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# Paleobiology in the Mediterranean

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## INTRODUCTION

It was in 1972 when Thomas J. Schopf (Fig. 1) and a bunch of fellows thought the time was ripe to thrust their paleontological form of mind into the body of evolutionary biology. It all started with a Symposium in 1970, and then a book, both entitled "Models in paleobiology": "*Implicit in it* [the book] *is the belief of the group* [Schopf et al.] *that paleontology has collected much of its data and basic theses. Explicit is the belief that henceforth paleontologists should turn to broader horizons and interpretive themes*" (Schopf, 1972, p. 4). Central to the lasting fame of that book was the chapter dedicated to speciation. The one paper that actually hit the target was entitled "Punctuated Equilibria: An Alternative to Phyletic Gradualism", written by Niles Eldredge and Stephen J. Gould (Eldredge & Gould, 1972; Eldredge, 2015). Did Schopf et al. need a new name for paleontology? Possibly not, but the book was a breakthrough and, together with "Punctuated Equilibria", the term "paleobiology" stuck and progressively placed itself at the core of paleontology. Indeed, it meant nothing bigger than, nor separated from "paleontology". What the subdiscipline actually embraced was listed by Thomas Schopf in the back cover of the journal *Paleobiology*, which he Chief-edited starting in 1975. The journal shunned taxonomy and published only papers dealing with "research on morphology, biogeochemistry, populations, faunal provinces, communities and ecosystems", with an emphasis on "processes and patterns, including speciation, extinction, development of individuals and of colonies, natural selection, evolution, and patterns of variation, abundance and distribution in space and time" (Schopf, 1975, back cover). Indeed, paleobiology was essentially paleontology minus two time-consuming and technical endeavours: stratigraphy and taxonomy.

Paleontology too, however, was there before the word was introduced in 1822 and used in its modern sense (see references in Rudwick, 2008). Before then, it was nothing but geology "tout court", the discipline that embraced the study of the history of life. The eminent proof of an historical nestedness of modern life sciences within earth sciences is found in Charles Darwin's "On the Origin of Species" of 1859, where the term "geology" or "geological" is mentioned 165 times, "palaeontology" and "palaeontological" 12 times, and "biology" is simply absent (even if the term was technically available; Darwin, 1859). Considering how much Darwin's approach to the theory of evolution had relied on the study of fossils (Lister, 2018), we must conclude that paleobiology was there right from the start of evolutionary thinking, at times hardly discernible from modern theory (Eldredge, 2015).

There is no doubt that Darwin shaped his geological state of mind around Charles Lyell's "Principles of Geology" (Lyell, 1830-1833). Now, our modern understanding of the way in which Lyell's "Principles" were conceived, clearly illustrates that what was new largely stemmed from his travel to Italy of 1828, when he came to see with his own eyes fossils and rock formations described in Giambattista Brocchi's "Subapennine Fossil Conchology" (1814; Fig. 2). Answering to Jean-Baptiste Lamarck's "Philosophie zoologique" (1801, 1809) and Georges Cuvier's "Recherches sur les ossemens fossiles" (1812; see Eldredge, 2015), Brocchi had adopted a quantitative approach to the study of the fossil record and calculated the percent of living species present among subapennine fossil molluscs, relying on a profound knowledge of the modern biota (Dominici, 2010). By counting all fossil species found in Italian "Tertiaries" (Rudwick, 2008) and knowing all the species that were living in the Mediterranean (which Brocchi thought he did, after all the work carried out by some of his colleagues in Veneto), the percent was a way to measure the gradual passing of time. Charles Lyell read Italian and Latin fluently (his father had translated Dante Alighieri's "Vita Nova" and "Convivio") and understood well what was hidden in Brocchi's approach. What Darwin later called "Lyell's Metaphor" (Darwin, 1859, p. 310) - the book "imperfectly written" on the pages of rock formations in the language of fossils - Lyell had learned to read thanks to "the finest collections of fossil shells in Italy" and by travelling the Peninsula with "mounting excitement" in 1828 (quotations from Rudwick, 2008, p. 272). Others were independently following Brocchi's pathway (Heinrich Georg Bronn, for instance; Tamborini, 2015a, b), but it was Lyell who left the longer-lasting heritage by perfecting in the years those "Brocchian statistics", in the chimeric search to objectively measure geological time (Rudwick, 2008, p. 474-479). The very stratigraphic terminology of the Epochs Eocene, Miocene, Pliocene and Pleistocene with which we order "Tertiary" are there for us to remind. To make a long story short, if the study of "patterns of variation, abundance and distribution of fossils in space and time" had a birthplace, that was the Mediterranean. Since its beginnings in 1814 with Brocchi, paleobiology was guided by an analytical, quantitative approach to reconstructing global patterns in the history of

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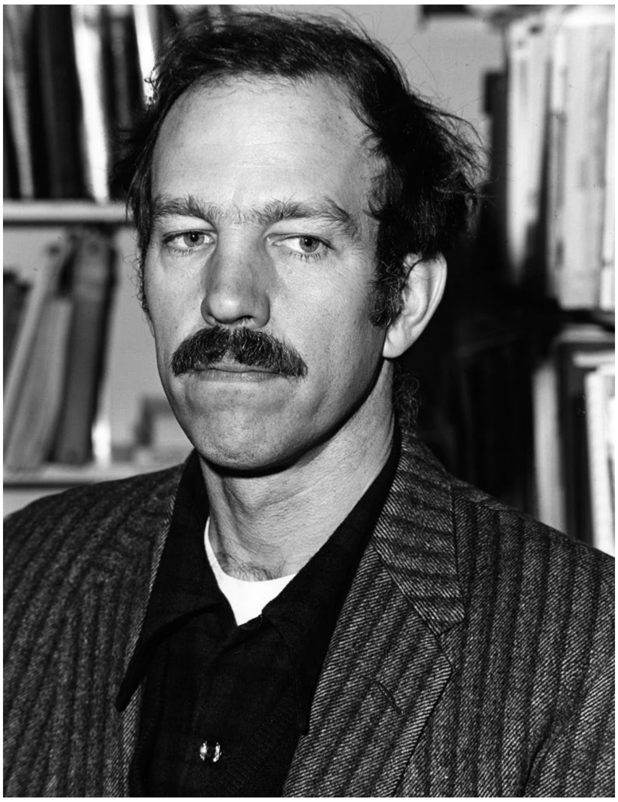

Fig. 1 - Thomas J.M. Schopf (1939-1984), paleobiologist at the Department of Geophysical Science, University of Chicago (USA).

life. Coming back to the 20th century, if not christening a new field of enquiry, the birth of the journal *Paleobiology* ensured a place for a young and active community of geoscientists to fruitfully exchange ideas and concepts, with new powerful mathematical tools and a more refined knowledge of the record. The "paleobiological revolution" (copyright Sepkoski & Ruse, 2015) indeed owes much to the journal in delivering those concepts and keeping early aims alive and kicking. A sign of good health is the recent birth of new areas of research of paleobiology within the field of geoscience: "conservation paleobiology" (e.g., Dietl & Flessa, 2017; O'Dea et al., 2017) and "stratigraphic paleobiology" (see below). These new areas share a common base: cross-fertilisation among different disciplines. Stratigraphic paleobiology is the watchword here, knowing that the Mediterranean fossil record is as inspiring and fertile today as it was in the early days of geology.

## STRATIGRAPHIC PALEOBIOLOGY

Stratigraphic paleobiology, a subdiscipline of paleobiology formalised by Patzkowsky & Holland in 2012, is a cross-over of the study of patterns of fossil distributions in space and time and stratigraphy. The idea, on one hand, is that the geological record has gaps and that these can be approached and better understood through the study of sequence stratigraphy and event stratigraphy (Ager, 1983). On the other hand, the fossils embedded in the geological record allow to depict environmental gradients and thus improve sequence-stratigraphic interpretation of the sedimentary successions. Sequence stratigraphy, bloomed in the late seventies in the laboratories of the Exxon Production Research Company from the analysis of stratal geometries from seismic profiles (Mitchum et al., 1977), soon expanded to well and outcrop studies, attracting mathematical minds (Jervey, 1988) as well as field-goers (Van Wagoner et al., 1990; Posamentier et al., 1992). Through the application of the principles of accommodation and sedimentation, sequence stratigraphy was a "revolution in sedimentary geology" (copyright Catuneanu, 2006), that was soon to bear consequences on our understanding of the fossil record (Holland, 1995, 2016), with transformative results in the subfields of macroevolution (Smith, 2001; Peters, 2005), macroecology (Holland, 2012; Nawrot et al., 2018) and paleoecology (Scarponi & Kowalewski, 2004; Scarponi et al., 2013). Patzkowsky & Holland (2012) must be credited with a full explanation of why paleobiological data must come with a stratigraphic context, but the feeling that sequence stratigraphy was revolutionising the way we see the marine fossil record came in the 1980s. First, it embraced biostratigraphy (Armentrout, 1987), while the earliest paleoecological studies on fossiliferous deposits in an explicit sequence stratigraphic context were published in the early 1990s (Banerjee & Kidwell, 1991). Soon after we find the first papers dedicated to the quantitative analysis of shell beds within a sequence-stratigraphic framework in the Mediterranean, published in this journal (Benvenuti & Dominici, 1992; Dominici, 1994). A deeper knowledge of the modern shelly benthos inhabiting that sea, with respect to most other places in the world, greatly facilitated the interpretation of fossiliferous successions taxonomically dominated by extant species whose ecological distribution was studied since more than two centuries (see Brocchi's 1814 account of the large work already carried out in the Adriatic Sea at his time by Giuseppe Olivi and Stefano Renier). The 1990s were the years when benthic paleoecology was mainly approached in the Mediterranean following the principles of benthic bionomics of the Endoume School (Pérès & Picard, 1964; Basso & Corselli, 2002). That methodology, distinguishing between "characterising" species of a given "biocenoses", from "not relevant species" (sic) resulted for the Mediterranean in the recognition of several benthic marine communities shaped by different substrate requirements and whose limits are determined by abiotic parameters (Pérès, 1967). The benthic bionomics approach was soon paralleled by the increasing application of multivariate analytical methods that facilitate comparisons with non-Mediterranean studies and it has been flanked in the years by the study of marine biotic gradients, more closely representing the natural spatial distribution of organisms (Miller, 1988; Patzkowsky, 1995; Holland & Patzkowsky, 2004). Furthermore, multivariate statistics represent an effective and powerful method for analysing large paleoecological dataset. A second wave of stratigraphic paleobiological studies soon followed in the Mediterranean, sometimes highlighting distinct groups of taxa that recur in time and space by the use of clustering techniques (Dominici, 2001; Ceregato et al., 2007; Pervesler et al., 2011; Scarponi et al., 2014; Cau et al., 2019), in other instances stressing biotic and taphonomic gradients by ordination methods


Fig. 2 - One of the plates engraved to illustrate the Subappennine Fossil Conchology by Giambattista Brocchi. Some of these Pliocene species are extant (e.g., *Murex rostratus*, the first to the left on top row, described by Giuseppe Olivi in his "Zoologia Adriatica" of 1792), others are extinct and were described by Brocchi for the first time.

Fig. 3 - Sedimentological shell bed at the bottom of a laminated sandstone, crossed by the trace fossil *Ophiomorpha nodosa* Lundgren, 1891. Lower Pleistocene of the Castell'Arquato Basin, in Emilia.

(Dominici & Kowalke, 2007; Dominici et al., 2008, 2018, 2019, 2020; Ayoub-Hannaa et al., 2013; Wittmer et al., 2014; Scarponi et al., 2017a, b). The application of high-resolution sequence stratigraphic methods and concepts is facilitated here by the good quality of shelly outcrops (Fig. 3) and by the particular collisional tectonic setting of depositional basins, leading to the formation of thick Pliocene and Pleistocene sedimentary successions (Fig. 4; Coletti et al., 2018; Dominici et al., 2018). In time, large datasets have assembled, forming the basis of macroecologic studies that investigated the fate of onshore-offshore gradient in geologic time, within a framework of sequence-stratigraphic units (Tomašových et al., 2014; Roden et al., 2018).

## A THEMATIC ISSUE OF BSPI

This issue is dedicated to the state of the art in a region of the globe that is particularly favourable for its natural opportunities, as centuries of paleontological literature testify, and for the cultural background that greatly facilitates the interpretation of the patterns of variation, abundance and distribution of fossils in space and time. Similarly to when Charles Lyell was here, an extended and lively community of paleontologists and biologists ensures widespread knowledge and expertise with generally very high taxonomic standards, the prerequisite to any good paleobiological enquiry. This national community if formed by many professional researchers and by an even higher number of experienced amateurs that are only rarely acknowledged (see Feldmann, 2014, for a noteworthy exception), but who often deserve high praise

Fig. 4 - Small-scale depositional sequences, formed by the stacking of grey mudstones from shelf settings to yellow shoreface sandstones. Upper Pliocene of the San Miniato Basin, in Tuscany. This is an historical locality visited by Brocchi in 1811.

for the quality of their insight and for their generosity. All studies deal primarily with marine molluscs among body fossils, secondarily with polychetes, brachiopods, ostracods and calcareous nannofossils. Two of the papers compare the distribution of different sets of fossils, one including also trace fossils. All rely on species-level quantitative datasets that are made available for further scrutiny. The stratigraphic interval presented includes the upper Pliocene and the Pleistocene, while localities range from North to South Italy and the Central Adriatic. Comparisons with modern counterparts rely on the best literature available on the ecology of marine benthic communities, also stemming from centuries of field research, particularly of the French and Italian schools. Most of the papers deal with classical outcrops that were first studied in the nineteenth century, also by Brocchi himself in 1814. One explores new territories merging macrobenthic and seismic insights to refine stratigraphical architecture of cored sedimentary successions. In this last respect, Azzarone et al. (2020) present a research that is novel for stratigraphic paleobiology, merging multivariate analysis of mollusc and ostracod assemblages from cores collected in the Central Adriatic with the study of seismic facies recorded along a multichannel seismic reflection profile. It is also particular in presenting the study of a lowstand wedge, a systems tract seldom available to outcrop studies. Cau et al. (2020) focus on the classical biodetrital-mudstone lithosomes, already noticed by Brocchi (1814, p. 158), and outcropping at Castell'Arquato (northwestern Emilia). The authors present gradient analysis of a previously-acquired large mollusc-based dataset (Cau et al., 2019), finding that factors controlling the distribution of biofacies are not dictated by water depth in a simple way, as frequently thought. They hypothesise instead a climatic forcing on shell-bed formation and a correlation between thick biocalcarenites and deep-water Pliocene and Pleistocene sapropel clusters. Biocalcarenites form during cold-arid phases, whereas sapropels indicate warm-humid conditions of the same climatic cycle, driven by astronomical cyclicity. The same region was studied by Bracchi et al. (2020), who present the paleocology of an interesting sedimentary unit recording abundant fossil remains of the iconic Mediterranean bivalve *Pinna nobilis* found in life position and belonging to a Lower Pleistocene depositional sequence of the Castell'Arquato Basin. Another classical locality presented in this issue is in southern Italy, at Altavilla Milicia, near Palermo, Sicily, bearing fossils that were studied by Calcara (1841) and Seguenza (1873-1877), among others. The comparative approach to the study of a shell-rich succession by Dominici et al. (2020) includes data from lithofacies and paleoecology of molluscs, chronostratigraphically framed thanks to calcareous nannofossil biostratigraphy. The results allow to correlate shell-rich units to two biocalcarenitic intervals studied in the Pliocene and Pleistocene of Emilia and Sicily.

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