

POSTULATES OF THE EVOLUTIONARY TAPHONOMY

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Fossils are not necessarily composed of organic matter and all of them lack the diagnostic features of biological entities, such as metabolism or viability. Therefore, fossils are not palaeobiological entities, although they bear palaeobiological information and were produced by biological entities of the past. In palaeontology, it is necessary to accept the **postulate of production**, according to which fossils or taphonomic individuals in general have been directly or indirectly generated by palaeobiological entities. The term biogenic production denotes the processes through which taphonomic individuals are generated by palaeobiological entities, whereas the term taphogenic production denotes the processes through which taphonomic individuals give rise to other taphonomic individuals. If taphonomic elements are reproductions or replicas of organisms of the past or parts of them, then taphonomic elements and their producer organisms or the corresponding anatomical parts have distinct nature.

Once the existence of biological entities or units of different levels of organization (organisms, populations, communities, species and clades, for instance) is admitted, and it is assumed that biological entities cannot be reduced to organisms, then it should not be excluded that palaeobiological entities had been able to give rise also to taphonomic entities of different levels of organization. The existence of hierarchically organized taphonomic systems is a logical assumption compatible and congruent with those used in the ecological theory and in the theory of organic evolution. According to these assumptions, taphonomic systems are integrated by elemental taphonomic individuals (that is taphonomic elements) or supraelemental taphonomic individuals (taphonic populations, taphonic

associations, taphons and taphoclades). This is the taphonomic **postulate of emergence** (Fig. 1). Any supraelemental taphonomic entity has a size (number of components), density (mean of components by unit of surface or volume), diversity and evenness, geographic distribution and temporal structure. The structural properties of any supraelemental taphonomic entity or unit are the result of both the external influences and the interaction between its components. The structural properties also determine the behaviour of any supraelemental entity in relation to the different environmental factors. The composition and the structural characters (i.e., the architecture) of the distinct taphonomic individuals make possible the analysis and the representation of its structure.

A taphonomic element is a remain or trace of an organism of the past which is (para)taxonomically significant and determinable. Every taphonomic element is constituted by molecules of a certain class (organic and/or inorganic), and it is possible to determine its chemical, mineralogical or petrological composition, but such constituents are not fossil if they lack (para-) taxonomic signification. Therefore, being fossil or fossilized is an emergent property, not an aggregative character, of the taphonomic elements with respect to their components. Taphonomic elements are the entities and the units of smaller level of organization constituting the fossil record. Taphonomic elements are basic entities of the taphonomic hierarchy and those of smaller duration. Taphonomic elements are the basic components of taphonic populations, taphonic associations, taphons and taphoclades, which respectively possess an elementary, populational or taphonic composition.

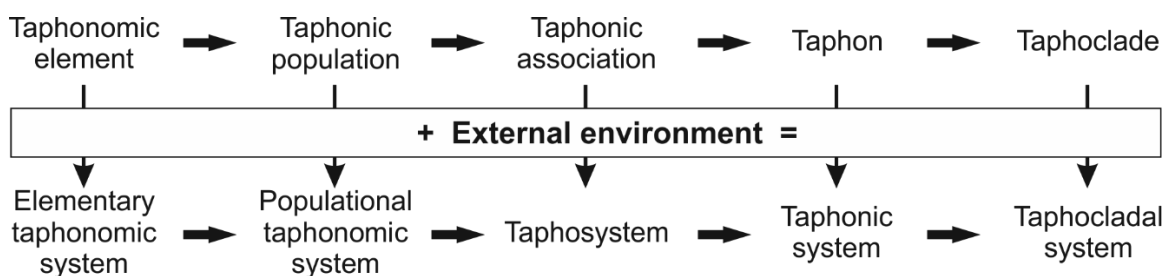


Figure 1. Evolutionary and functional hierarchy of taphonomic individuals (entities or units) and taphonomic systems.

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The taphonomic element that has acquired a new architecture (i.e., a new chemical composition and structure) should be considered as replica or element of a new taphonomic group, and not as a transformed element belonging to the original or antecessor taphonomic group. Concretionary internal moulds, pyritic moulds of ammonite shells, as well as impressions produced by certain shells in sedimentary surfaces are replicas of the original aragonitic shells. Calcitic aptychi, periostracal organic remains, phosphatic siphuncular tubes, aragonitic shells, pyritic moulds or concretionary internal moulds of the ammonite shells are taphonomic elements of different chemical composition and different structural characters, and they represent different taphonomic groups or taphons. Also macroconchs and microconchs of ammonites are distinct taphons, due to their structural and behaviour differences. A taphon is a group of taphonomic elements with a particular architecture (i.e., chemical composition and structure), functionally distinct and able of produce new taphonomic elements of its same taphonomic class, which constitute a historical entity, space-time limited. A taphonic population is a group of taphonomic elements belonging to the same taphon, within a particular environment. Taphons are integrated by local taphonic populations, which can be preserved in particular environments. Specific taphons are a particular class of taphons, in which all constituent taphonic populations correspond to elements representing the same biological species and being able to be preserved in a particular environment. A taphonic population can be analysed on the basis of its elementary composition (i.e., of its integrating taphonomic elements) and its structural properties: size, density, diversity, geographic distribution and temporal structure of the taphonic population. No taphonomic element can be preserved everywhere, but all taphons can become preserved somewhere even beyond the limiting constraints of the taphonomic elements originally produced.

A tafoclade is a group of taphons of common (para)taxonomic and genealogical origin. Taphoclades can present genetically differentiated parts, called subtaphoclades, and can constitute taphocladal groups. Taphoclades and taphocladal groups can be of specific or supraspecific category, according to the (para)taxonomic level of reference. A specific taphoclade includes a group of taphons representing the same species, whereas a specific taphocladal group includes a group of specific taphoclades of the same genus or supraspecific category. For instance, in the taphoclade of the subclass Ammonoidea (Triassic-Cretaceous) more than 30 ammonite taphons are known, from pseudomorphs of soft parts or organic periostraca more or less carbonized until external moulds of aptychi, through different pseudomorphs of siphuncular tubes and diverse internal

moulds of shells. The different anatomical parts of these ammonoids correspond to at least five subtaphoclades (i.e., soft-parts, periostraca, siphuncular tubes, shells and aptychi).

A taphonic association is a group of interrelated taphonic populations, pertaining to two or more taphons, interacting together and with their external environment. Taphonic associations should not be confused neither with fossil-assemblages or fossil-lagerstaetten, nor with biotextures or facies of fossiliferous rock-bodies. A fossil assemblage is a monotypic or polytypic group of fossils, or of taphonomic elements belonging to one or more taphons, from a restricted stratigraphic interval or geographic locality. A fossil-lagerstaette is any rock body unusually rich in palaeontological information, either in a quantitative or qualitative sense. The geologic term biotexture denotes the characteristics of a sediment or rock, concerning the size, shape, angularity and packing of the constituent bioclasts or fossils. Biofacies, ichnofacies and taphofacies are sediments or rocks characterized by particular palaeobiological, ichnological or preservational features, respectively, of the contained fossils.

A third necessary postulate for any taphonomic research, the so-called postulate of modification, assumes taphonomic individuals are not inert and every taphonomic entity or taphonomic unit is involved in some kind of process. Preservation is not the result of isolation of produced taphonomic elements or of the inhibition of alterative factors. Preservation is the result of a process, fossilization, where two interrelated components are involved: the biogenic and taphogenic production of taphonomic variability, and the regulation of such variability by taphonomic alteration. The second of these components can be regarded as an extrinsic principle of regulation, which is able to fix the direction of an evolutive taphonomic process. Representatives of new taphonomic groups appear during fossilization processes, showing different architecture from those biogenically produced, and they increase the diversity of the fossil record. In every fossilization stage, the persisting taphons will be those whose taphonomic elements have been stabilized, transformed, and replicated with a higher effectiveness in the prior stages, but not the initially most resistant or the less affected by environmental factors. The different taphonomic factors taking part in each stage of the fossilization processes are capable of eliminating those elements whose features are less appropriate for preservation. However, they may favour as well the appearance of preservative modifications. Fossilization, therefore, means an increase in taphonomic information or in taphonomic order that does not necessarily involve loss or decrease of palaeobiological information.

Taphonomic alteration means change by destruction or modification of taphonomic individuals (taphonomic elements, taphonic populations, taphonic associations, taphons or taphoclades) due to their interaction with the external environment. Structural properties of taphonomic individuals allow the distinction of separate alteration processes in four different levels: elementary, populational, taphonic and taphocladal. Elementary alteration acts on taphonomic elements, eliminating those of smaller durability and redundancy. Populational alteration represents the group effect on preservation potential of taphonomic elements belonging to the same taphon. Taphonic alteration acts on taphons, eliminating those of smaller preservation potential. Taphocladal alteration implies destruction or modification of taphoclades. In addition, these four types of taphonomic alteration give rise to different results. Elementary alteration causes destruction, stabilization, transformation and replication of taphonomic elements. Populational alteration give rise to destruction (populational destruction), maintenance (populational retention) and formation of new taphonic populations. Taphonic alteration causes destruction (taphonic destruction), maintenance (taphonic retention) and formation of new taphons (taphonization). Taphocladal alteration give rise to destruction of taphoclades (taxa without fossil record), maintenance of taphoclades (taxa with "unaltered fossils"), modification and diversification of taphoclades (taxa with "altered or varied fossils").

Applying principles of the theory of systems, any taphonomic entity can be considered as constituted by entities pertaining to the adjacent lower organization level, but anyone of these entities possesses at least an emergent property (i.e., a property not possessed by the entities of the adjacent lower organization level). As an example of emergent property in relation to taphonomic elements can be mentioned the taphonomic preservability or preservation potential of taphonic populations, taphons and taphoclades. Each taphonic population, taphon or taphoclade has a certain value of preservability or preservation potential, although the integrating taphonomic elements have only durability. Taphonomic populations, taphons and taphoclades have taphonomic preservability or preservation potential independently of the durability of their elements. Preservability or preservation potential, similarly as durability, is a relative and dispositional property. However, preservability must be compared with respect to the successive environments that temporarily range from the production of the supra-elementary taphonomic entity until the present evidence observed in the geologic record, whereas durability of a taphonomic element must be compared with respect to its particular external environment. Taphonomic elements

can undergo transformation (by changing their structural characters) whereas taphonic populations or taphons can evolve (changing the architecture of their taphonomic elements driven by their supraelemental architecture). For this reason, the durability of taphonomic elements can be interpreted with functional criteria, using experimental data and observations in modern environments, whereas the preservability of taphonic populations, taphons and taphoclades must be interpreted with evolutionary criteria. It may happen that the taphons or the taphoclades represented by taphonomic elements more durable and/or redundant in a phase of the fossilization process are not the most preservable. Preservability of taphons or taphoclades, similarly as adaptability of biological species, cannot be estimated by experimental methods or by observation in natural environments. Preservability of taphons and taphoclades neither can be tautologically estimated by the differential preservation observed or achieved in the fossil record. Preservability of taphons and taphoclades can only be assessed and tested in a retrospective way keeping in mind the physical properties of the successive taphonic populations and the successive taphons of each taphoclade. This procedure allows explaining the way representatives of some taphoclades (for example, the ammonite remains) have been able to be preserved and even to be abundant in supratidal environments of continental facies (as reelaborated internal moulds) beyond the limits of tolerance of the originally produced taphonomic elements (i.e., the aragonitic shells).

Alteration of taphonomic elements is conditioned by the respective values of elementary destruction, durability and redundancy. Alteration of taphons is conditioned by the respective values of taphonic destruction, taphonic retention and taphonization. Taphonic alteration and microevolutionary taphonomic changes are impelled by differential durability and redundancy of taphonomic elements, but are driven by the supraelemental architecture of taphons. On the other hand, taphocladal alteration and macroevolutionary taphonomic changes are impelled by differential taphonic retention and taphonization of taphons, and are driven by the supraelemental architecture of taphoclades. Taphocladal, macroevolutionary processes can be a result of differential rates of taphonic retention, taphonization and taphonic destruction, but not of intrataphonic changes (such as stabilization, transformation, replication or destruction of elements). Consequently, macroevolutionary (or taphocladal) and microevolutionary (or taphonic) taphonomic changes and processes can work in opposite directions. For instance, during taphonomic alteration, some trends can harm to taphoclades and favour the preservation of the integrating taphons. For example, marine environments of high sedimentation rate favoured

the rapid burial of ammonite remains, diminished the effects of the biostratinomic alteration, and promoted the preservation of soft parts, periostraca and organic siphuncular tubes, as well as the maintenance of jaw-elements in their original position and the integrity of the aragonitic shells during the biostratinomic phase and at the beginning of the fossilization. However, these sedimentary environments hindered the formation of sedimentary internal moulds of shells and, after the dissolution of aragonitic shells, decreased the geological longevity and preservability of the corresponding taphoclasts during the early fossilization. Consequently, marine environments of high sedimentary rate were favourable for the preservation of diverse anatomical parts of ammonites, but of low taxonomic significance at specific level. In contrast, marine environments of low sedimentation rate favoured the development of complete and homogeneous sedimentary infill of the ammonite shells, although promoted the destruction of soft parts, periostraca and organic siphuncular tubes, as well as the dispersal of jaw-elements and the fragmentation of the aragonitic shells during the biostratinomic phase. They were favourable environments for the development of concretionary internal moulds of the shells, of high taxonomic significance at specific level, although hindered the maintaining of others anatomical parts of the ammonites. Therefore, during the taphonomic alteration of ammonite shells, some trends can harm to the recorded taxonomic information (by taphoclastal alteration) although they favour the preservation of diverse anatomical information (by taphonic alteration) and vice versa.

In order to interpret the differential preservation of fossils and the fossilization mechanisms it is necessary to take in mind not only the original architecture of taphonomic elements and the environmental changes, but also the successive changes in architecture and the activities carried out by taphonomic elements, as well as the evolutionary modifications of taphons and taphoclasts. Taking into account the postulates of production, emergence and modification, an alternative model to that traditionally used in taphonomy may be developed for the fossilization processes: a systemic and evolutionist model of taphonomic modification and differential retention for a negentropic process of growing taphonomic information vs. an individualist or holistic and transformist model of palaeobiological modification and selective destruction for an entropic process of diminishing palaeobiological information (Fernandez-Lopez, 1982, 1991, 2000, 2005, 2006; Dominguez-Rodrigo et al. 2011).

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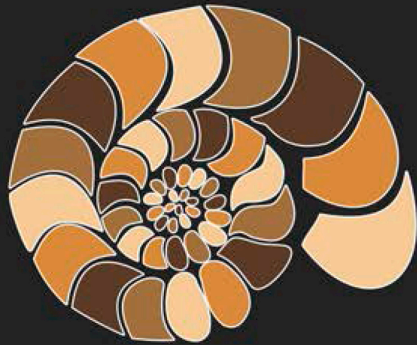
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