

Bolca fossils in the marine ecosystem of Val d'Alpone (Pesciara, Mt. Postale, San Giovanni Ilarione and Roncà)

Due to the excellent preservation and the evident marine origin, the fossils fauna collected from the Pesciara and Mt. Postale, from the hills of Roncà (Valle della Chiesa), as well as from San Giovanni Ilarione (Ciupio, Croce Grande, Bosco del Prete and Pozzani) have attracted the interest of natural philosophers since from the eighteenth century worldwide. The joint interest in the Bolca fishes and the close “Monti Veronesi” shellfish concerned the European debate on the Theory of the Earth, as witnessed by the writings by Antonio Vallisneri (1725) and Anton Lazzaro Moro (1740). The fossil fishes of Bolca certainly represent the most famous and most studied component of the Val d'Alpone fossil assemblage. Conversely, the studies focused on shellfishes were fringed by their greater abundance and ubiquity and in the possibility provided to compare fossil species with those living in the adjacent Adriatic Sea. This comparison was the subject of research by the pioneering works by Vitaliano Donati (1750) and Alberto Fortis (1774), translated into French, English and German. The interest intensified with the research of the first geologists Alberto Fortis (1778), Georges Cuvier (1796), Barthélemy Faujas de Saint-Fond (1798), Jean-Baptiste Lamarck, (1802-1806) and Antonio Catullo (1826) to finally take modern form during the nineteenth century with taxonomic and stratigraphic studies by Alexandre Brongniart (1823), Ferdinand Bayan (1870b), Karl Mayer (1870), Hébert E. and Munier-Chalmas (1877) and Antonio De Gregorio (1880, 1894) and in the twentieth century with Giotto Dainelli (1904-1905, 1915), Paolo Vinassa de Regny (1895-1897), Paul Oppenheim (1896) and Roberto Malaroda (1954). Taxonomic modernizations are recorded in recent years (Quaggiotto and Mellini 2008; Dominici *et al.*, 2012; Dominici 2014).

The numerous fossil exposures of the Val d'Alpone, iconically represented by the localities of Pesciara, Monte Postale, San Giovanni Ilarione and Roncà, represent a continuum in a relatively small area stratigraphic covering an interval comprised between the lower (Pesciara and Monte Postale) and the middle (San Giovanni Ilarione and Roncà; see e.g. Bayan, 1870a) Eocene and a variety of depositional environments, which include intertidal (Roncà), shallow subtidal (Monte Postale, associated environment to the “Bolca fish” deposit) and open sea environments (San Giovanni Ilarione).

Val d'Alpone in its entirety thus provides an ecological image of the entire bathymetric gradient, in an interval in which the Earth has experienced exceptionally high temperatures (Zachos *et al.*, 2001), marine biodiversity reached its climax (Lozouet, 2014) after a long period of post-mass extinction recovery (Kiessling *et al.*, 2008), and the groups of organisms that dominate modern seas have established themselves. Among them, the phylum Mollusca is one of the main contributors to modern marine biodiversity (Appeltans *et al.*, 2012; Costello and Chaudhary, 2017), which covers a wide range of niches ecological (Ponder and Lindberg, 2008) and is characterized by an excellent fossil record, providing a useful tool for comparisons in space and time, on a global scale.

In accordance with the latitudinal trends known for current seas (Roy *et al.*, 2004) and with the hypothesis widely shared that the center of biodiversity during the Eocene was located in the Tethys (Renema *et al.*, 2008; Friedman and Carnevale, 2018), the mollusks of Val d'Alpone indicate a greater diversity compared to that of the celebrated faunas of the Paris Basin (Sanders *et al.*, 2015; Merle *et al.*, 2016). The latter, known for the excellent degree of preservation and overall diversity (Merle, 2008; Dominici and Zuschin, 2016), constitute the main reference for reconstructing the variations of biodiversity of the last 65 million years (Lozouet, 2014). No other locality in the world contains the variety of forms known for the Val d'Alpone. This uniqueness is highlighted by the comparison with

both Atlantic and Tethys localities including the lower Eocene: Gan (France: Merle 1990; Tomašových *et al.*, 2014), Tremp-Graus (Spain: Dominici and Kowalke, 2007; 2014), and Lakhra (Pakistan: Merle *et al.*, 2014), and the Middle Eocene Grignon (Senders *et al.* 2015), Bribir (Croatia: Dainelli 1904-1905), Noax (Friuli: Dainelli, 1915), and Pamplona (Spain: Astibia *et al.*, 2018).

In general, crustaceans have a low probability of being preserved in a fossil state and their discovery is unusual, so their abundant presence in Val d'Alpone, known for centuries, is of particular importance. The finds are of an exceptional level both in Pesciara and in San Giovanni Ilarione. In the Bolca area (Beschinn *et al.*, 2016; 2021), associations of small brachyurs and anomurs, associated with corals, rich in taxa, many of which are new, were found inside small bioconstructions, coeval with the fossiliferous layers of Pesciara. for science that they show an evident resemblance to crustaceans that live today in the tropical seas of the Indo-Pacific area and above all affinity with faunas of the upper Eocene of Budapest (Müller & Collins, 1991). As regards the decapod fauna of the San Giovanni Ilarione (Ciupio) component of the Middle Eocene, historically studied by Bittner (1875, 1883, 1895) on specimens found mainly in the collections of the Natural History Museum of Vienna (Hyžný& Zorn, 2016, 2020), it is noted that its wealth is comparable only with that of Budapest (Lőrenthey&Beurlen, 1929). Evident affinities of the crustaceans of San Giovanni Ilarione are found for Europe with those of the surroundings of Palermo (Di Salvo, 1933), Huesca (Spain) (Zamora *et al.*, 2022), Hampshire Basin (UK) (Bell, 1858, Quayle & Collins, 1981), Lillebælt Clay Formation (Denmark) (Collins & Jakobsen, 2003) and for the Americas with those of North and South Carolina (USA) (Blow & Manning, 1996) and the Bateque Formation (Mexico) (Schweitzer *et al.*, 2006).

In the Roncà area (Valle della Chiesa), most of the historical sites are accessible. Only one is currently cultivated with Kiwi fruit. With regards to the sites of San Giovanni Ilarione, only that of Cupio is easily accessible, while those of Croce Grande, Bosco del Prete and Pozzani are buried under thick backfill debris above which valuable crops have been planted (vineyard) which renders their precise identification and delimitation result difficult. Paleontological excavations have been active since 2010 by the Ministry in Valle della Chiesa and on Monte Duello.

Comparison with other sites of global importance (sites written in the WHL UNESCO, Geoparks, Sites in the Tentative Lists, etc.)

Category (1) evaluates fossil records of Eocene marine faunas using four criteria:

Site	1. Diversity	2. Diversitytaxonom of upper level	3. Abundance of specimens	4. SignificanceEvolutionbroad than the fossils
VAL D'ALPONE Pesciara and Mt. Postale (Italy)	About 260 taxa (potentially notless than 280)	Over 110 families	Deposits extremely productive. Beyond 100,000 specimens extracted to date	First evidence in the paleontological record of ichthyofauna associated with modern type coral reef
Messel Pit Fossil Site (Germany)	8 taxa	5 o 6 families	Elevated	Evolutionary significance relatively marginal. Location that testifies to the structure of ancient communities' lakes of the European continent
Mo-Clay (FurFormation, Denmark)	About 80 taxa	Undefined. Fossiliferous association studied but only marginally	Not elevated	Not definable due to the very limited number of studies dedicated. Over 70% of taxa has

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				not been described yet
Green River Formation (USA)	31 taxa	20 families	Elevated, especially in relation to the enormous extension of sediments potentially fossiliferous of the Green River Formation	Fish association known more for the Cenozoic of North America
VAL D'ALPONE				
Pesciara and Mt. Postale	32 taxa	17 families;	Not elevated	Important contribution to the study of fossil crustaceans from various environments (lagoon, coral reef, inner shelf) with important insights into the evolution of the group
San Giovanni Ilarione (Italy)	19 taxa	9 families	Elevated	
Budapest (Hungary)	More than 60 genera (112 taxa)	31 families	Elevated	Fauna of historical importance of different environments that would need systematic revision and photographic testimony
Huesca-Aragona (Espana)	25 genera (27 taxa)	14 families	Not elevated	At the moment sporadic findings do not allow a global vision of the fauna or further evolutionary investigation
Palermo (Italy)	15 taxa	8 families	Scattered	Sporadic findings that highlight similarities with the faunas of western Veneto and Budapest
Hampshire Basin (United Kingdom)	39 taxa	18 families	Elevated	Faunas known since the last century which present systematic characteristics close to those of southern Europe
Lillebælt Clay Formation (Denmark)	9 taxa	8 families	Elevated	Fauna known from the last century which shows affinities both with those of England and those of southern Europe
Bateque Formation (México)	29 taxa	14 families	Unknown	The fauna has affinities with Pacific but also Tethyan faunas
Nord and South Carolina (USA)	25 taxa	13 families	Scattered	The fauna has greater systematic affinities with European ones than with American ones
VAL D'ALPONE				
Mt. Postale	65 spp. (Mt. Postale: Ypresian)	36 families (Mt. Postale)	1200 (Mt. Postale: Florence, Padua, Verona, Pisa, Paris)	Eocene roots of modern tropical marine benthos
San Giovanni Ilarione	519 spp. (San Giovanni Ilarione: Lutetian)	80 families (San Giovanni Ilarione)	2000 (San Giovanni Ilarione: Florence, Pisa, Paris)	
Roncà (Italy)	176 spp. (Roncà: Bartonian)	58 families (Roncà)	2500 (Roncà: Padua, Florence, Paris)	
Paris Basin (France)	788 spp. (Grignon: midLutetian) 254 spp. (Grignon)[bulk samples] 718 spp. (Baron: Bartonian)	87 (Grignon: Vienna)[bulk samples]	Consistence of Eocene Paris collections (order of magnitude): 105 specimens 7079 (Grignon: Vienna)[bulk samples]	Eocene roots of modern temperate marine benthos
Pyrénées-Atlantiques (France)	184 spp. (Gan: Ypresian)[bulk samples]	82 families (Gan: Ypresian)[bulk samples]	8117 (Paris)[bulk samples]	Eocene roots of modern temperate marine benthos
Friuli (Italy)	169 spp (Noax, Rosazzo)	53 families	1200 (Florence)	Eocene roots of modern tropical marine benthos

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Wadi Al-Hitan (UNESCO Egypt)	Unknown (Priabonian, see Peters 2009, doi: 10.2110/palo.2008.p08-080r)	Unknown (see Peters 2009, doi: 10.2110/palo.2008.p08-080r)	Unknown (see Peters 2009, doi: 10.2110/palo.2008.p08-080r)	Eocene roots of modern tropical marine benthos
Sobrarbe (UNESCO Spain)	Unknown (Lutetian, see Canudo et al. 2021)	Unknown (see Canudo et al. 2021)	Unknown (see Canudo et al. 2021)	Eocene roots of modern temperate marine benthos

Category (2) evaluates the nature and quality of the fossil archive at each site using five criteria:

		Site	5. Quality of conservation	6 Stratigraphic thickness of the layers containing fossils exposed	7. Geochronological Constraints	8. Age of fossils	9. Range of environments in which fossils are found
FISHES	VAL D'ALPONE	Pesciara and Mt. Postale (Italy)	Exceptional. In addition to the skeletal parts, there are evident traces of the viscera and of the musculature, in addition to embryos and eggs in situ. Finally, there are numerous examples of parasitism and trophic interactions. UNIQUE CONTEXT IN THE PALEONTOLOGICAL MARINE CENOZOIC RECORD		Definite age across the micropaleontological content of carbonate sediments of the succession	Between 50.5 and 48.5 million years	Environment lagoon behind the cliff. Coastal environment peri-reefal with grasslands, seagrass and algae
		Messel Pit Fossil Site (Germany)	Great			Around 48 million years	Maar crater lake
		Mo-Clay (Fur Formation, Denmark)	Very good preservation only in carbonate nodules. Most of the fish fossils come from diatomites where quality of conservation is not certainly extraordinary. In numerous cases it deals exclusively with skeleton imprints	Some hundreds of meters	Very well bound thanks to numerous Cineritic levels that characterize the sedimentary succession	Between 55 and 54 million years	Pelagic environment placed at several kilometers from emerged areas in the ancient North Sea
		Green River Formation (USA)	Exceptional, especially for the skeletal parts			About 52 million years	Various biotopes of a vast lake context
CRUSTACEANS	VAL D'ALPONE	Pesciara and Mt. Postale	The quality of conservation in general is good. The crustaceans of Pesciara and Mt. Postale are preserved on slab; those coming from the bioherme (Bolca area) are of modest size represented by carapaces and remains of chelipeds			Early Eocene	Lagoon environment, patch reef
		San Giovanni Ilarione (Italy)	The crustaceans from San Giovanni Ilarione are			Middle Eocene	Shelf environment

	primarily represented by carapaces				
Budapest (Hungary)	The quality of the preservation is good	Discontinuous outcrops partly in urban areas with a thickness of approximately 100 m		Middle and Late Eocene	Coral and platform environment
Huesca-Aragona (Spain)	Quality is good; the specimens often retain also the ventral parts	Discontinuous outcrops several meters thick		Eocene	Eocene platform and also external slope environment
Palermo (Italy)		Discontinuous outcrops no longer identifiable		Late Eocene	Reefal
Hampshire Basin (United Kingdom)	The quality of the preservation is not good	Thickness of a few hundred meters		Eocene	Inner shelf
Lillebælt Clay Formation (Denmark)	The quality of the preservation is very good	Thickness of a few tens of meters (with several discontinuities)	Findings often found in scattered nodules for which it is not possible to trace precise levels	Early/Middle Eocene	Inner shelf
Bateque Formation (México)	The quality of the preservation is not good	Not reported	Discrepancies in studies to evaluate the precise age of formation	Eocene	Outer shelf
Nord and South Carolina (USA)	The quality of the preservation is decent	Not reported		Middle Eocene	Inner shelf
VAL D'ALPONE Mt. Postale San Giovanni Ilarione Roncà (Italy)	Aragonite crystallised in calcite, lithified, only specimens larger than a few mm are preserved; external morphology very well preserved (Mt. Postale, San Giovanni Ilarione, Roncà)	Tens of m-thick succession (Postale) Dm-thick strata, part of a tens of m-thick succession (San Giovanni Ilarione, Roncà)	Biostratigraphic data (mainly large foraminifera)	51-49 Ma (Mt. Postale) 48?-41? Ma (San Giovanni Ilarione) 40-38 Ma (Roncà)	Shallow subtidal back-reef lagoon (Mt. Postale) Shoreface or inner shelf (San Giovanni Ilarione) Intertidal or shallow subtidal (Roncà)
Paris Basin (France)	Origine aragonite, unlithified, species smaller than a few mm are preserved; external morphology very well preserved (Grignon, La Guepelle)	Dm-thick shell beds, part of a meters-thick succession (Grignon, La Guepelle)	Sequence stratigraphic data? Biostratigraphy? Unpublished	45-42 Ma (Grignon) 40-38 Ma (La Guepelle)	Shoreface or inner shelf (Grignon, La Guepelle)
Pyrénées-Atlantiques (France)	Origine aragonite, unlithified, species smaller than a few mm are preserved; external morphology very well preserved (Gan)	Dm-thick shell beds, part of a meters-thick succession (Gan)	Biostratigraphy? Unpublished	50-49 Ma (Gan)	Outer shelf (Gan)
Friuli (Italy)	Aragonite crystallised in calcite, lithified, only specimens larger than a few mm are preserved;	Dm-thick shell beds, part of olistoliths (Noax, Rosazzo)	Biostratigraphic data (large foraminifera)	49-47 Ma (Noax, Rosazzo)	Intertidal or shallow subtidal (Noax, Rosazzo)

	external morphology very well preserved (Noax, Rosazzo)				
Wadi Al-Hitan (UNESCO Egypt)	Aragonite crystallised in calcite, lithified, only specimens larger than a few mm are preserved? (Wadi Al- Hitan)	Dm-thick shell beds part of a tens of m-thick succession (Wadi Al- Hitan)	Sequence stratigraphy (see Peters et al. 2009)	37-36 Ma (Wadi Al-Hitan)	Shoreface (Wadi Al- Hitan)
Sobrarbe (UNESCO Spain)	Aragonite crystallised in calcite, lithified, only specimens larger than a few mm are preserved?	Unknown, part of a tens of m-thick succession	Sequence stratigraphy? Unpublished (see Moreno-Azanza et al. 2021)	48?-41? Ma (Sobrarbe)	Deltaic, intertidal (Sobrarbe)

Category (3) evaluates permanence and scientific impact for each site using separate criteria for:

Site	10. Degree of investigation	11. The centrality of fossil associations for the reconstruction of the history of modern tropical marine biodiversity	12. The centrality of the study of fossils for the history of geology and evolutionary biology	13. Scientific Impact	14. Accessibility of the site
VAL D'ALPONE Pesciara and Mt. Postale (Italy)	Thorough	Most important site in the world for the interpretation of origin and evolutionary trends of current tropical marine diversity	Yes, the extraordinary relevance for the historical development of life sciences and more recently, of evolutionary biology. The fossil fish of Bolca, since the sixteenth century have played a central role in the interpretation of fossils as ex-live	Extraordinary	Good
Messel Pit Fossil Site (Germany)	Thorough	None, it is of a lake assemblage	The fish association of Messel, as far as relevance among the fresh-growing associations of the European Cenozoic is not to be considered fundamental for the history of geology and of evolutionary biology	Relevant to the definition of the structure and composition of the fresh fish communities of Europe of the first part of the Cenozoic	Good in some excavations sites
Mo-Clay (Fur Formation, Denmark)	Very limited	None. It is about fish association in a temperate marine context (proto-North Sea)	Potentially relevant, not adequately recognized	Potentially relevant, not adequately recognized	Good mostly on the Island of Mors
Green River Formation (USA)	Thorough	None, it is a lake assemblage	Numerous fish from the Green River Formation have been studied since the famous naturalist E.D. Cope	Very relevant for the definition of the structure and composition of the fresh fish communities of Northern America of the first part of the Cenozoic	Good in some quarries for the extraction (e.g. industrial use) of limestone laminates. The extension of the lake sediments of the Green River Formation is immense

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Pesciara and Mt. Postale	Sites subject to very accurate inquiries	The great biodiversity and abundance of investigated material allow to make important comparisons with current tropical faunas.	The remains of the Val d'Alpone allow to get information about global significance for the study of the evolutionary history of crustaceans. Furthermore, the Pesciara site has a fundamental place in the history of paleontology	High	Accessibility to the sites for visits is variable: The Pesciara is open to the public, the other sites are scattered in the territory with limited accessibility
San Giovanni Ilarione (Italy)					
Budapest (Hungary)	Site subject to deeper investigation	The abundance and diversity of the remains found allow to make some comparisons with current fauna	The material found in Budapest has been known for more than a century and therefore has a historical significance, its wealth allows important comparisons with contemporary faunas in other parts of Europe	High	Accessibility is not simple
Huesca-Aragona (Spain)	Sites not fully investigates	The small amount of remains allows only superficial considerations to be carried out	The remains found in this part of Spain are still scarce therefore they provide more uncomplete information	Medium	Accessibility not always simple
Palermo (Italy)	Thorough	The remains found confirm the observations already made for western Veneto and Budapest	The remains have made it possible to expand the distribution area of forms already known from western Veneto and Budapest	Medium	No more accessible
Hampshire Basin (United Kingdom)	Thorough	Faunas that include still existing families	Faunas partly known for more than a century with affinities with contemporary faunas of southern Europe	High	Accessible
Lillebælt Clay Formation (Denmark)	Thorough	The fauna highlights affinities on a generic level both with the contemporary English ones and with the Italian and Hungarian ones	Fauna known since the 19th century but investigated only recently	Medium	Accessible
Bateque Formation (México)	Thorough	Fauna significant as it developed between the North Pacific and Tethys dispersal zone	Fauna analyzed only recently that shows affinity with faunas of the Tethys and the North Pacific	Medium	Accessible
Nord and South Carolina (USA)	Only a preliminary analysis	Rich and differentiated fauna but known only from preliminary descriptions	Recently described fauna that highlights affinities with contemporary European ones	Medium	Unknown
VAL D'ALPONE					
Mt. Postale	High: well-established species-level taxonomy, in need of modern revision	Best means to measure shallow marine diversity during the early-mid Eocene (51-38 Ma): Neotethyan diversity hotspot	Covering the whole radiation of the forerunner of the modern tropical biota across the early and mid Eocene climatic optimum (Mt. Postale, San Giovanni Ilarione) into	High impact of older literature; in need of modern, peer-reviewed international studies	Badly exposed (Postale) Partly exposed (San Giovanni Ilarione, Roncà)
San Giovanni Ilarione					
Roncà (Italy)					

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	established modern stratigraphic setting (Mt. Postale), in need of revision (San Giovanni Ilarione, Roncà)		the Bartonian cooling (Roncà)		
Paris Basin (France)	High: well-established species-level taxonomy (Grignon), in need of modern revision (La Guepelle)	Best measure of shallow marine diversity during the middle Eocene (SBZ13-SBZ14, ca. 48-40 Ma): N Atlantic	Covering the radiation of the forerunner of the modern temperate biota across the mid Eocene climatic optimum (Grignon) into the Bartonian cooling (Baron, La Guepelle)	High impact of older literature; partly in need of modern, peer-reviewed international studies	Well-exposed (Grignon, La Guepelle)
Pyrénées-Atlantiques (France)	Low: species-level taxonomy available only as a list in unpublished studies	Best means to measure shallow marine diversity during the early Eocene (SBZ11, ca. 50-48 Ma): N Atlantic	Covering the radiation of the forerunner of the modern temperate biota across the early Eocene climatic optimum (Gan)	Absent in older literature and in peer-review papers	Unknown (Gan)
Friuli (Italy)	High: well-established species-level taxonomy, in need of modern revision; well-established modern stratigraphic setting (Noax, Rosazzo)	Best means to measure shallow marine diversity at the passage early-middle Eocene (SBZ12-SBZ13, ca. 48,5-47,5 Ma): Neotethyan diversity hotspot	Covering the radiation of the forerunner of the modern tropical biota across the early-mid Eocene transition (Noax, Rosazzo)	High impact of older literature; in need of modern, peer-reviewed international studies	Partly exposed (Noax, Rosazzo)
Wadi Al-Hitan (UNESCO Egypt)	Practically zero	Best means to measure shallow marine diversity during the late Eocene cooling (see Peters 2009, doi: 10.2110/palo.2008.p08-080r): Neotethyan diversity hotspot	Covering the radiation of the modern tropical biota during the Priabonian cooling (Wadi Al-Hitan)	Absent in older literature and in peer-review papers	Well-exposed (Wadi Al-Hitan)
Sobrarbe (UNESCO Spain)	Practically zero	Best means to measure shallow marine diversity during the mid Eocene (see Canudo et al. 2021): N Atlantic	Covering the radiation of the forerunner of the modern temperate biota during the mid Eocene (Wadi Al-Hitan)	Absent in older literature and in peer-review papers	Unknown (Sobrarbe)