Death: a key information in marine palaeoecology

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INTRODUCTION

As a dissipative structure, according to the second law of thermodynamics (Prigogine & Wiame, 1946; Prigogine, 1961), the Individual is the unique biological deme that originates at birth and stops at death, which marks the end of entropy production and consequently of the non-equilibrium state. Therefore it is the only entity able to pass on to the lithosphere as fossil; its death is the initial stage at which begin the taphonomic processes.

According to the validity of this axiom, the definition of the taphonomy, as proposed by Efremov (1940) and modified by Emig & Racheboeuf (1990), is fully consistent with the replacement of "organic remains" by "biological entities", that is: "TAPHONOMY is the study of the transition of the biological entity from the biosphere to the lithosphere". According to this definition, taphonomy and its processes belong to a scientific field shared by two disciplines, Biology and Geology, both being complementary. The biological processes, playing a taphonomic role, have been underestimated (see Kidwell & Behrensmeyer, 1988) compared to the geological processes, whereas, since the 1990s, the biological importance became predominant (see Bromley, 1996; Kowalevski, 1997; Nebelsick, 1999). Nevertheless, Bromley (1996), in his definition of taphonomy, that is "the study of processes that lead to the loss of information incurred has sediments pass from the active benthic boundary layer into the geological record", takes into consideration only the processes provoking a loss of information in soft substrates, which represents only a part of the taphonomy. According to Bromley (pers. comm.), taphonomy begins before death, e.g. mollusc and brachiopod shell commonly start to become degraded by bioerosion during the life of the "host".

Presently, the importance of the factors responsible for the death of individuals, whether or not they reach the fossil register, and the identification of the prevailing ecological conditions at this moment have been largely overlooked in the taphonomic processes and in the paleoecological reconstruction.

T_0: THE DEATH OF THE INDIVIDUAL

Death is the initial stage represented by T_0, from which begin the processes of the taphonomy (from *taphos* = tomb and *nomos* = law, in Greek), the beginning of the transition of an entity towards the fossil register. The Individual cannot be separated from its environment, because living within a population, defined as "a group of individuals of the same species occupying a niche in a given biocenosis" (Arnaud & Emig, 1987), and therefore in a biocenosis, which is defined as "all the populations linked by a reciprocal dependence and now permanent manner in reproducing in a biotope". The population is the highest natural level within the biological hierarchy: compared to the individual, it is characterised by continuity in time and by the capacity to evolve. Its total disappearance is an extinction, which is generally due to factors external to this population (i.e. perturbations of the biotope, competition with other populations, diseases...).

Three types of death may occur for the individual. Nevertheless the instantaneous character of the death remains a delicate point to be estimated when compared to the geological time scale.

1 – natural death that, for a lot of groups, leads rarely to the fossil register, except as fragments and debris of various sizes, according to the action of the prevailing factors governing the biotope in which death occurred;

2 - death by predation often leads to the same result as the above-mentioned. Sometimes, the predator can be identified and its effects analysed, e.g. perforations by gastropods. For those two types, the death of individuals belonging to the same species is displayed, sometimes over several tens of thousands of years (Emig, 1987).

3 - death under drastic changes, sometimes "catastrophic", of the environmental conditions, concerning generally many individuals, a whole population or several populations, a biocenosis or several ones with harsh biotope modifications. In this case, all age classes are affected. Such changes may induce a shortening of the stage of alteration and an acceleration of that of fossilisation, e.g. effects of a period of rapid sedimentation. In addition, the responsible factors should be identified in the geological layer, while the conditions in T_0 cannot be interpreted as normal life conditions. For example, the death of a population of brachiopods, i.e. *Lingula* or *Gryphus*, at the base of a marl or shale, overlying a sandstone has occurred during a large fine sedimentation while the normal life conditions of these populations occur in sandy substrates, not in muddy substrates in which occurs the death. Consequently fossilisation takes place in a layer, which informs about the death conditions (Emig, 1989a, 1990; Fernández-López, 1995) (Fig. 1).

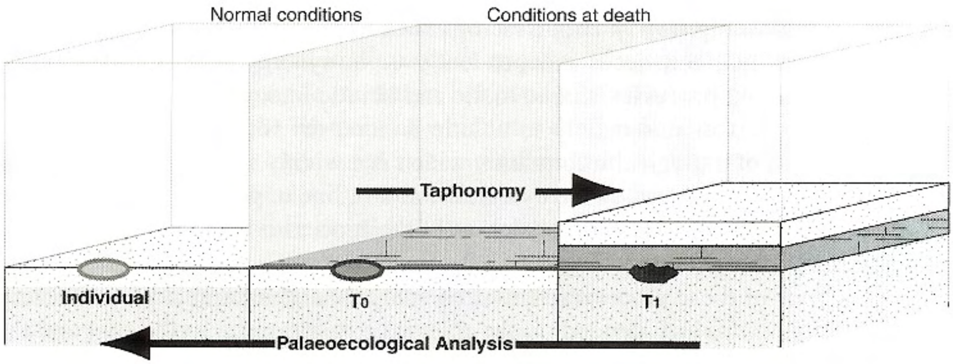

Figure 1. Diagram of an individual under taphonomic processes, from T_0 to T_1, and the paleoecological approach, from the fossil register to reconstruct the original life conditions.

More than the direct causes inducing the death of the individual, the environmental conditions prevailing at the moment of the death will induce the *post-mortem* loss of information during the taphonomic transition, as well as the potential of fossilisation of the dead individuals. They may also determine whether or not such individuals will remain in life position. The identification of all these conditions should avoid bias, distortions and errors in the paleoecological interpretation. The morpho-anatomical characteristics of the individual in T_0 directly influence the taphonomy of the individual.

In each of those three types of death, there is always the possibility of a mixing of populations or individuals, even in life position, which may belong to the different biocenoses or/and to different geological periods. Still it is difficult to localise the death within the geological time scale, as the dating of each fossil is obviously impossible. Consequently, only an excellent knowledge of the ecology of the populations, the cause of the death of the individuals, as well as the general ecological conditions that prevailed, may allow one to specify the moment of death for each fossil (see examples in Emig, 1986; Largois, 2000).

FROM T_0 TO T_1: THE TAPHONOMIC PROCESSES

In Biology, *post-mortem* transformation is generally not taken into account except when directly concerning living populations and biocenoses, i.e. by biodetritic addition to the sediment (shells, spicules, bones, etc.) or as nutritional contribution (necrophagy, organic enrichment, etc.).

Taphonomic processes always occur from T_0 to T_1 (which corresponds to the entry of the Individual into the fossil register) (Fig. 1). The responsible factors are generally abiotic (including the sediment), which are external to individuals, populations and biocenoses and delimit their extension and ecological evolution (Pérès, 1982; Arnaud & Emig, 1987). Biotic factors, such as predation, bioturbation, organic degradation, etc., can occur independently or in synergy with abiotic factors. There are alteration processes, due to biotic and abiotic factors, and conservation or fossilisation processes due mainly to abiotic factors; the former processes lead to major reduction of biological information which is a widely accepted concept. Both types of taphonomic processes are dynamic and non-linear, permanently from T_0 to T_1, governed by the changes and evolution of the biocenosis in which a dead individual undergoes taphonomy (Fig. 1).

The actions of these processes should be analysed and interpreted from "actuodata", the limits of which depend on the relevance to transpose to the past and the reliability of the paleoecological data obtained from the fossil layer, including the validity of species identification. There is no model, even in the Actual; each fossil layer needs an acute analysis, especially of its particularities and of its situation (Emig, 1990; Bromley, 1996; Kowalesvski, 1997, 1999; Nebelsick, 1999). Finally, the knowledge of the death factors, or at least the occurrence of ecological conditions at that moment, should be considered as basic taphonomic data with which to perform a paleoecological analysis.

One of the aims of a paleoecological interpretation of a fossil layer is to identify the factors at T_0 in order to establish the prevailing environmental conditions when the death of individuals occurred, perhaps to discriminate the time interval between the death of the different individuals. As in ecology, the paleoecological approaches have to take into account the multiplicity and the insertion of space and time scales, as well as the interactions of physical, chemical and biological features in relation to the organisation levels of the biological and ecological systems (Emig *et al.*, 1995). Within a fossil assemblage, the thickness of which is sometimes centimetrical, time and space insertions may develop over several tens of thousands of years, so that the conditions at T_0 can be very different over a long period. For example, the Würmian thanatocenoses of *Venus casina*, occurring originally in the Infralittoral zone, are now located in the Bathyal zone, on the continental slope, at about 180 m depth, and continue to be "fattened" by a living population of *V. casina* (Emig, 1987); however, this species is eurytopic because related to biotopes with strong hydrodynamics. The death of the molluscs was and is natural, except for some killed by gastropod naticids. The biocenoses are different: originally a biocenosis of the" Sands and Gravel under the influence of Bottom Currents ", presently that of the "Bathyal Detritic Sand", characterised by the brachiopod *Gryphus vitreus* (Emig, 1985, 1989b). The thickness of the layer is about 5 cm because the sedimentation is very weak in this slope area for about the last 18,000 years.

CONCLUSIONS

The challenge of the paleoecological approach is to reconstruct from the fossil register (in T_1) the factors and conditions when the death of the individual (in T_0)

occurred. Our (palaeo)biological (including the taxonomy) and (palaeo)ecological knowledge of the fossilised individuals, as well as that of the biocenoses and the bionomy, are of fundamental importance in order to identify all the factors. In fact, by definition, the taphonomic transition is biospherical. There remains a major difficulty: how to define the moment at which the dead individual entered the fossil register, which could be interpreted as being different from its entrance into the lithosphere. When individual remains reach the historic layer of a sediment (see Bromley, 1996), they can be considered as being within the "lithosphere", but how may we interpret the bivalve remains in the above cited example of the Würmian thanatocenoses located near and on the sediment surface.

This approach, close to that of forensic medicine, requires an integration of the complementary methods of the Life Sciences and of the Earth Sciences. This is the originality of taphonomy. The research of criteria and their analysis have to be made with the same rigor as the police to identify and analyse the causes of the death and environmental conditions in T_0.

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