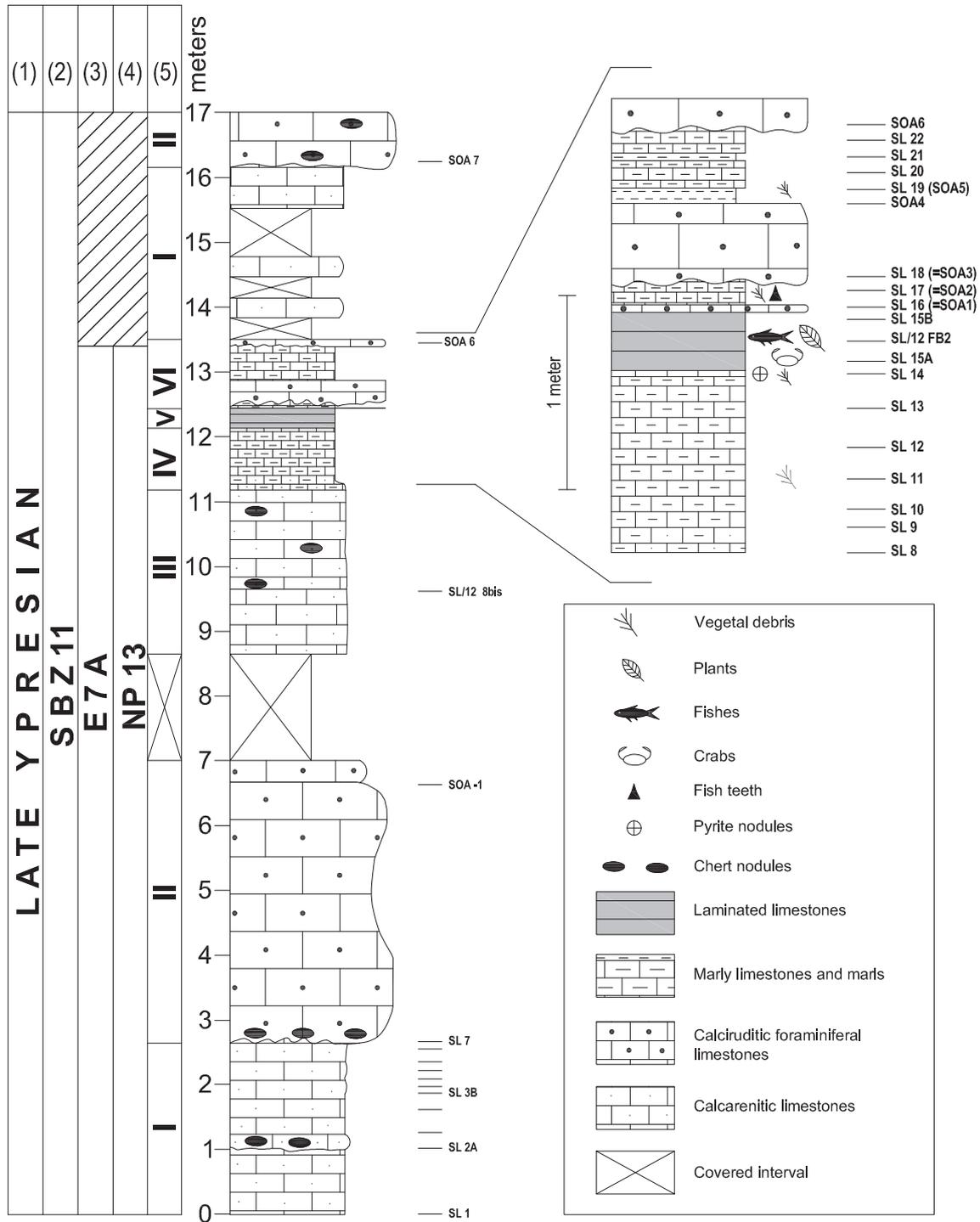


Fig. 2. Stratigraphic column of the Solane section with indication of the collected samples. The blow up shows the segment straddling the fossiliferous interval. 1: Chronostratigraphy; 2: larger foraminiferal zonation SBZ after Serra-Kiel et al. (1998); 3: planktonic foraminiferal zonation E after Wade et al. (2011); 4: calcareous nannofossils zonation NP after Martini (1971) and 5: lithozones.

analyses. No specific permits were required for the described field studies and sampling. All macrofossils discovered in the site have been officially deposited in public museums and a protocol number has been assigned (see below).

3.1. Macrofauna and macroflora

Macrofossils have been mostly recovered from the laminites of the lithozone V (Fig. 2). The only exception is represented by a shark

tooth probably coming from lithozone VI. Rock slabs containing these fossils, including the material here studied and figured, are stored in the paleontological collections of Museo Civico di Storia Naturale di Verona and the small Antiquarium of San Giorgio di Valpolicella (Verona province). At Verona Museo Civico di Storia Naturale are stored slabs with 72 fishes (IGVR 64065–64087; 64095–64112; 82399–82416; 82429–82454), 2 crustaceans (IGVR 82417–82420) and 15 plant remains (IGVR 64088–64094; 82421–82428; 82433, 82434, 82455). At the Antiquarium of San Giorgio di Valpolicella are stored slabs with 25

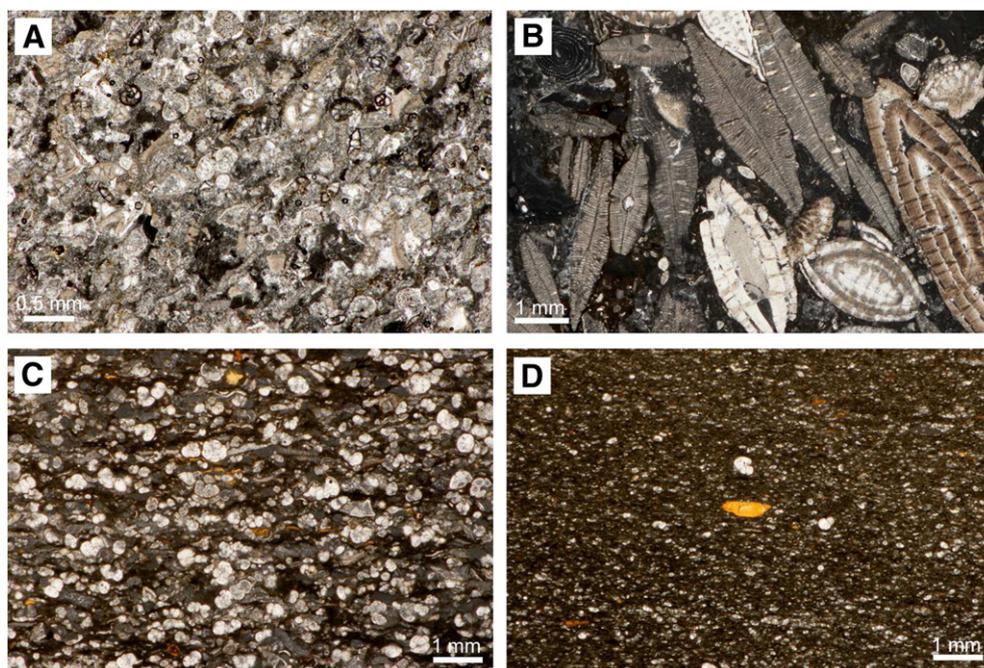


Fig. 3. Thin sections showing the microfacies of some lithozones recognized in the Solane section. A, Microfacies of the lithozone I (sample SL 1). B, Microfacies of the lithozone II (sample SL 7). C, Microfacies of the lithozone IV (sample SL 9). D, Microfacies of the lithozone V (sample SL 15A). See the text and Fig. 2 for more details.

fishes (IGVR 67856–67864, 67866, 67872–67880, 82465) and 7 plant remains (IGVR 67865, 67867–67869, 67871).

3.2. Foraminifera

The foraminiferal content was analyzed for 10 samples (Appendix A). Semiquantitative analysis of planktic and small benthic foraminifera was performed in washed residues of the $>63 \mu\text{m}$ fraction obtained from limestones, marly limestones and indurated marls processed following the cold acetolysis method of Lirer (2000) as described in Luciani et al. (2007). We calculated the planktic to planktic and benthic ratios, expressed as the proportion of planktic specimens in the total foraminiferal assemblage ($P/(P + B)\%$, briefly P/B). For paleodepth estimation we followed the bathymetric division defined in Van Morkhoven et al. (1986): upper bathyal = 200–600 m, middle bathyal = 600–1000 m and lower bathyal = 1000–2000 m. The studied residues are deposited in the micropaleontological collections of the Dipartimento di Geoscienze of the Padova University (Italy) and labeled with the sample number assigned during the fieldwork (Appendix A).

3.3. Larger foraminifera

The larger foraminifera are always included within hard biocalciferous limestones, sometimes with incipient silicification, so they were studied on thin sections of 8 samples (Appendix B). The nummulites were identified mainly on axial sections; also oblique or (rarely) equatorial sections were used to infer the inner characters of the tests. The alveolins are unfortunately quite rare, and usually not very well preserved, anyway some sections allowed identification of species. The measurements of the main biometric parameters were made on photomicrographs. For nummulite determinations we refer mainly to Schaub (1981) and Kleiber (1991) for axial sections. For alveolina determinations we refer to Hottinger (1960), Scotto di Carlo (1966), and Drobne (1977). Thin sections for the study of larger foraminifera are stored at the Dipartimento di Scienze Chimiche e Geologiche of Modena and Reggio Emilia University (Italy) and labeled with the sample number assigned during the fieldwork (Appendices A, B).

3.4. Calcareous nannofossils

Seventeen samples (Appendix C) were prepared from unprocessed material as smear slides and examined using a light microscope at $1250\times$ magnification. After a preliminary qualitative analysis in order to evaluate the abundance and the state of preservation of calcareous nannofossil assemblages the following quantitative and semiquantitative counting methods (Thierstein et al., 1977; Backman and Shackleton, 1983; Rio et al., 1990) have been applied to check the presence or absence of index species: 1) Counting species versus total assemblage, taking into account at least 300 specimens. This method has been applied from sample SL3A to sample SL8 (11.3 m); 2) Counting the number of specimens of rare but biostratigraphically useful species in an area of about 6–7 mm², which is roughly equivalent to 3 vertical traverses (modified after Backman and Shackleton, 1983), i.e. discoasterids and *Tribrachiatus orthostylus*. All studied smear slides are deposited in the micropaleontological collections of the Dipartimento di Geoscienze of the Padova University (Italy) and labeled with the sample number assigned during the fieldwork (Appendices A and C).

3.5. Dinoflagellates

Dinocysts were examined in 11 samples (Table S4) using established palynological processing methods. Briefly, samples were dried in a stove at 60 °C and a known amount of *Lycopodium* spores was added to ca. 10 g of material. Then the samples were treated with 30% HCl and twice with 38% HF for carbonate and silicate removal, respectively. Residues were sieved using a 250 and a 15 μm nylon mesh to remove large and small particles respectively. For removal of heavy minerals and to break up clumps of organic material, the sample was placed in an ultrasonic bath for a maximum of 5 min, sieved again, and subsequently concentrated to 1 ml, of which 10–35 μl was mounted on microscope slides. Taxonomy follows Fensome and Williams (2004). The material studied for dinoflagellate analysis is stored in the collection of the Laboratory of Palaeobotany and Palynology, at the Department of Earth Sciences, Faculty of Geosciences, Utrecht University (Netherlands) and labeled with the sample number assigned during the fieldwork.

3.6. Organic geochemistry

Before extraction, 15–20 g of 12 freeze-dried samples (Appendices A and E) was powdered. Extractions were performed with a Dionex Accelerated Solvent Extractor (ASE). Samples were extracted with a 9:1 (vol:vol) dichloromethane:methanol (DCM:MeOH) mixture at 7×10^6 Pa at 100 °C for 20–25 min. The obtained extract was dried, weighed and separated over an activated aluminumoxide (Al_2O_3) column using 9:1 hexane:DCM, 1:1 DCM:MeOH as eluents for the apolar and polar fractions, respectively. The obtained fractions were then dried again under a stream of nitrogen. The polar fraction was dissolved in 99:1 hexane:2-isopropanol and filtered over a 0.45 μm PTFE filter, to remove any large particles before analysis on an Agilent 1290 UHPLC-MS. An Alltech Prevail Cyano column (150 mm \times 2.1 mm \times 3 μm) was used to separate the glycerol dialkyl glycerol tetraethers (GDGTs), the target compounds. 10 μl of each in 99:1 hexane:2-isopropanol dissolved sample was injected. Detection of GDGTs was performed in Selected Ion Monitoring (SIM) (Schouten et al., 2007b). Chemstation software was used to integrate the GDGT abundances to obtain the TEX_{86} value (Schouten et al., 2002). The most recent high temperature (TEX_{86}^H) calibration was applied (Kim et al., 2010). The relative influence of soil organic matter and overprint by methanotrophic bacteria on the distribution of the different GDGTs is assessed with the Branched Isoprenoid Tetraether (BIT)-index (Hopmans et al., 2004) and the methane (MI)-index (Zhang et al., 2011), respectively.

4. Results

4.1. Fish assemblage

Fishes are the most common fossils in the laminated limestone (lithozone V) at Solane. The degree of disarticulation of fish skeletons studied herein is highly variable. Some specimens are fully articulated with soft body outline visible, whereas most of the specimens are moderately to poorly preserved, being usually more or less deformed or partially disarticulated, often with distorted proportions of the skeletons. Isolated elements of the skeletons (teeth, vertebrae) only sporadically have been found. Bones are usually preserved as brown to amber colored elements. In several cases, the scarce preservation prevents from the confident identification of the specimens. The fish assemblage of Monte Solane comprises Anguilliformes (fam., gen. et sp. indet.), Clupeidae (gen. indet., Order Clupeiformes; Fig. 4A), Gonostomatidae (gen. indet. cf. *Scopeloides*, Order Stomiiformes; Fig. 4B), Myctophidae (gen. indet. cf. *Eomyctophum*, Order Myctophiformes; Fig. 4C), Perciformes (fam., gen. et sp. indet.), Apogonidae gen. indet. (Order Perciformes, Suborder Percoidei; Fig. 5A), Euzaphlegidae (gen. et sp. nov., Order Perciformes, Suborder Trichiuroidei; Fig. 5B), Gempylidae (gen. et sp. indet., Order Perciformes, Suborder Trichiuroidei; Fig. 5C), Gempylidae (gen. indet. cf. *Thyrsitoides*, Order Perciformes, Suborder Trichiuroidei; Fig. 6A), Trichiuridae (gen. indet. cf. *Anenchelum*, Order Perciformes, Suborder Trichiuroidei; Fig. 6B), ? Propercarinidae (gen. indet., Order Perciformes, Suborder Stromateoidei), and Acanthomorpha (order, fam., gen. et sp. indet.; Fig. 6C). This list includes three taxa (Apogonidae gen. indet., Gempylidae gen. indet. cf. *Thyrsitoides* and Acanthomorpha order, fam., gen. et sp. indet.) not reported in the preliminary list of Zorzin et al. (2011). Among the Solane fish assemblage, the stomiiforms strongly predominate; the myctophiforms are much rarer, whereas all other taxa are represented by one to three specimens each in the collections. A detailed description of the ichthyofauna with a comparative systematic discussion will be the object of a separate paper (Bannikov et al., in prep.).

4.2. Macrofauna associated with fishes

Associated with fishes, two crabs have been found in the fossiliferous interval. Both specimens are strongly flattened: one is fully articulated but badly preserved; the other is represented by an isolated

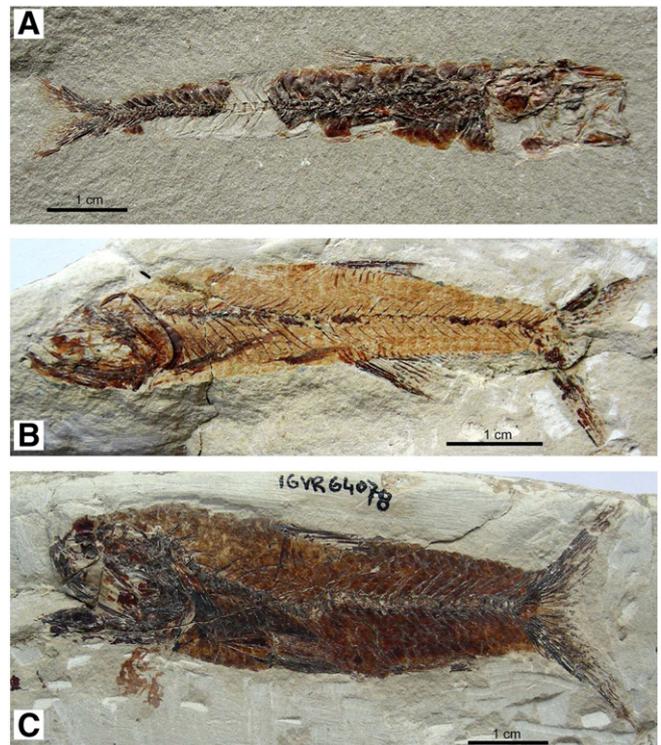


Fig. 4. Fossil fishes from the Ypresian of Solane. A, Clupeidae gen. indet. (IGVR 64083). B, Gonostomatidae gen. indet. cf. *Scopeloides* (IGVR 64073). C, Myctophidae gen. indet. cf. *Eomyctophum* (IGVR 64078).

sculptured carapace. The state of preservation precludes reliable taxonomic assignments (De Angeli A., 2013 pers. comm.).

4.3. Macroflora

Macroflora from the Monte Solane fish beds is represented mainly by non-calcareous marine macroalgae together with few angiosperm leaves and indeterminate seeds.

The more common forms (ca. 60% of the recovered assemblage) belong to the non-calcareous macroalga *Delessertes*; a genus defined on foliose thallus algae attached to the substrate by a rounded cartilaginous stipe (von Sternberg, 1833). Abramo Massalongo (1859) in the Bolca macroflora defined (without description) 8 different species of *Delessertes* and 22 different subspecies of *Delessertes bolcensis*. The thallus of the Monte Solane specimens is composed by oval and linear-lobate laminae impressions (Fig. 7A) from 4 to 18 cm long and with 3 cm of maximum width. Few brownish to reddish carbonaceous material was observed in the laminae impression and reddish lucent material in the cartilaginous stipe (Fig. 7B). On the basis of the morphological features, the Monte Solane specimens could be ascribed to *Delessertes bolcensis* Massalongo, a species very similar to the now existing type species *Delessertes sanguinea* (Hudson) Lamouroux.

Angiosperm non-lobate leaves recovered at Solane could be ascribed to the Byttneriaceae (now Malvaceae) genus *Dombeyopsis* (Massalongo, 1854; Meschinelli and Squinabol, 1892). The leaves show asymmetric primary venation and two different kinds of margin; respectively dentate (Fig. 7C) and non dentate (Fig. 7D). Cuticle in the leaves seems to be not preserved.

A five-lobed structure (Fig. 7E) is composed of dark pointed lobes with no clear venations and central part damaged. This specimen could be ascribed to the genus *Chaneia*, an extinct winged fruit common in the Tertiary of Europe (Heer, 1859; Wang and Manchester, 2000; Vasilis and Kvacsek, 2005). In the Monte Solane macroflora also two dark carbonaceous round structures were found, associated with

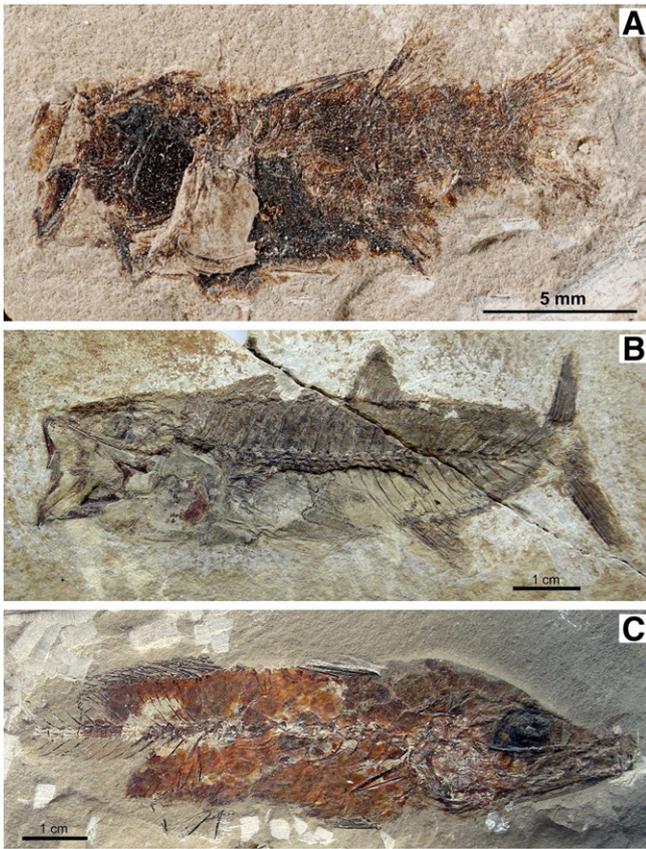


Fig. 5. Fossil fishes from the Ypresian of Solane. A, Apogonidae gen. indet. (IGVR 82413). B, Euzaphlegidae gen. indet. (IGVR 64084). C, Gempylidae gen. indet. (IGVR 64080).

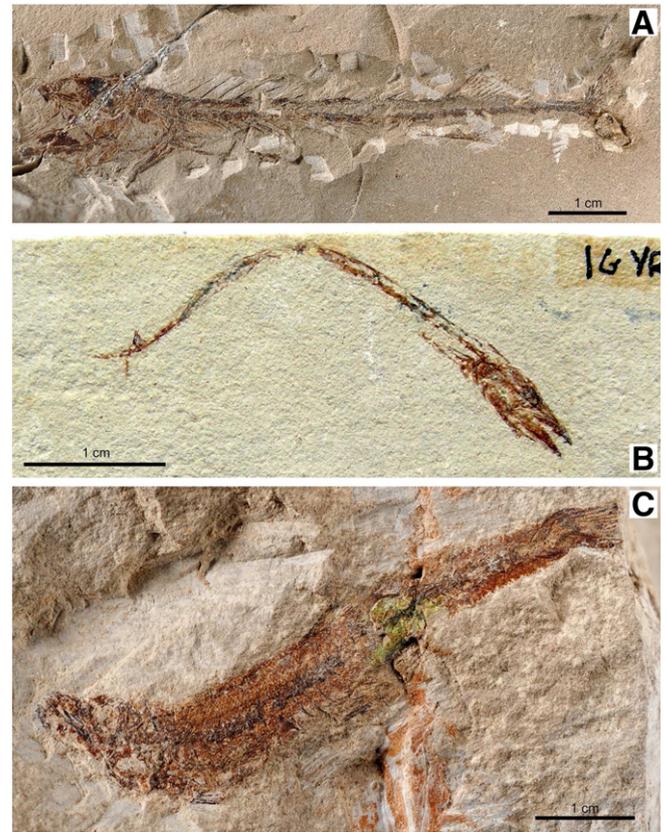


Fig. 6. Fossil fishes from the Ypresian of Solane. A, Gempylidae gen. indet. cf. *Thyrstitoides* (IGVR 82445). B, Trichiuridae gen. indet. cf. *Anenchelum* (IGVR 64082). C, Acanthomorpha order, fam., gen. et sp. indet. (IGVR 82452).

“fruit” and seed. In Fig. 7F is illustrated a circular structure, 3 cm in diameter, with a clear caved shell (1.5–2 mm thick) with a carbonaceous globose millimeter size structure inside that resembles a nut seed. The precise systematic position of the 6 centimeter dark rounded “fruit” (Fig. 7G) is uncertain.

4.4. Foraminifera

4.4.1. Planktic foraminifera

Planktic foraminifera are diverse and typical of the Tethyan low-temperature latitude assemblages. They are dominated by acarininids and subbotinids/parasubbotinids, with less frequent morozovellids, pseudohastigerinids, planorotalitids, globanomalinids and igorinids and by very rare biserial forms as *Praemurica? lozanoi* and *Guembeltrioides nuttallii*. Within the *Lagerstätte* laminated interval, planktic foraminiferal assemblages display significant changes consisting in the evident increase of pseudohastigerinids and biserial forms and in the entry of *Pseudoglobigerinella bolivariana* and of the small-sized triserial genus *Jenkinsina* (particularly abundant in the >38 micron fraction of samples FB2 and 15A). Due to the occurrence of *Acarinina cuneicamerata* and absence of both *Morozovella subbotinae* and *Turborotalia frontosa* (also in the basal beds ca. 55 m below the fossiliferous interval), the Chiusole Formation at Solane up to the lithozone VI belongs entirely to the E7a Zone (Wade et al., 2011).

4.4.2. Benthic foraminifera

All samples analyzed contain benthic foraminifera. They are moderately to poorly preserved and represent a minor component of the residues, representing <10% of the total foraminiferal content. Calcareous-hyaline infaunal morphotypes (buliminids, stilostomellids and nodosariids) dominate in all samples, along with less abundant

epifaunal morphotypes as cibicidids, *Cibicidoides*, *Hanzawaia* and anomalinids. The rare agglutinants observed consist of ammodiscids, clavulinids and spiroplectamminids. Within lithozone IV, the buliminid fauna, enriched by the presence of *Globobulimina* and *Uvigerina*, is associated with common fragments of large chambers of calcareous uniserial taxa (stilostomellids). A peculiar assemblage is recorded within the overlying lithozone V (*Lagerstätte* interval), where a fairly diversified fauna, virtually lacking epifaunal taxa, is dominated by small-sized buliminids (e.g. *Bulimina virginiana*, *Globobulimina*, *Bolivina* and fursenkoinids). In the overlying lithozone VI, the assemblage returns more diversified, with stilostomellids again common, associated with angulogerinids and epifaunal taxa. Shallow-water bioclastic debris is a significant component of most of the residues examined, with the exception of the samples from lithozone V. The occurrence of asterigerinids observed in some samples at Solane is likely an effect of downward transport from neritic environment, as supported by the presence of fragments of larger foraminifera and bioclastic detritus.

4.4.3. Larger foraminifera

The distribution of larger foraminifera is summarized in Appendix B. The assemblages are dominated by nummulites and orthophragminae sensu Less (1987), with a few alveolinas. The preservation is usually quite good for nummulites and orthophragminae, whereas it's usually poor for alveolinas, which are frequently broken and/or incomplete. As noted above, the taxonomic assignment on thin sections bears some uncertainties. Some of the specimens here labeled as *Nummulites burdigalensis cantabricus* (Fig. 8C) do not display all the typical features of the subspecies, namely the proloculus size could be smaller, out of the range for *N. b. cantabricus* and within the range of its ancestor *N. b. burdigalensis*. Here we face two problems: first, the random section could bring to underestimate the size of the proloculus, due to the out-

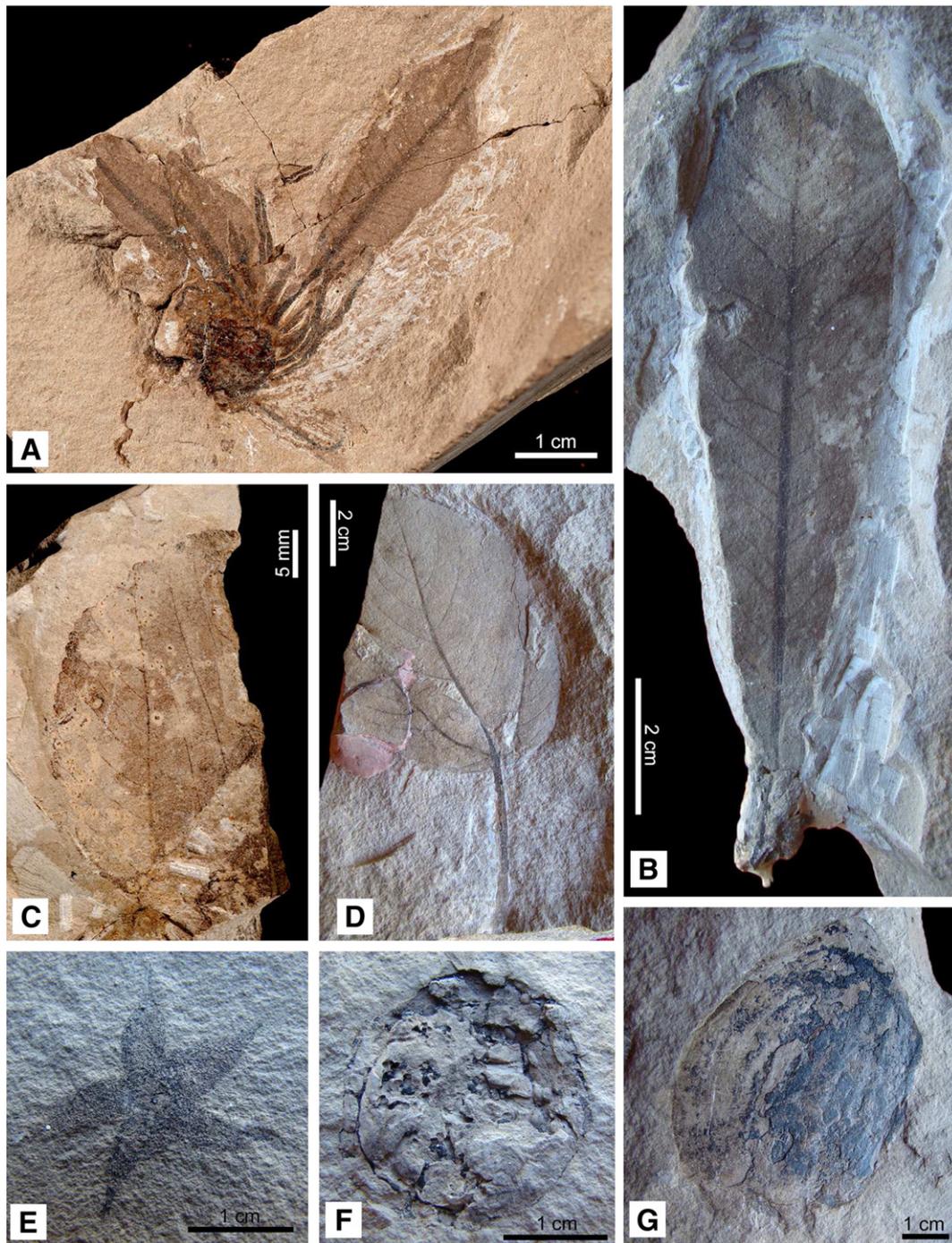


Fig. 7. Macroflora from the Ypresian of Solane. A, *Delessertes bolcensis* Massalongo (IGVR 82426). B, *Delessertes bolcensis* Massalongo (IGVR 67865). C, *Dombeyopsis* sp. (IGVR 82423). D, *Dombeyopsis* sp. (IGVR 67867). E, cf. *Chaneaia* (IGVR 67869). F, ? Nut seed (IGVR 82467). G, “Fruit” (IGVR 82466).

of-center cut; second, the very low number of specimens in the thin section (usually one-two specimens, the maximum observed for this subspecies is 5 in the sample SOA7) does not allow the study of a population. The general distribution of biometric parameters towards the lower edge of the range could suggest we are close to the limit between the two subspecies. The assemblages are substantially homogeneous. Based on the presence of *Alveolina decastroii*, *Nummulites burdigalensis cantabricus*, and *N. nitidus* (Fig. 8) the studied section is assigned to upper Ypresian Shallow Benthic Zone SBZ 11 of Serra-Kiel et al. (1998) (Fig. 2). Larger foraminiferal assemblages of the calcirudites collected at the base of the formation (e.g. sample SL/12–48 collected ca. 50–55 m below the fish-bearing interval; Appendix B) indicate that at

Solane the Chiusole Formation from the base to the fossiliferous interval belongs to the SBZ 11 Zone.

4.5. Calcareous nannofossils

All samples contain common to few calcareous nannofossils having a poor to moderate state of preservation. The results are shown in Appendix C. The genus *Discoaster* generally exhibits low relative abundances. Among the discoasterids, the absolute abundances show that *Discoaster lodoensis* is present in almost all samples. The presence of rare specimens of five-rayed *Discoaster* with ambiguous taxonomic/morphological features prevented a confident identification of *Discoaster sublodoensis*

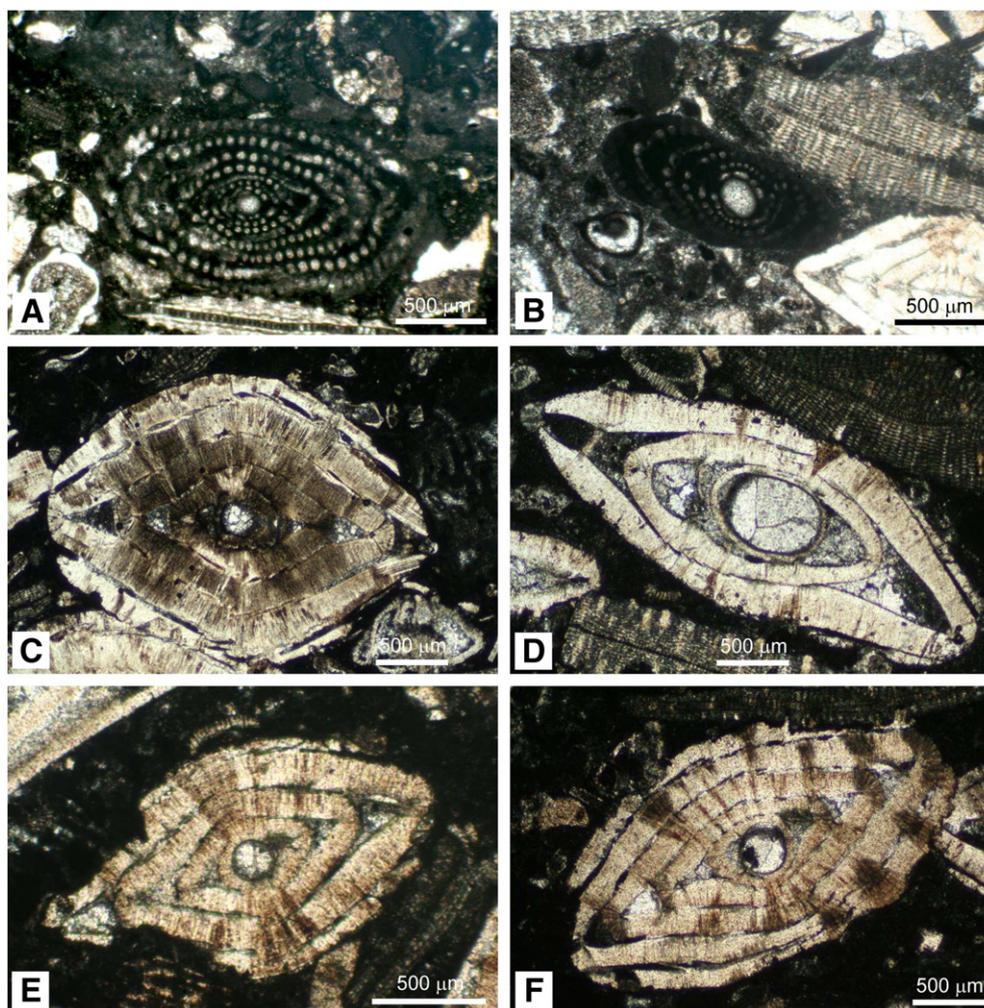


Fig. 8. Thin sections of samples with larger foraminifera from the Solane section. A, *Alveolina decastroi*. (Sample SR B2). B, *Alveolina distefanoi* (Sample SOA 7). C, *Nummulites burdigalensis cantabricus* (Sample SR B2). D, *Nummulites pratti* (Sample SOA 7). E, *Nummulites nitidus* (Sample SOA 7). F, *Nummulites partschi* (Sample SOA 7).

except in sample SL21 (Fig. 2; Appendix C) where a single specimen of *D. sublodoensis* is recorded. Among placoliths, *Coccolithus crassus* and the Noelaerhabdaceae (*Cyclicargolithus*, *Dictyococcites* and *Reticulofenestra*) are always present even if with different/variable abundances, whereas the genus *Toweius* is rare or virtually absent (Appendix C). In agreement with Agnini et al. (2006), the distribution patterns of Noelaerhabdaceae, *Discoaster*, and *Toweius*, the absence of *Tribrachiatulus orthostylus* and the sporadic presence of *D. sublodoensis* (Appendix C) allow for ascribing the Solane section to the calcareous nannofossil zone NP13 (Martini, 1971) (Figs. 2, 9). In addition, the occurrence of *C. crassus* indicates that the Solane section can be attributed to the calcareous nannofossil zone CP11 of Okada and Bukry (1980) (Fig. 9). A sample of marls collected at the base of the Chiusole Formation, ca. 50–55 m below the fossiliferous interval (Appendix C), is characterized by the presence of *D. lodoensis* (common), *T. orthostylus* (rare), *C. crassus* (few) and *Toweius* spp. (rare). This assemblage allows for ascribing the basal beds of Chiusole Formation at Solane to the upper part of Zone NP12, according to Agnini et al. (2006).

4.6. Dinoflagellate cysts

Palynological associations (Appendix D) contain large amounts of amorphous organic matter (AOM), varying in color from very light to nearly black. Fungal remains are abundant in nearly every sample, probably comprising outcrop contamination. The dominant palynomorph groups are marine dinoflagellate cysts (dinocysts) and foraminiferal linings, and only a few pollen and cysts of fresh water algae are recorded.

The dinoflagellate assemblages are generally poor in diversity and the preservation is moderate. Many of the identified taxa, notably *Operculodinium centrocarpum* and *Spiniferites ramosus*, have long biostratigraphic ranges from the Cretaceous to the present. However, *Charlesdowniea edwardsii* is recorded, of which the first occurrence was correlated to the middle of calcareous nannofossil NP12 Zone of Martini (1971) and becomes extinct in the NP14 Zone (Bujak and Mudge, 1994). We also recorded *Enneadocysta* spp., of which the earliest occurrences are known from the Southern Ocean as early as 53 Ma (Bijl et al., 2013) but emerges in the Southern mid-latitudes at ca. 49 Ma (Williams et al., 2004). These dates are consistent with the recorded calcareous nannoplankton biostratigraphy. *Operculodinium* spp., *Spiniferites* spp. and *Impaginium* spp. dominate the dinocyst assemblages.

4.7. TEX₈₆ paleothermometry

A total of 12 sediment samples from the Monte Solane section were selected for TEX₈₆ analysis (Appendices A, E). Only 8 of these yielded sufficiently abundant GDGTs (>1 ng/g dry weight sediment) to accurately quantify the ratio of the components and, hence, the TEX₈₆ values (Appendix E). The relative contribution of soil-derived lipids, as expressed in the BIT index, is low, averaging 0.06 and a maximum of 0.2, excluding the possibility that TEX₈₆ values are affected by lipids derived from soil bacteria (Weijers et al., 2006). The MI has values <0.11 suggesting no significant influence of anaerobic methane oxidation.

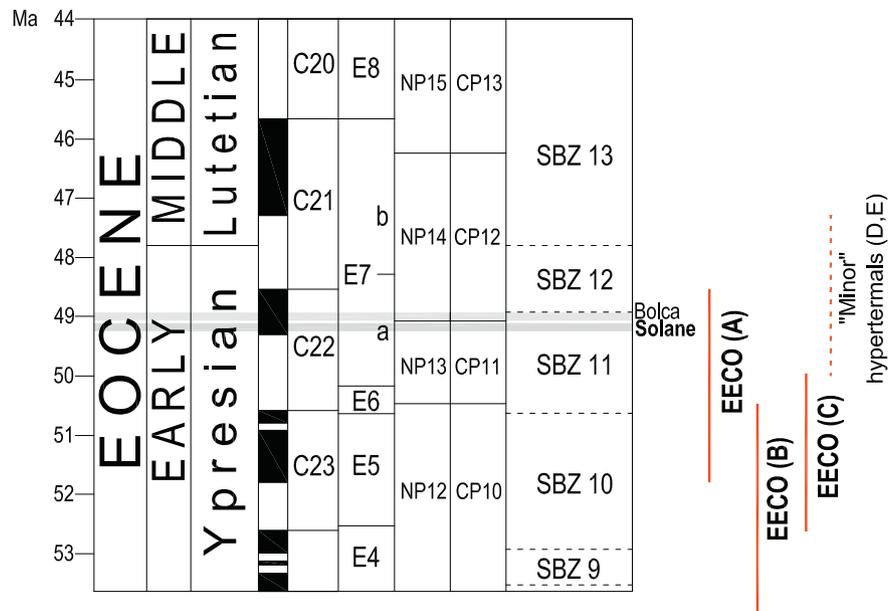


Fig. 9. Biomagnetostratigraphy of the Ypresian-Lutetian interval. Geomagnetic polarity scale, zonations of planktic foraminifera (E), larger benthic foraminifera (SBZ) and calcareous nannofossils (NP and CP Zones) after Vandenberghe et al. (2012). The stratigraphic positions of Solane and Bolca (Pesciara) sites are indicated by gray bars. Planktic foraminiferal Zonation of Wade et al. (2011), Tethyan zonation of larger benthic foraminifera from Serra-Kiel et al. (1998), and the calcareous nannofossil stratigraphy (NP and CP Zones of Martini, 1971 and Okada and Bukry, 1980 as modified by Vandenberghe et al., 2012). The red bars correspond to various EECO stratigraphical positions and concepts according to the following authors: A) Bijl et al. (2009); B) Schneider et al. (2011); C) Agnini et al. (2006). The dotted bar denotes the late Ypresian-earliest Lutetian time interval characterized by minor hyperthermals according to: D) Sexton et al. (2011) and E) Payros et al. (2012).

TEX₈₆ values are high, at 0.97 on average and imply SSTs (Sea Surface Temperatures) exceeding 37 °C.

5. Discussion

5.1. Dating the Solane Lagerstätte

The Solane site is unique among the Paleogene *Fossil Lagerstätten* of Veneto region (NE Italy) because of the concomitant presence and abundance in the sediments of calcareous plankton, larger foraminifera and dinoflagellates that allow a firm dating (Fig. 9). The biozonal assignments, based on the various groups herein investigated, allow ascribing the studied section to the upper part of the Ypresian (Fig. 9). Specifically, the sporadic presence of *Discoaster subloboensis* within lithozone VI allows the assignment of the upper portion of the studied section to the upper part of calcareous nannofossil zone NP13 (Fig. 9), in agreement with the data of Agnini et al. (2006) and Shamrock and Watkins (2012). All biostratigraphical data concur in evidencing that the Solane site is slightly older than the Ypresian Pesciara of Bolca that falls within the larger foraminiferal SBZ 11 and basal calcareous nannofossil NP14 Zone (Medizza, 1975; Papazzoni and Trevisani, 2006) (Fig. 9). In terms of absolute age, the Chiusole Formation at Solane spans the interval between the first occurrence of *Acarinina cuneicamerata* (at 50.2/50.4 Ma; Wade et al., 2011; Vandenberghe et al., 2012) and the first common occurrence of *Discoaster subloboensis* (49.11 Ma; Vandenberghe et al., 2012). An older age was estimated for the lowest occurrence of *A. cuneicamerata* in the Tethyan Possagno section (Treviso province, eastern part of the Veneto region) and ODP Site 1051 (Luciani et al., 2011) where the species first occurs below the highest occurrence of *M. subbotinae*. Specifically, the estimated age is 51.81 Ma and 51.14 Ma for Possagno and Site 1051 respectively, according to Vandenberghe et al. (2012).

5.2. Paleoenvironmental inferences

5.2.1. Fish fauna

The ichthyofauna of Monte Solane includes mainly mesopelagic fishes (stomiiforms, myctophiforms, trichiuroids), with a few epipelagic

taxa (?Propercarinidae gen. indet. and a clupeid herring). Among the materials collected, the fishes which now inhabit shallow-water coastal area and bottom-dwellers are almost absent (with the probable exception of the apogonid and anguilliform). The strong predominance of Gonostomatidae (cf. *Scopeloides*; Fig. 4B) in the fish fauna (more than 60% of the fish specimens in the MCSNV collection) suggests that the fishes were buried in an open marine basin with a depth most probably greater than 300 m. Extant bioluminescent gonostomatids are known to inhabit depths from 200 (rarely 100) to 2700 m and more (e.g., Schaefer et al., 1986); some of them undertake vertical migration to upper 200 m at night (as also most of myctophids do; Hulley, 1986). The gonostomatid genus *Scopeloides* is also characteristic for the mesopelagic zone of the Oligocene Paratethys (Danil'chenko, 1960, 1967; Prokofiev, 2005). According to the fish fauna composition, the Monte Solane sediments were probably deposited in a deep marine basin with normal salinity and relatively warm climate, perhaps in a relatively close proximity to an insular shore, as evidenced by the discovery of an apogonid. Most of the modern apogonids are shallow-water fishes, although *Ostorhinchus gularis* inhabits depths from 60 to 290 m (Nelson, 2006). Given the considerations above, we infer that the majority of the fishes probably lived in the water column above the depositional site and only some specimens were more or less transported horizontally. Moreover, the highly variable state of preservation of fishes at Solane suggests that the ichthyotaphocoenosis likely resulted from the settling of carcasses in a quiet environment under low sedimentation rate and variable physicochemical sea bottom water conditions.

5.2.2. Comparison with the Bolca fish faunas

The ichthyofauna of Monte Solane is totally different from the Lower Eocene fish fauna of the Bolca sites (Pesciara and Monte Postale), although these localities are close both geographically and in their age. The Bolca *Fossil Lagerstätten* are exceptionally rich in shallow-water taxa (Blot, 1980; Landini and Sorbini, 1996; Bannikov, 2010), whereas only few taxa of predominantly mesopelagic fishes occur at Monte Solane. Only three families are common in both the two fish faunas (Clupeidae, Apogonidae and Euzaphlegidae); however, these are represented by different genera, as most probably is correct for

the anguilliforms. In addition, the state of preservation of fossils is usually much better in Bolca than in Monte Solane. The hints for the presence of microbial mats in Bolca, absent in Monte Solane, could partially account for the preservation differences between these localities. Fossil fishes from Bolca are represented by both small and large specimens, whereas those from Monte Solane are relatively small. These differences can be explained by the fact that the Bolca and Monte Solane sites were deposited in quite different settings. For the Bolca locality, Papazzoni and Trevisani (2006) proposed a shallow marine basin neighboring emerged land (e.g. coral reef lagoon; cf. Bellwood, 1996), whereas for Monte Solane it is possible to infer a much deeper, open marine environment.

5.2.3. Macroflora

Macrofloral findings are mainly represented by the delicate algal bodies belonging to *Delessertes* (*Delesseria*) that needs stagnant water and/or low rate of decomposition for preservation (Krings and Mayr, 2004). The paleoecology of these rare fossils is not well known and the only possibilities to compare with are the similar rhodophcean forms; the habitat of the living *Delesseria* is both lower intertidal to subtidal environments, normally on rocky sea bottom. The abundance of *Delessertes* in the lagoonal setting of the Bolca Fossil-Lagerstätte further supports its nearshore living environment. The source area of these macroalgal remains could be roughly placed south of the Monte Solane fossiliferous locality (Sarti, 1980).

5.2.4. Foraminifera

5.2.4.1. Planktic foraminifera. The planktic foraminiferal assemblages of the Chiusole Formation up to the Lagerstätte interval are generally well diversified, implying that a full set of ecological niches was occupied both in surface and subsurface waters, thus suggesting relatively stable and oligotrophic environmental conditions. Within the lithozone V the increase of groups considered as opportunists, according to the known life-strategies of Eocene planktic foraminifera (biserials, pseudohastigerinids, *Jenkinsina*, *P. bolivariana*) (see Luciani et al., 2010 and references herein), suggests an environmental shift towards a perturbed environment. The paleoecological significance of the aforementioned forms indicates a possible expansion of the oxygen-minimum zone and increased eutrophy of the upper water column during deposition of the Lagerstätte sediments. We cannot exclude that the environmental perturbation might have implied variations in salinity, as suggested by the palynological data (see below), because less is known about this parameter for the aforesaid opportunist forms.

5.2.4.2. Benthic foraminifera. The high planktic/benthic foraminiferal ratio (>90%) in all samples indicates a deep marine environment, at least upper bathyal (Alegret and Thomas, 2001). At Solane, the overall scarcity of benthic foraminiferal taxa common in middle–lower bathyal settings (e.g. *Nuttallides truempyi*, *Bulimina impendens-trinitatensis* group) suggests deposition in a full upper bathyal environment (from 200 to 600 m) *sensu* Van Morkhoven et al. (1986). This estimation is in good agreement with indications given by fish fauna and is consistent with the paleogeographic setting of the area, located in the structural high of former Trento Plateau. The high abundance of infaunal taxa (e.g. buliminids, stilostomellids) in all the lithozones examined is indicative of significant food supply at the sea floor. In fact, in the present oceans high abundances of buliminids characterize areas with high food supply, possibly associated low oxygen conditions (Alve, 1995; Bernhard et al., 1997; Bernhard and Sen Gupta, 1999; Van der Zwaan et al., 1999; Gooday, 2003). In addition, also the extinct group of stilostomellids preferred enhanced food supply and tolerated lowered oxygen concentrations (e.g. Hayward et al., 2012). Significant signs of changing sea floor conditions are recorded within lithozone IV, where an increase in large stilostomellids, along with the presence of *Globobulimina* and *Uvigerina*, indicate more eutrophic and possibly

less oxygenated sea floor conditions. The benthic assemblages of the overlying lithozone V (fish bed) indicate a change towards hypoxic conditions (*sensu* Jorissen et al., 2007) as testified by the presence of stressed, low-diversity, small-sized “buliminid”-dominated fauna. The primary fine lamination of the sediment, along with the virtual absence of a benthic foraminiferal epifaunal community, further supports a scenario of low oxygen levels that prevented sea floor colonization by benthic burrowers. Slight differences in the composition of benthic foraminiferal faunas within the fish bed suggest that the environmental conditions were not homogeneous, but characterized by variable degrees of sea floor hypoxia and/or food supply. Short-lived phases of total anoxia in a general context of marked hypoxia cannot be completely ruled out, but they are probably beyond the resolution of our foraminiferal record/sampling. The more structured and diversified benthic foraminiferal assemblages of lithozone VI indicate less stressed and more oxygenated sea floor conditions.

5.2.4.3. Larger foraminifera. The mixing of larger foraminifera living presumably in different parts of the carbonate platform, together with a general common orientation of the tests parallel to the stratification, clearly suggests some degree of transportation. The presence of a few planktic foraminifera in the matrix among larger foraminifera, the erosive base of most of the larger foraminiferal-rich beds, interbedded between calcareous plankton-rich strata, clearly indicate the tests were moved towards the basin.

The larger foraminiferal assemblages of Pesciara and Monte Postale sites mainly differ from those of Solane section in the abundance of alveolinas, which are widespread below and above the laminated limestones with fishes (Papazzoni and Trevisani, 2005, 2006; Trevisani et al., 2005). The nummulitic facies once present in the uppermost levels of the Pesciara outcrop contains *Nummulites pratti* and *N. praelucasi* (Papazzoni and Trevisani, 2005); the same species are present also in the Solane section (Fig. 8D, Appendix B). Among alveolinas, all the species present in Solane, namely *Alveolina decastrói*, *A. distefanoí* (Fig. 8A, B) and *A. rugosa* (Appendix B) were also found in the Pesciara section and at the Monte Postale. As discussed in the previous section, the larger foraminiferal assemblage suggests the tests accumulated come from different parts of the platform, with the nummulite facies best represented in comparison with the more proximal *Alveolina* facies. In this respect, the source area of the resedimented larger foraminifera in the Solane section is more distal than the paleoenvironments represented in the Pesciara and Monte Postale sites.

5.2.5. Dinoflagellate cysts

The occurrence of abundant *Impagidinium* spp., both in modern and Paleogene oceans, is restricted to the outer shelf to open ocean environments (Sluijs et al., 2005; Zonneveld et al., 2013). *Operculodinium* spp. and *Spiniferites* spp. are also abundant, which is often the case in outer shelf environments. Moreover, relative abundances of terrestrial material are very low, with only sporadic occurrences of terrestrial palynomorphs (spores and pollen). The combined information suggests that sediments at Solane were deposited in an outer neritic to mesopelagic environment, with significant open oceanic influences. Inner neritic dinocyst species, e.g. *Areoligera*, *Homotryblium* are occasionally recorded and therefore most likely indicate downslope transport. The dominance of Gonyaulacoid cysts over Peridinioid cysts suggests relatively low productivity, e.g. Sluijs et al. (2005). Much diversity in dimensions and characteristics is recorded within taxa, particularly in *Spiniferites* spp., *Operculodinium* spp. and to a lesser extent in *Impagidinium* spp. In *Spiniferites* such variation includes poorly developed to full-grown processes and normal to very small cyst sizes. Changes in wall texture and general appearance such as thick *Hafniasphaera*-like wall structures and spherical vs. ovoidal cyst shapes are also common. *Operculodinium* shows variation in cyst sizes from large 120 + μm, to normal size ~40–50 μm. In addition, some *Operculodinium* specimens exhibit fibrous processes similar to those in *Fibrocysta*, and intermediate forms between

these two genera are recorded. Generally, processes in *Operculodinium* are short, although normal forms are also common. Such variations in size, shape and process length have previously been explained by variations in salinity (Ellegaard et al., 2002; Mertens et al., 2009). If so, the various morphotypes in these samples could represent a mixture of specimens derived from the entire inshore-to-offshore transect or seasonal variability in sea surface salinity, perhaps associated with seasonal river influx and/or precipitation.

5.3. Depositional model of the Solane site

Lithological, sedimentological and paleontological evidences all concur in indicating that the Ypresian Solane succession deposited in a basinal, upper bathyal setting sensu Van Morkhoven et al. (1986) in close vicinity to a carbonate platform that supplied abundant fine-grained bioturbidites. Such calciturbiditic influx, typically represented by lithozone I, was periodically disrupted by landslides and debris flows testified by deposition of coarse biocalciruditic banks (e.g. lithozone II; Fig. 2). Such deposits likely testify to the tectonic instability of the area (Sarti, 1980). Lithozones IV–VI, including the fish bed (Fig. 2), represent the “autochthonous” hemipelagic sedimentation. The entire interval from +2.7 up to ca. 13.5 m (lithozones II–VI; Fig. 2) is clearly a fining upward succession testifying a gradual and progressive diminishing of the platform sedimentary influx into the basin. Calciturbiditic deposits reappear intermittently during the deposition of the lithozone VI, as evidenced by the presence of biocalcirudites intercalated within the marly limestones (Fig. 2). The fine-grained calcarenites overlying lithozone VI record the reestablishment of normal bioturbidite sedimentation within the basin (Fig. 2). Lowered oxygen conditions certainly prevailed during the deposition of the lithozone IV to VI with harsher, severely hypoxic conditions recorded within the fish-bearing bed, as evidenced by benthic foraminiferal content and well-preserved primary lamination of the sediment that excludes the presence of burrows. The only fossils of macrobenthics observed (two crabs) were probably transported from the platform, as well the delicate macroalgal remains of *Delessertes*. Few burrows filled by shallow-water bioclasts cutting the fish bed obliquely testify later reoxygenation phase, in part connected with the deposition of bioclastic turbidites within the overlying lithozone VI (Fig. 2). The absence of total anoxia within lithozone V (or, most probably, alternating short intervals of anoxia and hypoxia; see above) and a relatively low sedimentation rate may account for the different degrees of articulation and preservation of Solane fishes.

5.3.1. Stagnation versus high productivity at Solane

Two models have been essentially proposed to explain the development of oxygen-depleted bottom waters and the deposition of organic-rich levels: 1) the stagnation model; 2) the productivity model (Meyers, 2006). Model 1 emphasizes a strong stratification of the water-column limiting mixing of surface and bottom eventually leading to anoxic bottom waters and favoring the preservation of organic matter. Model 2 stresses the importance of high primary productivity in surface waters creating elevated levels of organic matter accumulation and marked oxygen consumption. Considerations merely based on ecology of benthic and planktic foraminiferal assemblages are not straightforward in discriminating which model may best explain the origin of the Solane fish bed. Nevertheless, the relatively low productivity conditions in the upper water column inferred by dinoflagellate assemblages seem to favor a scenario of stagnation. Causes of stagnation are difficult to assess, considering that only one section is available for this study, but the data collected allow a reasonable hypothesis. The “taphonomic trap” of Solane likely developed in a relatively small, intraslope restricted basin in which a temporary basin-platform threshold, maybe associated with sea-level rise, stopped the detrital input from the platform and limited the mixing of a consistent portion of the water column up to the sea bottom. In such low hydrodynamic conditions, hypoxic to anoxic facies likely developed, enabling aerobic bacterial decay and favoring the

preservation of fishes and macroflora. A thermal or salinity seasonal stratification may have further decreased bottom water ventilation in the Solane basin, as possibly indicated by TEX₈₆ and dinoflagellate data (see below). Based on previous observations on macrofaunal preservation and benthic foraminiferal content, we infer that the degree of hypoxia at the sea floor varied, indicating that stratification of the water column varied over time.

5.4. Paleoclimatic framework

The Solane sediments deposited during the Ypresian Stage (56–47.8 Myr; Vandenberghe et al., 2012), an interval in which the Earth's climate attained its warmest state of the Cenozoic, often referred to as the Early Eocene Climatic Optimum (EECO; Zachos et al., 2001; Bijl et al., 2009). The exact stratigraphical position of EECO is still not well constrained (Fig. 9) and it lacks a formal definition in terms of absolute age and duration (Slotnik et al., 2012). However, the Solane Lagerstätte was deposited in the upper Ypresian, close to the top of calcareous nannofossil Zone NP13 (Fig. 9), calibrated to Chrons C22r–C21r, which should encompass the EECO. High-resolution correlations to potentially identify previously recorded brief (ca. 10–100 kyr) and transient periods of marked warming associated with prominent negative carbon isotope excursions and deep-sea carbonate dissolution surrounding the EECO (Payros et al., 2012 and references herein; Sexton et al., 2011) is not possible with the current dataset. This would require high-resolution paleomagnetic, isotopic and geochemical investigations. Further comparative studies on Solane and other Eocene Lagerstätten (e.g. Bolca sites) may then offer the stimulating chance to test the highly speculative hypothesis that exceptional fossil preservation may have been promoted during CO₂ greenhouse crises and climatic disruptions (Retallack, 2011).

5.4.1. TEX₈₆ paleothermometry at Solane

Even though the Solane sediments were deposited during a time interval characterized by high global temperatures, the TEX₈₆ values of 0.97 and calibrated temperatures of ~37 °C are remarkably high. Such values were previously only encountered in sediments deposited in (sub-)tropical regions during the Cretaceous (Schouten et al., 2003; Dumitrescu et al., 2006; Forster et al., 2007), and unprecedented in the Cenozoic where only PETM sediments from the New Jersey Shelf come close (Zachos et al., 2006; Sluijs et al., 2007). The maximum value of the proxy is 1 and so values of 0.97 approach the limits of the proxy. Moreover, the modern core-top calibration is limited to ~28 °C, so the reconstructed absolute temperatures are extrapolations of the modern ocean that have yielded credibility with multi-proxy comparison (e.g. Zachos et al., 2006; Weijers et al., 2007; Hollis et al., 2012) and culturing experiments (Schouten et al., 2007a). As an effect, the absolute temperature reconstructions should be taken with extreme caution (Schouten et al., 2013). If the recorded SSTs are realistic, the extremely high temperatures here recorded may explain the low amount of dinoflagellate cysts in the samples (Hallegraeff et al., 1997). Also, as Mertens et al. (2009) showed, changes in cyst characteristics are for a large part influenced by both temperature and salinity in *Lingulodinium machaerophorum*. Therefore, it may be difficult to distinguish between salinity and temperature effects as such.

6. Conclusions

The Chiusole Formation outcropping at Monte Solane, in the western Lessini Mountains of NE Italy, bears an interval of laminated dark limestones with fishes, a macroalgal non-calcareous flora and scarce remains of terrestrial plants (angiosperm leaves and fruit seeds). The rich micropaleontological content (foraminifera, calcareous nannofossils and dinoflagellate cysts) allows ascribing the section to the upper part of the Ypresian (Early Eocene), close to the NP13/NP14 calcareous nannofossil zonal boundary. The Solane site predates the worldwide-

famous lagoonal Bolca *Konservat Lagerstätte* by a few hundred kyr. The revealed ichthyofauna evidences a strong dominance of mesopelagic taxa, mainly represented by stomiiforms. Epipelagic taxa are a minor component of the assemblage and fishes inhabiting shallow-water coastal area and bottom-dwellers are almost absent. If confirmed, the presence of a specimen of *Propercarinidae* at Solane represents the first Eocene record of the family, previously known only from the Oligocene of Paratethys (Bannikov, 1995, 2012). The Solane fish fauna, older than the Lutetian Dabakhana fish fauna of Georgia (Danil'chenko, 1962; Bannikov, 2010), represents the oldest Cenozoic record of an ichthyofauna with strong predominance of meso-bathypelagic taxa. Paleontological (fishes and foraminifera) and sedimentological evidences clearly indicate deposition of the fossiliferous bed at upper bathyal paleodepth, likely between 300 and 600 m, supported by dinoflagellate cyst assemblages indicating open ocean conditions and only few terrestrial pollen and spores. The Solane site is the first Eocene bathyal fossiliferous site so far discovered in the Veneto region of northeastern Italy and probably is one of the few bathyal Eocene *Lagerstätten* of the world (Retallack, 2011). To date, only one other Eocene bathyal *Lagerstätte* (Solteri site; Trentino region) is known from Italy, which unfortunately was never investigated in detail (Venzo et al., 1986).

At Solane larger foraminifera and macroalgae (*Delessertes*), along with rare crabs and few shallow-water fishes are the only macroremains transported from a nearby carbonate platform, source area of the calciturbidites characterizing the Chiusole Formation in the area. A significant distance of the site from emerged lands, probably situated NE of Solane (Luciani, 1989), can be inferred by the scarcity of terrestrial macro and microfloral components within the fish bed. Reduced terrestrial input is also testified by low BIT values. All data indicate deposition of the fossiliferous interval during a phase in which the calciturbiditic input to the basin ceased and a consistent portion of water column became stagnant up to the sea bottom developing hypoxic to possibly anoxic conditions. TEX_{86} records very high temperatures at Solane, approaching the limit of the proxy.

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References

Agnini, C., Muttoni, G., Kent, D.V., Rio, D., 2006. Eocene biostratigraphy and magnetic stratigraphy from Possagno, Italy: the calcareous nannofossil response to climate variability. *Earth Planet. Sci. Lett.* 241, 815–830.

- Alegret, L., Thomas, E., 2001. Upper Cretaceous and lower Paleogene benthic foraminifera from northeastern Mexico. *Micropaleontology* 47, 269–316.
- Alve, E., 1995. Benthic foraminiferal distribution and recolonization of formerly anoxic environments in Drammensfjord, southern Norway. *Mar. Micropaleontol.* 25, 169–186.
- Backman, J., Shackleton, N.J., 1983. Quantitative biocronology of Pliocene and early Pleistocene calcareous nannoplankton from the Atlantic, Indian and Pacific Oceans. *Mar. Micropaleontol.* 8, 141–170.
- Bannikov, A.F., 1995. Morphology and phylogeny of fossil stomatoid fishes (Perciformes). *Geobios-Lyon, Mémoire spécial*, 19, pp. 177–181.
- Bannikov, A.F., 2010. Fossil Vertebrates of Russia and Adjacent Countries. Fossil Acanthopterygian Fishes (Teleostei, Acanthopterygii). GEOS, Moscow (LXI+244 pp. [In Russian]).
- Bannikov, A.F., 2012. The first record of the genus *Isurichthys* (Perciformes, Ariommatidae) in the Lower Oligocene of the Northern Caucasus. *Paleontol. J.* 46, 171–176.
- Bellwood, D.R., 1996. The Eocene fishes of Monte Bolca: the earliest coral reef fish assemblage. *Coral Reefs* 15, 11–19.
- Bernhard, J.M., Sen Gupta, B.K., 1999. Foraminifera of oxygen-depleted environments. In: Sen Gupta, B.K. (Ed.), *Modern Foraminifera*. Kluwer Academic Press, pp. 201–216.
- Bernhard, J.M., Sen Gupta, B.K., Borne, P.F., 1997. Benthic foraminiferal proxy to estimate dysoxic bottom water oxygen concentrations, Santa Barbara Basin, US Pacific continental margin. *J. Foramin. Res.* 27, 301–310.
- Bijl, P.K., Schouten, S., Sluijs, A., Reichert, G.-J., Zachos, J.C., Brinkhuis, H., 2009. Early Paleogene temperature evolution of the southwest Pacific Ocean. *Nature* 461, 776–779.
- Bijl, P.K., Sluijs, A., Brinkhuis, H., 2013. A magneto- and chemostratigraphically calibrated dinoflagellate cyst zonation of the early Paleogene South Pacific Ocean. *Earth-Sci. Rev.* 124, 1–31.
- Blot, J., 1980. La faune ichthyologique des gisements du Monte Bolca (Province de Vérone, Italie). Catalogue systématique présentant l'état actuel des recherches concernant cette faune. *Bulletin du Muséum national d'Histoire naturelle (Paris) sér 4, section C*, 2, pp. 339–396.
- Bosellini, A., 1989. Dynamics of Tethyan carbonate platforms. In: Crevello, P.D., et al. (Eds.), *Controls on carbonate platform and basin development*. SEPM Spec. P., 44, pp. 3–13.
- Bujak, J., Mudge, D., 1994. A high-resolution North Sea Eocene dinocyst zonation. *J. Geol. Soc. Lond.* 151, 449–462.
- Carraro, F., Malaroda, R., Piccoli, G., Sturani, C., Venzo, S., 1969. Note illustrative della Carta Geologica D'Italia, Scala 1:100.000. Foglio 48, Peschiera del Garda (97 pp.).
- Channell, J.E.T., D'Argenio, B., Horvath, F., 1979. Adria, the African promontory in Mesozoic Mediterranean paleoceanography. *Earth-Sci. Rev.* 15, 213–292.
- Danil'chenko, P.G., 1960. Kostistye ryby maykopskikh otlozheniy Kavkaza [see Danil'chenko, 1967, below, for translation]. *Trudy Paleontol. Inst. Akad. Nauk SSSR* 78, 1–208 [In Russian].
- Danil'chenko, P.G., 1962. Fishes of the Dabakhana Formation of Georgia. *Paleontol. J.* 1, 111–126 [In Russian].
- Danil'chenko, P.G., 1967. Bony fishes of the Maikop deposits of the Caucasus. Translated from Russian. U.S. Department of Interior and the National Science Foundation, Israel Program for Scientific Translations, Jerusalem.
- De Zanche, V., Sorbini, L., Spagna, V., 1977. Geologia del territorio del Comune di Verona. *Memorie del Museo Civico di Storia Naturale di Verona*, 1, pp. 1–52.
- Doglionni, C., Bosellini, A., 1987. Eoalpine and mesoalpine tectonics in the Southern Alps. *Geol. Rundsch.* 77, 734–754.
- Drobne, K., 1977. Alvéolines paléogènes de la Slovénie et de l'Istrie. *Schweizerische Paläontologische Abhandlungen*, 99, pp. 1–175.
- Dumitrescu, M., Brassell, S.C., Schouten, S., Hopmans, E.C., Sinninghe Damsté, J.S., 2006. Instability in tropical Pacific sea-surface temperatures during the early Aptian. *Geology* 34, 833–836.
- Ellegaard, M., Lewis, J., Harding, I.C., 2002. Cyst–Theca relationship, life cycle, and effects of temperature and salinity on the cyst morphology of *Gonyaulax baltica* sp. nov. (Dinophyceae) from the Baltic Sea area. *J. Phycol.* 38, 775–789.
- Fensome, R.A., Williams, G.L., 2004. The Lentini and Williams Index of fossil dinoflagellates 2004 Edition. American Association of Stratigraphic Palynologists, Contributions Series, 42, pp. 1–909.
- Forster, A., Schouten, S., Baas, M., Sinninghe Damsté, J.S., 2007. Mid-Cretaceous (Albian–Santonian) sea surface temperature record of the tropical Atlantic Ocean. *Geology* 35, 919–922.
- Garavello, A.M., Ungaro, S., 1996. Biostratigrafia del Paleocene ed Eocene inferiore dei M. Lessini: sezione stratigrafica di Gazzo (Verona). *Ann. Univ. Ferrara Sez. Sci. Terra* 7, 23–34.
- Goody, A.J., 2003. Benthic foraminifera (Protista) as tools in deepwater palaeoceanography: environmental influences on faunal characteristics. *Adv. Biol.* 46, 1–90.
- Hallegraeff, G.M., Valentine, J.P., Marshall, J.A., Bolch, C.J., 1997. Temperature tolerances of toxic dinoflagellate cysts: application to the treatment of ships' ballast water. *Aquat. Ecol.* 31, 47–52.
- Hayward, B.W., Kawagata, S., Sabaa, A., Grenfell, H., Van Kerckhoven, L., Johnson, K., Thomas, E., 2012. The last global extinction (Mid-Pleistocene) of deep-sea benthic foraminifera (Chrysalogoniidae, Ellipsoidinidae, Glandulonodosariidae, Plectofrondiculariidae, Pleurostomellidae, Stilostomellidae), their Late Cretaceous–Cenozoic history and taxonomy. *Cushman Foundation for Foraminiferal Research Special Publication*, 43 (408 pp.).
- Heer, O., 1859. Die Tertiäre Flora der Schweiz. *Flora Tertiaria Helvetiae* 3. Verl. Wurster & Co., Winterthur.
- Hollis, C.J., Taylor, K.W.R., Handley, L., Pancost, R.D., Huber, M., Creech, J.B., Hines, B., Crouch, E.M., Morgans, H.E.G., Crampton, J.S., Gibbs, S., Schouten, S., Pearson, P.N., Zachos, J.C., 2012. Early Paleogene temperature history of the Southwest Pacific Ocean: reconciling proxies and models. *Earth Planet. Sci. Lett.* 349–350, 53–66.

- Hopmans, E.C., Weijers, J.W.H., Schefuss, E., Herfort, L., Sinninghe Damsté, J.S., Schouten, S., 2004. A novel proxy for terrestrial organic matter in sediments based on branched and isoprenoid tetraether lipids. *Earth Planet. Sci. Lett.* 224, 107–116.
- Hottinger, L., 1960. Recherches sur les Alvéolines du Paléocène et de l'Éocène. Schweizerische Paläontologische Abhandlungen (75–76 Texte (I), 1–243; Atlas (II), 18 Pls).
- Hulley, P.A., 1986. Family No. 86: Myctophidae. In: Smith, M.M., Heemstra, P.C. (Eds.), *Smiths' Sea Fishes*. Smith Institute of Ichthyology, Grahamstown, pp. 282–321.
- Jorissen, F.J., Fontanier, C., Thomas, E., 2007. Paleoenvironmental proxies based on deep-sea benthic foraminiferal assemblage characteristics. In: Hillaire-Marcel, C., de Vernal, A. (Eds.), *Developments in Marine Geology. Proxies in Late Cenozoic Paleoenvironmentology*, vol. 1. Elsevier, Amsterdam, pp. 264–325.
- Kim, J.H., van der Meer, J., Schouten, S., Helmke, P., Willmott, V., Sangiorgi, F., Koc, N., Hopmans, E.C., Sinninghe Damsté, J.S., 2010. New indices and calibrations derived from the distribution of crenarchaeal isoprenoid tetraether lipids: Implications for past sea surface temperature reconstructions. *Geochim. Cosmochim. Acta* 74, 4639–4654.
- Kleiber, G.W., 1991. Nummuliten der paläogenen Tethys in Axialschnitten. *Tübinger Mikropaläontol. Mitt.* 9, 1–161.
- Krings, M., Mayr, H., 2004. *Bassonia hakeiensis* (BASSON) nov. comb., a rare non-calcareous marine alga from the Cenomanian (Upper Cretaceous) of Lebanon. *Zitteliana A* 44, 105–111.
- Landini, W., Sorbini, L., 1996. Ecological and trophic relationships of Eocene Monte Bolca (Pesciara) fish fauna. In: Cherchi, A. (Ed.), *Autecology of Selected Fossil Organisms: Achievements and Problems*. Bollettino della Società Paleontologica Italiana, Volume Speciale 3. Mucchi, Modena, pp. 105–112.
- Less, G., 1987. Paleontology and Stratigraphy of the European Orthophragminae. *Geologica Hungarica Series Palaeontologica*, 51. Geological Institute of Hungary, Budapest (1–373 pp.).
- Lirer, F., 2000. A new technique for retrieving calcareous microfossils from lithified lime deposits. *Micropaleontology* 46, 365–369.
- Luciani, V., 1989. Stratigrafia sequenziale del Terziario nella catena del Monte Baldo (province di Verona e Trento). *Mem. Sci. Geol.* 41, 263–351 Padova.
- Luciani, V., Giusberti, L., Agnini, C., Backman, J., Fornaciari, E., Rio, D., 2007. The Paleocene–Eocene Thermal Maximum as recorded by Tethyan planktonic foraminifera in the Forada section (northern Italy). *Mar. Micropaleontol.* 64, 189–214.
- Luciani, V., Giusberti, L., Agnini, C., Fornaciari, E., Rio, D., Spofforth, D.J.A., Palike, H., 2010. Ecological and evolutionary response of Tethyan planktonic foraminifera to the middle Eocene climatic optimum (MECO) from the Alano section (NE Italy). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 292, 82–95.
- Luciani, V., Giusberti, L., Rio, D., 2011. Remarks on the Early–Middle Eocene biomagnetostratigraphy based on planktic foraminiferal evidences from the Tethyan successions of northeastern Italy. In: Egger, H. (Ed.), *Climate and Biota of the Early Paleogene*, Conference Program and Abstracts, 5–8 June 2011, Salzburg, Austria, 85. *Berichte der Geologischen Bundesanstalt*, Wien, p. 110.
- Malaroda, R., 1962. Gli hard grounds al limite fra Cretaceo ed Eocene nei Lessini occidentali. *Mem. Soc. Geol. Ital.* 3, 111–135.
- Martini, E., 1971. Standard Tertiary and Quaternary calcareous nannoplankton zonation. In: Farinacci, A. (Ed.), *Proceedings of the 2nd Planktonic Conference*, vol. 2. Edizioni Tecnoscienza, Roma, pp. 739–785.
- Massalongo, A., 1854. *Monografia delle Dombeyacee fossili fino ad ora conosciute*. Tipografia Antonelli, 1854, Verona.
- Massalongo, A., 1859. *Syllabus plantarum fossilium*. Tipografia A. Merlo, Verona.
- Massari, F., Medizza, F., 1973. Stratigrafia e paleogeografia del Campaniano-Maastrichtiano nelle Alpi Meridionali (con particolare riguardo agli hard grounds della Scaglia rossa veneta). *Mem. Ist. Geol. Mineral. Univ. Padova* 28, 1–62.
- Mattioli, P.A., 1555. I discorsi di M. Pietro Andrea Mattioli medico sanese, ne i sei libri della materia medicinale di Pedacio Dioscoride Anazarbeo. Con i veri ritratti delle piante & de gli animali, nuovamente aggiuntivi dal medesimo. Vinegia nella bottega d'Erasmo, appresso Vincenzo Valgrisi, Venezia.
- Medizza, F., 1975. Il nannoplankton calcareo della Pesciara di Bolca (Monti Lessini). *Studi e Ricerche sui Giacimenti Terziari di Bolca 2*, Museo Civico di Storia Naturale di Verona, pp. 433–444.
- Mertens, K.N., Ribeiro, S., Bouimetarhan, I., Caner, H., Combourieu Nebout, N., Dale, B., De Vernal, A., Ellegaard, M., Filipova, M., Godhe, A., Goubert, E., Grosfeld, K., Holzwarth, U., Kotthoff, U., Leroy, S.A.G., Londeix, L., Marret, F., Matsuoka, K., Mudie, P.J., Naudts, L., Pena-Manjarrez, J.L., Persson, A., Popescu, S.-M., Pospelova, V., Sangiorgi, F., Van der Mee, M., Vink, A., Zonnenveld, K., Vercauteren, D., Vlassenbroeck, J., Louwye, S., 2009. Process length variation in cysts of a dinoflagellate, *Lingulodinium machaerophorum*, in surface sediments: investigating its potential as salinity proxy. *Mar. Micropaleontol.* 70, 54–69.
- Meschinelli, A., Squinabol, X., 1892. *Flora Tertiaria Italica*. Tipi Seminari, Padova.
- Meyers, P.A., 2006. Paleoenvironmental and paleoclimatic similarities between Mediterranean sapropels and Cretaceous black shales. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 235, 305–320.
- Nelson, J.S., 2006. *Fishes of the World*, 4th ed. Wiley, Hoboken, NJ.
- Okada, H., Bukry, D., 1980. Supplementary modification and introduction of code numbers to the low-latitude coccolith biostratigraphic zonation (Bukry, 1973; 1975). *Mar. Micropaleontol.* 5, 321–325.
- Papazzoni, C.A., Trevisani, E., 2005. The Ypresian succession of the Monte Postale and its relationship with the Pesciara di Bolca (Verona/Vicenza Provinces, Northern Italy). *Epitome 1*, Geitalia 2005, 5th Forum Italiano di Scienze della Terra, Spoleto 21–23 settembre 2005, pp. 274–275.
- Papazzoni, C.A., Trevisani, E., 2006. Facies analysis, palaeoenvironmental reconstruction, and biostratigraphy of the “Pesciara di Bolca” (Verona, northern Italy): an early Eocene *Fossil-Lagerstätte*. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 242, 21–35.
- Payros, A., Ortiz, S., Alegret, L., Orue-Extebarria, X., Apellaniz, E., Molina, E., 2012. An early Lutetian carbon-cycle perturbation: insights from the Gorronatxe section (western Pyrenees, Bay of Biscay). *Paleoenvironmentology* 27, PA2213. <http://dx.doi.org/10.1029/2012PA002300>.
- Prokofiev, A.M., 2005. Systematics and phylogeny of the stomiiform fishes (Neoteleostei: Stomiiformes) from the Paleogene–Neogene of Russia and adjacent regions. *J. Ichthyol.* 45 (Suppl. 1), 89–162.
- Rasser, M.W., Harzhauser, M., et al., 2008. Paleogene and Neogene of Central Europe. In: McCann, T. (Ed.), *The Geology of Central Europe. Mesozoic and Cenozoic*. Geological Society, London, Volume 2, pp. 1031–1140.
- Retallack, G.J., 2011. Exceptional fossil preservation during CO₂ greenhouse crises? *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 307, 59–74.
- Rio, D., Raffi, I., Villa, G., 1990. Pliocene–Pleistocene calcareous nannofossil distribution patterns in the western Mediterranean. In: Kastens, K.A., Mascle, J., et al. (Eds.), *Proceedings of the ODP, Scientific Results*, v. 107. Ocean Drilling Program, College Station, TX, pp. 513–533.
- Sarti, M., 1980. Frane sottomarine e debris flow in una successione carbonatica torbidaica eocenica (Val d'Avesa, Verona). *Ann. Univ. Ferrara Sez. IX Sci. Geol. Paleontol.* 7, 65–89.
- Schaefer, S., Johnson, R.K., Badcock, J., 1986. Family No. 74: Gonostomatidae. In: Smith, M.M., Heemstra, P.C. (Eds.), *Smiths' Sea Fishes*. Smith Institute of Ichthyology, Grahamstown, pp. 247–253.
- Schaub, H., 1981. Nummulites et Assilines de la Téthys Paléogène. *Taxonomie, phylogénèse et biostratigraphie*. Schweizerische Paläontologische Abhandlungen, 104 (1–236(text); 105–106, (Plates)).
- Schneider, L.J., Bralower, T.J., Kump, L.R., 2011. Response of nannoplankton to early Eocene ocean deoxygenation. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 310, 152–162.
- Schouten, S., Hopmans, E.C., Schefuss, E., Sinninghe Damsté, J.S., 2002. Distributional variations in marine crenarchaeal membrane lipids: a new tool for reconstructing ancient sea water temperatures? *Earth Planet. Sci. Lett.* 204, 265–274.
- Schouten, S., Hopmans, E.C., Kuypers, M.M.M., Van Breugel, Y., Forster, A., Sinninghe Damsté, J.S., 2003. Extremely high sea water temperatures at low latitudes during the middle Cretaceous as revealed by archaeal membrane lipids. *Geology* 31, 1069–1072.
- Schouten, S., Forster, A., Panoto, F.E., Sinninghe Damsté, J.S., 2007a. Towards calibration of the TEX86 palaeothermometer for tropical sea surface temperatures in ancient greenhouse worlds. *Org. Geochem.* 38, 1537–1546.
- Schouten, S., Hugué, C., Hopmans, E.C., Kienhuis, M.V.H., Sinninghe Damsté, J.S., 2007b. Analytical methodology for TEX86 paleothermometry by high-performance liquid chromatography/atmospheric pressure chemical ionization-mass spectrometry. *Anal. Chem.* 79, 2940–2944.
- Schouten, S., Hopmans, E.C., Sinninghe Damsté, J.S., 2013. The organic geochemistry of glycerol dialkyl glycerol tetraether lipids: a review. *Org. Geochem.* 54, 19–61.
- Schwark, L., Ferretti, A., Papazzoni, C.A., Trevisani, E., 2009. Organic geochemistry and paleoenvironment of the Early Eocene “Pesciara di Bolca” Konservat-Lagerstätte, Italy. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 273, 272–285.
- Scotto di Carlo, B., 1966. Le Alveoline del Gargano nord-orientale. *Palaeontogr. Ital.* 61, 65–73.
- Serra-Kiel, J., Hottinger, L., Caus, E., Drobne, K., Ferrández, C., Jauhri, A.K., Less, G., Pavlovic, R., Pignatti, J., Samsó, J.M., Schaub, H., Sirel, E., Strougo, A., Tambareau, Y., Tosquella, J., Zakrevskaya, E., 1998. Larger foraminiferal biostratigraphy of the Tethyan Paleocene and Eocene. *Bull. Soc. Geol. Fr.* 169, 281–299.
- Sexton, P.F., Norris, R.D., Wilson, P.A., Pälike, H., Westerhold, T., Röhl, U., Bolton, C.T., Gibbs, S., 2011. Eocene global warming events driven by ventilation of oceanic dissolved organic carbon. *Nature* 471, 349–353. <http://dx.doi.org/10.1038/nature09826>.
- Shamrock, J.L., Watkins, D.K., 2012. Eocene calcareous nannofossil biostratigraphy and community structure from Exmouth Plateau, Eastern Indian Ocean (ODP Site 762). *Stratigraphy* 9, 1–54.
- Slotnik, B.S., Dickens, G.R., Nicolo, M.J., Hollis, C.J., Crampton, J.S., Zachos, J.C., Sluijs, A., 2012. Large-amplitude variations in carbon cycling and terrestrial weathering during the latest Paleocene and earliest Eocene: The Record at Mead Stream, New Zealand. *J. Geol.* 120, 487–505.
- Sluijs, A., Pross, J., Brinkhuis, H., 2005. From greenhouse to icehouse; organic-walled dinoflagellate cysts as paleoenvironmental indicators in the Paleogene. *Earth-Sci. Rev.* 68, 281–315.
- Sluijs, A., Brinkhuis, H., Schouten, S., Bohaty, S.M., John, C.M., Zachos, J.C., Reichert, G.-J., Sinninghe Damsté, J.S., Crouch, E.M., Dickens, G.R., 2007. Environmental precursors to light carbon input at the Paleocene/Eocene boundary. *Nature* 450, 1218–1221.
- Sorbini, L., 1972. I fossili di Bolca. *Edizioni Corev*, Verona.
- Tang, C., 2002. Monte Bolca: an Eocene fishbowl. In: Bottjer, D.J., et al. (Eds.), *Exceptional Fossil Preservation: A Unique View on the Evolution of Marine Life*. Columbia University Press, New York, pp. 365–377.
- Thierstein, H.R., Geitzenauer, K.R., Molino, B., Shackleton, N.J., 1977. Global synchronicity of late Quaternary coccolith datum levels: validation by oxygen isotopes. *Geology* 5, 400–404.
- Trevisani, E., Papazzoni, C.A., Ragazzi, E., Roghi, G., 2005. Early Eocene amber from the “Pesciara di Bolca” (Lessini Mountains, northern Italy). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 223, 260–274.
- Ungaro, S., 2001. Le biofacies paleoceniche ed eoceniche dei Monti Lessini (Veneto, Italia). *Ann. Univ. Ferrara Sez. Sci. Terra* 9, 1–40.
- Van der Zwaan, G.J., Duijnste, I.A.P., Den Dulk, M., Ernst, S.R., Kouwenhoven, N.T., 1999. Benthic foraminifers: proxies or problems? A review of paleoecological concepts. *Earth-Sci. Rev.* 46, 213–236.
- Van Morkhoven, F.P.C.M., Berggren, W.A., Edwards, A.S., 1986. Cenozoic cosmopolitan deep-water benthic foraminifera. *Bull. Cent. Rech. Explor. Prod. Elf-Aquitaine Mem.* 11 (423 pp.).

- Vandenbergh, N., Hilgen, F.J., Speijer, R.P., 2012. Chapter 28. The Paleogene Period. In: Gradstein, F.M., Ogg, J.G., Smith, A.G., Ogg, G.M. (Eds.), *The Geologic Time Scale 2012*. Elsevier, pp. 855–921. <http://dx.doi.org/10.1016/B978-0-444-59425-9.00028-7>.
- Vasilis, T., Kvacsek, Z., 2005. The extinct genus *Chaneya* Wang et Manchester in the Tertiary of Europe—a revision of *Porana*-like fruit remains from Öhningen and Bohemia. *Rev. Palaeobot. Palynol.* 134, 85–103.
- Venzo, G.A., Princivale, F., Pugliese, N., 1986. L'Eocene inferiore con pesci, crostacei e filliti in località Solteri di Trento. *Studi Trentini Sci. Nat. Acta Geol.* 62, 71–89.
- von Sternberg, K., 1833. Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt, V. I., fasc. 5–6. Johann Spurny, Prag.
- Wade, B.S., Pearson, P.N., Berggren, W.A., Pälike, H., 2011. Review and revision of Cenozoic tropical planktonic foraminiferal biostratigraphy and calibration to the geomagnetic polarity and astronomical time scale. *Earth-Sci. Rev.* 104, 111–142.
- Wang, Y., Manchester, S.R., 2000. *Chaneya*, a new genus of winged fruit from the Tertiary of North America and Eastern Asia. *Int. J. Plant Sci.* 161, 167–178.
- Weijers, J.W.H., Schouten, S., Spaargaren, O.C., Sinninghe Damsté, J.S., 2006. Occurrence and distribution of tetraether membrane lipids in soils: implications for the use of the TEX86 proxy and the BIT index. *Org. Geochem.* 37, 1680–1693.
- Weijers, J.W.H., Schouten, S., Sluijs, A., Brinkhuis, H., Sinninghe Damsté, J.S., 2007. Warm arctic continents during the Palaeocene–Eocene thermal maximum. *Earth Planet. Sci. Lett.* 261, 230–238.
- Williams, G.L., Brinkhuis, H., Pearce, M.A., Fensome, R.A., Weegink, J.W., 2004. Southern Ocean and global dinoflagellate cyst events compared: index events for the Late Cretaceous–Neogene. In: Exon, N.F., Kennett, J.P., Malone, M.J. (Eds.), *Proceedings of the Ocean Drilling Program, Scientific Results*, 189, pp. 1–98 (Online).
- Winterer, E.L., Bosellini, A., 1981. Subsidence and sedimentation on Jurassic passive continental margin, Southern Alps, Italy. *AAPG Bull.* 65, 394–421.
- Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292, 686–693.
- Zachos, J.C., Schouten, S., Bohaty, S., Sluijs, A., Brinkhuis, H., Gibbs, S.J., Bralower, T.J., Quattlebaum, T., 2006. Extreme warming of mid-latitude coastal ocean during the Paleocene–Eocene Thermal Maximum: inferences from TEX86 and isotope data. *Geology* 34, 737–740.
- Zhang, Y.G., Zhang, C.L., Liu, X.-L., Li, L., Hinrichs, K.-U., Noakes, J.E., 2011. Methane index: a tetraether archaeal lipid biomarker indicator for detecting the instability of marine gas hydrates. *Earth Planet. Sci. Lett.* 307, 525–534.
- Zonneveld, K.A.F., Marret, F., Versteegh, G.J.M., Bogus, K., Bonnet, S., Boumetarhan, I., Crouch, E., de Vernal, A., Elshani, R., Edwards, L., Esper, O., Forke, S., Grosfeld, K., Henry, M., Holzwarth, U., Kieft, J.F., Kim, S.-Y., Ladouceur, S., Ledu, D., Chen, L., Limoges, A., Londeix, L., Mildenhall, D.C., Mudie, P., Neil, H.L., Pospelova, V., Qi, Y., Radi, T., Richerol, T., Rochon, A., Sangiorgi, F., Solignac, S., Turon, J.-L., Verleye, T., Wang, Y., Wang, Z., Young, M., 2013. Atlas of modern dinoflagellate cyst distribution based on 2405 datapoints. *Rev. Palaeobot. Palynol.* 191, 1–197.
- Zorzini, R., Bannikov, A.F., Fornaciari, E., Giusberti, L., Papazzoni, C.A., Roghi, G., 2011. Il giacimento a pesci e piante fossili dell'Eocene inferiore di Monte Solane (Verona). *Boll. Museo Civ. Stor. Nat. Verona* 35, 57–64.