

Taphonomic Alteration and Evolutionary Taphonomy

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Every process of taphonomic alteration implies change and modification of the affected taphonomic elements, but it does not necessarily lead to the destruction of taphonomic elements. Taphonomic alteration can be of four types: elementary, populational, taphonic and taphocladal. In order to interpret the differential preservation of fossils and 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 of taphonomic elements and the activities carried out by taphonomic elements, as well as the evolutionary modifications of taphons and taphoclades. This systemic and evolutionist procedure allows to explain how the representatives of some taphons or taphoclades have been able to end up being preserved outside of the limits of tolerance of the originally produced taphonomic elements.

Keywords: PRESERVATION POTENTIAL, TAPHONOMIC DURABILITY, FOSSILIZATION POTENTIAL, FOSSILIZATION THEORY, AMMONITES

Introduction

Most of the current taphonomic interpretations consider that taphonomic alteration has acted during fossilization processes like a filter or a sieve, eliminating a large amount of the originally produced biological remains and traces, which were non-preservable or of smaller durability due to their composition and structure. The destructive role of taphonomic alteration is currently accepted in research, and it is considered that taphonomic alteration can deteriorate and eliminate the biological remains and

traces of lower physical resistance, chemical stability or durability. The only entities or units of taphonomic alteration usually investigated are biological remains and traces, as well as thanatocoenosis or taphocoenosis (Efremov, 1940, 1950) and fossil assemblages. From this point of view, the alteration cannot produce new elements, which represent new taphonomic groups. Taphonomic alteration cannot generate new taphonomic entities. It can only deteriorate or destroy and retain deteriorated parts of the initially produced biological remains and traces. Taphonomic alteration is a destructive or negative force, which does

not contribute to preservation, being only responsible for the destruction of biological remains and traces. The destructive action of the taphonomic alteration or the relative behaviour of the biological remains and traces cannot serve as causal argument to explain the fossilization mechanisms or processes. Taphonomic alteration can only eliminate the non-preservable remains and traces, and some other cause should play the positive role of producing or maintaining the preservable remains and traces. From this point of view, the composition and structure of original biological remains and traces, not the external environment or the differential behaviour of taphonomic entities, play a causal role in the changes happened during fossilization. From a different approach, however, an alternative model to that traditionally used in taphonomy can be developed: the model of taphonomic modification and differential retention vs. the model of palaeobiological modification and selective destruction.

The purpose of the present work is to show that taphonomic alteration acts at different levels of organization and, as a consequence, it is convenient to employ a systemic and evolutionary approach in taphonomic analyses and interpretations. Several new concepts of evolutionary taphonomy, such as taphon and taphoclade, allow to give a non-tautological meaning to the concept of preservability or preservation potential.

Evolutionary taphonomy

Taphonomic 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 may be regarded as an extrinsic principle of regulation, which is able to fix the direction of evolutionary taphonomic processes. Representatives of new taphonomic groups appear during fossilization processes. Components of these taphonomic groups show different composition and structure from those biogenically produced, and they increase diversity of the fossil record. In every fossilization stage, the persisting taphonomic groups (or taphons) will be those whose preserved elements have been stabilized, transformed, and replicated with a higher effectiveness in the prior stages, but not the most resistant or those preserved elements less affected by environmental factors.

Taphonomic alteration deteriorates and eliminates the taphonomic elements of smaller durability, but it is also able to cause favourable modifications for the preservation and to produce new elements that represent new taphonomic groups, and it can be considered as a factor responsible for the fossilization. Some of the taphonomic alteration processes are of destructive effect, and some are of conservative effect (cf. Skelton, 1993: 574). Biological remains and traces, fossils or taphonomic elements, are not the only entities or units of taphonomic alteration. Alteration affects taphonomic entities at different level of organization, and can generate new entities, no longer limited to act as a sieve or filter destroying the taphonomic elements of smaller physical resistance, chemical stability or durability. Taphonomic alteration causes favourable modifications for the preservation and produces new taphonomic entities, besides sieving and retaining modified parts

of the initially produced taphonomic elements. From this point of view, it is considered that taphonomic alteration is a modifier force, not necessarily negative, that can become a generating force responsible for the appearance of new taphonomic elements of different chemical composition, representing new taphonomic groups and new taphons. Taphonomic alteration can be considered as a positive force and, therefore, as the primary cause of changes during fossilization. Functionality and evolution of taphonomic entities also have a relative importance as causal argument. From this point of view, the modifier action of the taphonomic alteration, the external environment and the relative behaviour of the taphonomic entities can be causal arguments to explain the mechanisms of fossilization. Not only the original architecture (composition and structure) of the taphonomic entities and their external environments, but also their modified architectures, the successive changes of the external environment and the functional or evolutionary activities carried out, have a causal role in the changes happened during fossilization.

This second approach is evolutionary and systemic, allowing to develop a theory of the fossilization denominated theory of taphonomic evolution (Fernández-López, 1982, 1984, 1988, 1989, 1991a,b, 1995, 1999, 2000). Taphonomic changes, selective preservation during fossilization and the resultant differential preservation occur as a consequence of taphonomic alteration, as taphonomic entities are fitted to the changes of their external environment. The composition and structure of taphonomic entities, as well as their functional or evolutionary activities and the environmental changes, can limit, restrict, hinder, attenuate, damage, diminish,

inhibit or prevent the preservation, but they can also condition, channel, facilitate, intensify, favour, enhance, activate or promote the alteration processes and the trends or the paths of fossilization processes. Taphonomic alteration causes the change and, as a result, taphonomic entities are preserved.

Taphonomic alteration

Differential destruction of taphonomic entities is just a particular case of taphonomic alteration that can be distinguished with the name of taphonomic sieve. Other cases of taphonomic alteration correspond to the differential modification of taphonomic entities, by causal interaction among the components and the external environment, giving rise to the selective preservation. Changes in differential preservation of two or more taphonomic entities during fossilization depends on both intrinsic and extrinsic taphonomic factors. Every taphonomic entity is subjected to the action of physical, chemical and biological agents from the external environment. Any component of the external environment able to act directly on taphonomic elements is an extrinsic or environmental taphonomic factor. However, the external environment is not the only source of taphonomic change or selection. Actual properties of taphonomic entities (such physical or real properties as their composition, structure and behaviour with respect to environmental changes) also intervene during taphonomic alteration.

Biological remains and traces or, in general, taphonomic elements are not the only entities or units of alteration. Taphonomic alteration also acts at supra-elementary levels, on entities or units of different duration. From a functional point of view, it

Taphonomic alteration

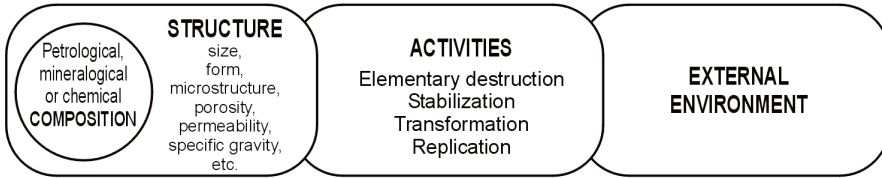
is accepted the existence of taphonomic entities of different level of organization: taphonomic elements, taphonic populations and taphonic associations (also called preserved associations; [Fernández-López, 1982, 2000](#)). From an evolutionary point of view, it is accepted the existence of taphons, which can constitute units of higher order called taphoclades (groups of taphons of common taxonomic origin). Taphonomic elements are basic entities of the taphonomic hierarchy and those of smaller duration (Fig. 1). The concepts of taphonomic element, taphonic population, taphon, taphonic association and taphoclade show increasing generality. Taphonomic alteration acts simultaneously on individuals (entities or units) at different levels of organization, and it causes changes and different results according to the levels. The same environmental factors of alteration determine different

modifications in the taphonomic entities of different level of organization. For example, dispersion of taphonomic elements can modify their geographic location, mechanical position, orientation and removal degree. However, dispersion of taphonomic elements can also cause changes in the density of taphonomic elements of each taphonic population or taphon, and in its geographic distribution, as well as in the proportions of representatives of each taphon, and it can modify the composition and structure of taphons and taphonic associations. During processes of taphonomic dispersion, which separate and disseminate the taphonomic elements, representatives of some taphons have been destroyed while others have reached new areas and environments, favouring the persistence of taphons constituted by allochthonous elements.

TAPHOCLADE	Taphonic composition	Taphoclade size Taphoclade density Taphoclade diversity Geographic distribution Temporal structure	Taphoclade destruction Disruptive fossilization Directional fossilization Stabilizing fossilization		Taphoclade effectiveness
TAPHON	Population composition	Taphonic size Taphonic density Taphonic diversity Geographical distribution Temporal structure	Taphonic destruction Taphonization Taphonic retention	Preservability or Preservation potential	Taphonic valence
TAPHONIC POPULATION	Elementary composition	Population size Population density Population diversity Geographic distribution Temporal structure	Population destruction Population disgregation Population aggregation Population development		
TAPHONOMIC ELEMENT	Petrological composition Mineralogical composition Chemical composition	Morphology: size, form, microstructure, porosity, specific gravity, etc. Geographic ubication Temporal structure	Elementary destruction Elementary aggregation Replication Transformation Stabilization Production	Redundance Durability	Taphonomic effectiveness
INDIVIDUALS CHARACTERS	COMPOSITION	STRUCTURAL PROPERTIES	FUNCTIONAL OR EVOLUTIONARY ACTIVITIES	DISPOSITIONAL PROPERTIES (capacities, aptitudes)	TAPHONOMIC ROLE (capacity use, effects, results of the activity)
ACTUAL PROPERTIES					

Figure 1. Characters of taphonomic individuals at different levels of organization of the taphonomic hierarchy.

CONSTRAINTS OF ELEMENTARY ALTERATION



RESULTS:

- 1) *Destruction of taphonomic elements.*
- 2) *Maintenance and transformation of taphonomic elements.*
- 3) *Formation of new taphonomic elements, even of new composition and structure.*

Figure 2. The composition and structure of taphonomic elements and the external environment are constraints of elementary alteration. Nevertheless, activities or functional properties of the taphonomic elements are also constraints of elementary alteration influencing their selective preservation. Many taphonomic elements have been destroyed by elementary alteration, but this alteration has also increased the variability of other taphonomic elements and has given rise to taphonomic elements of new architecture (composition and structure).

In fossilization, as in organic evolution (Gould, 2002: 636), changes at the different levels of the taphonomic hierarchy are allometric, nonfractal, and asymmetric. Changes at a low level may or may not have an effect at higher levels (upward causation), but alteration at upper levels must become extensive to the units included in the lower levels (downward causation; cf. Campbell, 1974). Production or alteration of taphonomic entities can also be a consequence of modifications happened in a lower level or in a higher level of complexity. Among such processes should be differentiated those of aggregation or disgregation of taphonomic entities and the evolutionary processes. Taphonomic systems of any level of organization have been able to arise during fossilization by a process of aggregation or disintegration of pre-existent taphonomic entities, or by an evolutionary process (Fernández-López, 1989). This approach increases the possibilities of analysis and synthesis in taphonomic research, justifying the distinction between taphonomic modifications

of two types: functional and evolutionary modifications.

Actual (physical, real or non-dispositional) properties of taphonomic entities and their interactions with the external environment allow to distinguish alteration processes at different levels. Taphonomic alteration can be of four types: elementary, populational, taphonic and taphocladal.

Elementary alteration

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 aggregate trait, 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. In turn, taphonomic

elements are the basic components of taphonic populations, taphons, taphonic associations and taphoclades, which respectively possess an elementary, population or taphonic composition.

Taphonomic alteration has changed the composition and structure of taphonomic elements of any taxonomic group from its production until its current state (Fig. 2). Selective preservation of taphonomic elements by destruction or differential modification is conditioned by the external environment, but also by the actual characters of taphonomic elements such as the architecture (composition and structure) and the functional properties (*i.e.*, stabilization, transformation and replication; Fernández-López, 1995, 2000: 87-90).

Taphonomic stabilization means maintenance of the composition and structure of taphonomic elements when they are subjected to environmental changes, by means of two strategies or mechanisms that can be combined: (1) realization of new functions or activities, counteracting the action of the external environment; and (2) acquisition of new structural characters, protecting the elements of the action exercised by the factors of taphonomic alteration (Fernández-López, 1995, 2000: 86, fig. 37). *Taphonomic transformation* denotes any process leading to changes in the properties of taphonomic elements. Taphonomic elements undergoing transformation can acquire new preservation states, changing the nature, the number or the disposition of their structural characters (by loss, substitution, addition or reordering of these characters). *Taphonomic replication* is the process by which a taphonomic element produces a copy of itself. It is the process by which one or more taphonomic elements are generated by a pre-existent taphonomic

element. During fossilization of a certain taphon, the appearance of new taphonomic elements can occur by simple replication, if one element is generated, or by multiple replication, when more than one elements are generated. The taphonomic elements that have acquired a new chemical composition and a structure should be considered as replicas, as new elements, and not as transformed elements. Concretionary internal moulds, pyritic moulds of ammonite shells, as well as impressions produced by some 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 taphons.

Taphonomic analyses of the functional properties mentioned before (stabilization, transformation and replication) allow describing the activities and behaviour of representatives of each taphonomic group, which are characterized by some particular actual and dispositional properties. In this kind of research, the functional properties, the activities or the short-term reactions of taphonomic elements should be distinguished from the dispositional properties, such as durability and redundancy.

Taphonomic durability means the capacity or probability of any taphonomic element to persist as an element of the same taphonomic class, as an element of the same taphon, being subjected to environmental changes (Fernández-López, 1982, 1991b, 2000). The term skeletal durability has been used by several authors to denote a capacity of the skeletal remains exclusively, whereas the concept of taphonomic durability is

applicable to any taphonomic element (cf. Chave, 1964; Behrensmeyer, 1978, 1984; Lawrence, 1979; Shipman, 1981, 2001; Flessa & Brown, 1983; Brett, 1990; Kowalewski, 1997; Butler & Schroeder, 1998; Kershaw & Brunton, 1999; Best & Kidwell, 2000; Simões *et al.*, 2000; Oyen & Portell, 2001; Seilacher *et al.*, 2001; Kidwell, 2002a,b; Nebelsick & Kroh, 2002; Pickering & Carlson, 2002; Behrensmeyer *et al.*, 2003; Brand *et al.*, 2003; Hoppe *et al.*, 2003; Kowalewski & Bambach, 2003; Kowalewski & Rimstidt, 2003; Robinson *et al.*, 2003; Smith, 2003; Zuschin *et al.*, 2003; Beavington-Penney, 2004; Hoffmeister *et al.*, 2004; Krause, 2004; Martínez-Delclòs *et al.*, 2004; Meléndez Hevia, 2004; Palanti *et al.*, 2004; Rodland *et al.*, 2004; Tomasovych, 2004a,b; Harvey & Fuller, 2005; Holmes *et al.*, 2005). Durability should not be mistaken with some actual properties of taphonomic elements such as hardness, tenacity, physical resistance or robustness. Possession of resistant hard parts is an obvious help for preservation in some environments, although it is not a guarantee; and lack or loss of hard parts does not necessarily imply non-preservation. Durability is a dispositional property, showing different values under different environmental conditions. Durability of a taphonomic element depends of environmental conditions, and in a particular environment can persist the softest and fragile taphonomic elements, whilst the elements of highest hardness and robustness are destroyed. For example, in euxinic and anoxic environments, calcareous elements usually disappear before phosphatic or organic ones; on the contrary, in alkaline and oxic environments, organic remains can become completely destroyed when inorganic (calcareous or phosphatic) ones still persist.

Although durability of taphonomic elements is not a measurable property, the concept is useful in taphonomy because it allows using the relative concept of degree of durability of taphonomic elements of a certain class, taphon or taphoclade and estimating its corresponding values taking in mind their actual properties. It is also possible to predict the variation of the degree of durability of elements of a certain taphonomic group after an environmental change, and it is possible to assess if the degree of durability of representatives of a taphon is higher or lower with respect to other, taking in account data obtained from the fossil record, as well as experimental and natural setting observations. For example, in the cases when destruction of taphonomic elements takes place by abrasion, it is possible predicting and testing that the degree of durability usually diminishes with the increasing size or decreasing sorting of the abrasive particles. On the other hand, elements of the same taphonomic group being more spheroidal, with finer and more compact microstructure, and with a smaller amount of organic matter usually have higher degree of durability to abrasion than discoidal elements, with porous microstructure. Nevertheless, other factors such as the size of taphonomic elements, their concentration, their packing pattern or the differential attack by alterative agents can also affect the degree of durability of representatives of a taphonomic group. In this sense, the concept of half-life or the mean value of the time in which taphonomic elements of a certain taphonomic group remain as recognizable elements serves as indicator of the degree of durability of elements of such taphonomic group (cf. Cummings *et al.*, 1986; Meldahl, 1987; Davies *et al.*, 1989; Kidwell, 1989, 2002a,b;

Fernández-López, 1991b, 2000; Petrovich, 2001; Kowalewski & Bambach, 2003; Kowalewski & Rimstidt, 2003; Tomasovych, 2004b).

Biological redundancy is the capacity of organisms to give rise to multiple evidence of their existence, whereas *taphonomic redundancy* is the capacity of taphonomic elements to repeat the same message or to give rise to multiple evidence of their existence (cfr. Tasch, 1965, 1969, 1973; Lawrence, 1968; Beerbower & Jordan, 1969; Holtzman, 1979; Fernández-López, 1982, 2000). Taphonomic redundancy, as well as replication, does not imply that every resulting element is identical to the original element before being replicated, but only that it is of the same taphonomic class and (para-)taxonomically significant. In accordance with these ideas, production of taphonomic elements can result from redundancy and replication of a pre-existent taphonomic entity. The concept of redundancy is of taphonomic interest because it allows estimating different degrees of redundancy in representatives of different taphonomic groups under particular environmental conditions, on the basis of their actual properties. It is also useful to predict the variations in the degree of redundancy of the elements of a certain taphonomic group according to environmental changes, and it is possible to assess if the degree of redundancy of representatives of a taphon is higher or lower than the degree of another under some particular environmental conditions, keeping in mind data obtained from the fossil record, in modern environments or by experimentation. It is not the absolute value of durability or redundancy of taphonomic elements that is important in taphonomic

alteration, but their relative value. Elements of a particular taphonomic group will be favoured by alteration only if they are more durable and/or redundant than others.

Other relevant problems, different to those of analyzing the functional properties of taphonomic elements, are those related to the use that elements have made of their capacities, to the results or effects of the activities carried out by the elements, or to the taphonomic role that has had a taphonomic property. The capacity that have had the taphonomic elements to perpetuate their characters, by stabilization, transformation and/or replication, as well as the effects or results that the elements have achieved by their durability and redundancy, are represented by their taphonomic effectiveness. *Taphonomic effectiveness* is the use made by taphonomic elements of their durability and of their redundancy. Some elements have given rise to multiple evidence of their existence, whereas others have disappeared without leaving any evidence. Although it is probable that the elements of the same taphonomic group being differentially effective due to their structural and behaviour differences, it is possible to consider the taphonomic effectiveness of representatives of a certain taphonomic group or taphon, or the effectiveness that they have had to be stabilized, transformed and/or replicated. Taphonomic effectiveness can be assessed keeping in mind the taphonomic survival (*i.e.*, the proportion of taphonomic elements persisting after an environmental change). The degree of taphonomic effectiveness can be estimated by the proportion of elements preserved after an environmental change, with respect to the total number of taphonomic elements before the change. However, it should be remarked that a higher taphonomic effectiveness

of elements does not guarantee a better preservation of the taphon or of the taphoclade. Taphons or taphoclades composed of taphonomic elements that have had higher degree of durability and/or redundancy in a phase of the fossilization process might not be the most preservable. The taphonomic effectiveness of representatives of a taphon or taphoclade in a particular environment can be expressed by their degrees of durability and redundancy, but taphonomic effectiveness does not allow to interpret the differential preservation or the selective preservation between representatives of different taphons or taphoclades. Moreover, the range of tolerance and the degree of taphonomic effectiveness of representatives of the same taphon can be different in different places of their area of geographic distribution. A certain taphon may be eurytopic in their optimal environment and stenotopic in another region where some restrictive factor plays the maximal influence (Fernández-López, 1991b, 2000). Taphonomic effectiveness can also vary within a taphon or taphoclade, when undergoing evolutionary modifications. The process of taphonomic evolution allows explaining the persistence of some taphonomic elements under environmental conditions beyond the limits of tolerance of the biogenically produced taphonomic elements. For example, in the Iberian Basin during the Middle Jurassic, some reelaborated, concretionary internal moulds of ammonites persisted in supratidal environments, beyond the limits of tolerance of the aragonitic shells, and formed local concentrations of moulds before being definitively buried.

Examples of elementary alteration that can be observed in the fossil record correspond to cases of differential modification,

and in particular of replication, transformation and stabilization, rather than of differential destruction. The two main ways of elementary alteration observed in the fossil record result from differential durability and redundancy of taphonomic elements. Secondary structural characters, appeared by taphonomic alteration, due to processes of maximum stabilization and minimum transformation giving rise to persistence of the original architecture of taphonomic elements represent the elementary changes of smallest magnitude, whereas new architectures arisen by maximum transformation and simple replication correspond to the elementary modifications of greatest magnitude.

Supra-elementary alteration

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 vary or undergo transformation (by changing their structural characters) whereas taphonic populations or taphons can evolve (by changing the architecture of their taphonomic elements). 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. On the other hand, in any taphon or taphonic association there will be elements with higher durability and/or redundancy than others in the face of physical, chemical and biological factors responsible for their alteration. The intra- and intertaphonic variability and the differential preservation observable in the fossil record are properties determined by alternative factors (*i.e.*, by extrinsic factors of regulation), but they are also influenced by intrinsic factors (*i.e.*, by palaeobiological, of production and taphonomic factors that have previously acted).

In taphonomy, the terms *preservability* or *preservation potential* (capacity or potential to be preserved) mean the probability of a certain taphonomic entity to be preserved in the geological record (cf. Müller, 1951, 1979; Behrensmeyer,

1978, 1984; Shipman, 1981, 2001; Fernández-López, 1982, 1992, 2000; Janin, 1983; Behrensmeyer & Kidwell, 1985; Whittington & Conway Morris, 1985; Brett & Baird, 1986; Peebles & Lewis, 1988; Wilson, 1988; Andrews, 1990; Allison & Briggs, 1991; Donovan, 1991, 2002; Kidwell & Boscence, 1991; Berger & Strasser, 1994; Lymann, 1994; Butterfield, 1995, 2003, 2005; Kidwell & Flessa, 1996; Meléndez *et al.*, 1996; Haglund & Sorg, 1997; Meléndez, 1997; Perry, 1998, 1999; Powell *et al.*, 1998; Trapani, 1998; Martin, 1999; Moffat & Bottjer, 1999; Nebelsick, 1999; Benton *et al.*, 2000; Brachert & Dullo, 2000; Harding & Chant, 2000; Kidwell & Holland, 2000; Zuschin *et al.*, 2000, 2003; Bell *et al.*, 2001; Bradshaw & Scoffin, 2001; Jones *et al.*, 2001, 2004; Zuschin & Stanton, 2001; Bandyopadhyay *et al.*, 2002; De Renzi *et al.*, 2002; Holz & Simões, 2002; Kidwell, 2002a,b; Nebelsick & Kroh, 2002; Rickards & Wright, 2002; Schieber, 2002; Badgley, 2003; Curran & Martin, 2003; Delvene, 2003; Greenstein & Pandolfi, 2003; Harper, 2003; Kroh & Nebelsick, 2003; Lockwood, 2003; McKinney, 2003; Nielsen & Funder, 2003; Noffke *et al.*, 2003; Smith & Nelson, 2003; Tsujita, 2003; Trueman *et al.*, 2003; Gupta & Pancost, 2004; Martin *et al.*, 2004; Martínez-Delclòs *et al.*, 2004; Messina & Labarbera, 2004; Schweitzer, 2004; Tapanila *et al.*, 2004; Terry, 2004; Tomasovych, 2004ab; Waugh *et al.*, 2004; Wings, 2004; Gaines *et al.*, 2005; Jensen *et al.*, 2005; Smith *et al.*, 2005; Weissbrod *et al.*, 2005; Zhu *et al.*, 2005). The taphonomic preservability or preservation potential cannot be reduced to a qualitative concept, as the concept of durable, resistant or robust used by some authors to distinguish among species, organisms or remains preservable and non-preservable. It is a relative and dispositional

property of each taphon that must be compared with respect to an environment or a group of environments that temporarily ranges from the appearance of the taphonomic entity until the current obtention of evidence in the fossil record. If preservability is understood exclusively as a relative and dispositional property of taphonic populations, taphons or taphoclades, not of taphonomic elements, then this concept is no longer tautologic. In accordance with this meaning, both taphonomic effectiveness and preservability depend on durability and redundancy, but they are not linked to each other by a relationship of causality. Every taphonomic modification representing an increase in preservability implies an increase of taphonomic effectiveness, but a higher effectiveness may not be associated with an increase in preservability.

The selective preservation of some taphons can be interpreted on the basis of the processes of taphonic retention and taphonization. The term *taphonic retention* denotes the processes by which the composition and structure of taphons are maintained unchanged, preventing their destruction by environmental changes, as a consequence of the stabilization and transformation of its taphonomic elements. Taphonic retention should be understood as a process, not as a mere persistence of taphons. Maintenance of taphons during taphonomic alteration (i.e., the taphonic retention) take place by modification processes, such as the stabilization and the transformation of taphonomic elements. However, the degree or the rate of retention of a taphon and the differential retention among taphons cannot usually be reduced to elementary properties or characters because they depend on supra-elementary structural

characters (e.g., population size, density and diversity, or geographic distribution of the considered taphon). The cause of differential retention should be looked for in factors or forces that have promoted this result either directly (by the properties of taphons) or indirectly (due to the properties of taphonomic elements and taphonic populations) and have given rise to processes that can be denominated of stabilizing or normalizing alteration. For example, some taphons are not destroyed or changed, or they make it in minimum degree, because they may stay in more stable environments, because they may have a more stable composition and structure, by some internal or functional inability to change, because the taphonomic elements undergo processes or carry out activities that counteract the action of the external environment, because the taphonomic elements have acquired new structural characters protecting them of the action of alterative factors and/or because the elements have acquired new preservation states by changing the nature, the number or the disposition of their structural characters. Environmental tracking, for example, is a strategy of taphons allowing them to counteract the destructive action of the external environment and to achieve taphonic retention. It basically consists in reacting to adverse environmental conditions arisen in their area of geographic distribution going until more favourable environments, instead of being modified or destroyed in consonance with the environmental change. Dispersion of taphonomic elements or nekrokinosis processes are not necessarily destructive, and they can increase the degree of taphonic retention and the preservability of taphons.

Taphonomic alteration

The formation of new taphonomic groups is denominated taphonization, and it is what allows the demarcation of taphons (Fernández-López, 1989, 1991b, 2000). *Taphonization* is the production of one or more taphonic populations of a new taphon. Taphons can be produced by palaeobiological entities or by taphonomic entities. The origin of taphons by taphonomic alteration, the taphogenic taphonization, take place by processes of modification of taphonomic elements, such as the transformation and the replication. Taphons can be stable during long intervals of geologic time or undergo structural modifications and even give rise to new taphons constituted by taphonomic elements of different composition and structure. New taphons arise during fossilization by transformation and/or replication of taphonomic elements belonging to previous population (sub)groups (Fig. 3). It is possible to distinguish between the taphonization due to accumulation of changes or continuous modification of a taphon by transformation of their taphonomic elements (simple taphonization) and the taphonization due to a process of division and appearance of one or more new taphons by replication of their taphonomic elements (multiple taphonization) that have taken place by directional alteration or by disruptive alteration, respectively. Nevertheless, some taphons do not change or make it in minimum degree, and they are not destroyed, as a result of processes of taphonic retention and stabilizing or normalizing alteration.

According to the ideas above, morphological characters of taphonomic elements are insufficient to explicit the meaning of the term taphon; besides the morphological criteria, other structural and genetic criteria are required. Analogous concepts at the level of taphon of the

appearance and destruction of taphonomic elements are the appearance and destruction of taphons, that can be denominated taphonization and taphonic destruction, respectively. Taphonic destruction is the disappearance of a taphon without producing any new taphon.

Taphonization can be considered as the analogous process, at the taphon level, of the appearance of a new taphonomic element. However, these concepts present structural differences. The appearance of new taphonomic elements will be required in each case of taphogenic production or replication, but such new elements may have or not different architecture (composition and structure) and may represent or not new mechanisms of elementary behaviour. On the contrary, the appearance of a new taphon by taphonomic alteration, or every event of taphogenic taphonization, implies some kind of differentiation in the composition and structure of the new generated, descendant taphon, with respect to the producer, original taphon. On the other hand, the appearance of new taphons may take place either by a gradual change, or else by a punctuated, in frequencies and types of characters of a taphonic population. Two taphonic populations do correspond to different taphons when they display some properties promoting or involving different behaviour with respect to the durability and/or redundancy of their constituent elements. Consequently, taphons are spatio-temporally limited (they have appeared and may be destroyed) being the taphonization what allows to demarcate them. Each taphonomic element is unique, and each taphon is unique too. Taphons or taphoclades could be considered as abstractions but, as they represent the natural order resultant of functional or evolutionary taphonomic

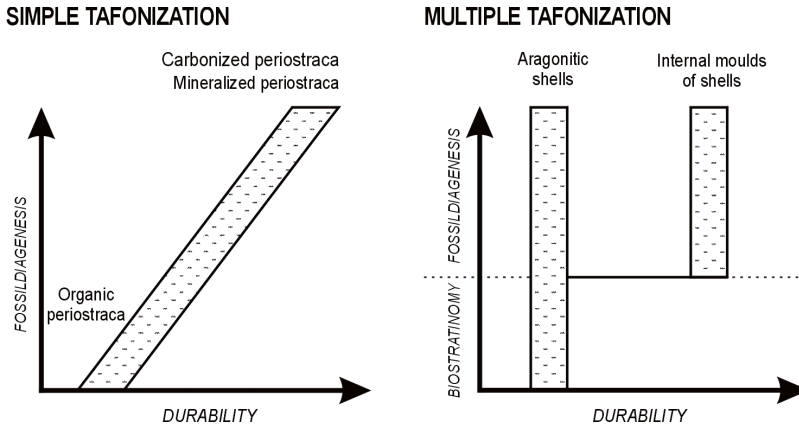


Figure 3. Patterns of taphonization during fossilization. The formation of a new taphon from a previous one, or taphogenic taphonization, can be by continuous modification of a taphon in other (simple taphonization) or by multiplication of a taphon, appearing one or more new taphons (multiple taphonization). For example, in the case of ammonites, some periostraca were progressively carbonized or mineralized during fossilization, forming pseudomorphs of different composition, structure and durability, with respect to the original organic periostraca. These carbonized or mineralized periostraca represent new taphons, arose by simple taphonization. On the other hand, sedimentary internal moulds of ammonite shells formed at the beginning of the fossilization show different composition, structure and durability that aragonitic shells from which they have been formed by multiple taphonization.

processes, they are not conventional or arbitrary classes of similar elements.

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. The diversity of interactions between taphonomic entities and their external environment results in taphonic alteration leading to change or to constancy, depending on whether the environment undergoes any change or not, and depending on the nature of that change. When relationships between taphonic populations of a certain taphon and their external environment remain stable, the alteration is stabilizing or normalizing and, as concomitant process, the fossilization is stabilizing or normalizing. A certain sequence of interactions between the

taphonic populations and the external environment showing a constant change in the same sense, will lead to directional alteration and, as concomitant process, to directional fossilization. This continuous evolutionary trend can result from repeated retroactive interactions between preserved and altered taphonomic elements. Diversification of an initially homogeneous environment in turn, will lead to a subsequent diversification of interactions between taphonic populations and their respective environments. This will result in a process of disruptive alteration and their concomitant disruptive fossilization. When the origin of the taphons take place by multiple taphonization and disruptive alteration, it is possible to consider the new produced, descendant taphons as evolutionary entities with real, non-

Taphonomic alteration

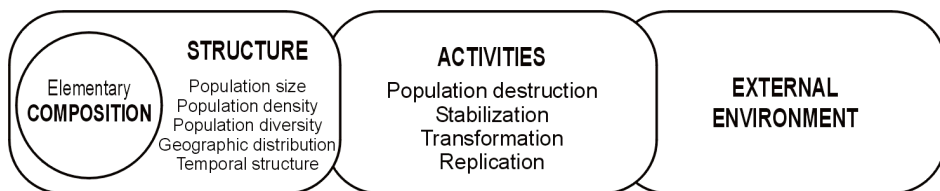
conventional limits. In contrast, if the new taphons arise by simple taphonization (gradual modification by transformation) and directional alteration then the direction of alteration in the taphonic populations and the pattern of temporal variation during the period of existence of the taphon will reflect the intrataphonic morphological changes in the course of a genealogical trend, allowing only a conventional delimitation, but not necessarily arbitrary, of successive segments.

Populational alteration

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. Taphonic populations can be analyzed on the basis of their elementary composition (i.e., of their integrating taphonomic elements) and their structural properties: size, density, diversity, geographic distribution and temporal structure of the taphonic population (Fig. 1). Population size is the total number of taphonomic elements composing a taphonic population. Population density is the average number of taphonomic elements of a particular taphon per surface or volume unit in the area occupied by the taphonic population. Population diversity is the variety or dissimilarity of types of preservation state or taphomorphotypes (including taphomorphs sensu [Crampton, 2004](#)) composing a taphonic population. It can be estimated by the values of the population richness (i.e., the number of types of preservation state or taphomorphotypes) and/or the population

CONSTRAINTS OF POPULATIONAL ALTERATION



RESULTS:

- 1) *Destruction of taphonic population.*
- 2) *Maintenance and transformation of taphonomic elements of the same taphon, by group effect.*
- 3) *Formation of new taphonomic elements, even of new composition and structure, by group effect.*

Figure 4. Populational alteration represents the group effect on durability and redundancy of taphonomic elements of a same taphon. Populational alteration can cause destruction or local modification of taphonomic elements of the same taphon. Selective preservation by populational alteration has influenced in the formation of a great variety of taphonic associations that can be grouped in two categories, as effects of stabilization processes prevail on those of replication. These two categories of taphonic associations correspond respectively to the so-called conservation fossil-lagerstaetten and concentration fossil-lagerstaetten.

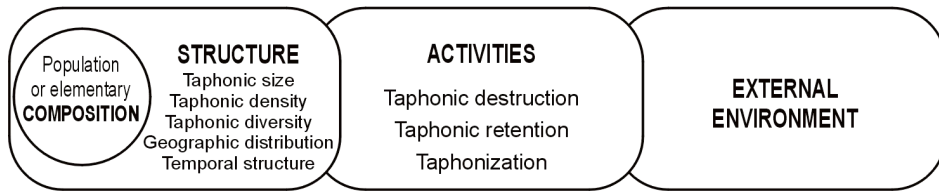
evenness (i.e., the similarity of types of preservation state or taphomorphotypes in relative abundance).

Alteration of taphonic populations can be due to destruction or modification of taphonomic elements (by upward causation) as well as to destruction or modification at the population level (populational alteration). *Populational alteration* represents the group effect on the capacity or aptitude to be preserved (durability and redundancy) of taphonomic elements of the same taphon (Fig. 4). The degree of durability and the degree of redundancy of the representatives of a taphon can be conditioned by intrinsic populational factors such as size, density, diversity and populational geographic distribution. For example, interactions among taphonomic elements have influenced in the taphonic populations, as well as in the composition and structure of taphonic associations. During taphonomic alteration, the density of a taphonic population or the regional density of a taphonic association (average of taphonomic elements per surface or volume unit in the area occupied by the taphonic association) can be a limiting constraint of its geographic distribution, if it reaches very high or very low values. An increase in the concentration of organic remains can locally reduce the concentration of available oxygen and inhibit the processes of aerobic biodegradation (Allison & Briggs, 1991). Some cases of differential preservation observed in common graves among the elements being located in a more internal position in the group are due to the greater concentration of taphonomic elements, and some cases of differential preservation among the common graves of greater population size and density result from populational alteration. On the other hand, a

higher concentration of skeletal remains increases the degree of cohesion and permeability of the sediment, hinders the activity of the burrowing macroorganisms, and can favour the differential mineralization of the remains constituting an association (Kidwell & Jablonski, 1983). Consequently, some fossiliferous concretions can result from processes of populational alteration, by differential mineralization of taphonic populations of higher size and density. However, regroupment processes increasing the concentration of taphonomic elements conditioned by their own structural properties (for example, the discoid form) can also promote the differential destruction of elements of the same taphon, when they hinder or prevent the sedimentary filling of internal cavities or the sedimentary replication by means of external moulds of the taphonomic elements.

Taphonomic alteration by differential durability, differential redundancy or selective destruction of taphonomic elements in relation with some structural character of the taphonomic population represents a genuine populational alteration. Modification or destruction of taphonic populations conditioned by such characters as population density or geographical distribution, cannot be attributed to elementary alteration, because taphonomic elements do not have population density. Neither can the geographic distribution of a taphonic population be correlated with the size of the component elements. Nevertheless, destruction of taphonic populations can be explained in many cases as consequence of a mere destruction of taphonomic elements, and can be causally reduced to the elementary level. In general, any taphonomic character of a taphonic population conferring it a capacity or aptitude irreducible

CONSTRAINTS OF TAPHONIC ALTERATION



RESULTS:

- 1) Destruction of taphons (anatomical elements without fossil record).
- 2) Maintenance and transformation of taphons (stabilized and transformed anatomical elements).
- 3) Formation of new taphons (replied anatomical elements).

Figure 5. Taphonomic alteration acts on taphons and can cause their destruction or their microevolutionary modification. Actual properties of taphons (composition, structure, function and evolution) and successive external environments determine their preservation potential. Taphonomic alteration can destroy some anatomical elements of a certain taxonomic group (species or genre, for example), at the same time that retains or replicates other anatomical elements of the same taxonomic group. Taphonomic alteration can stabilize and transform elements of some taphons, as well as it can generate new taphons, of different composition and structure, and of higher preservation potential.

to elementary properties by interaction with the external environment allows a process of populational alteration, being or not emergent the character in question.

The two main ways of populational alteration observable in the fossil record are due to differences in durability and redundancy. Populational alteration will favour the taphonic populations and the taphons that (a) generate stabilized or transformed taphonomic elements in changing local conditions, that maintain their composition and structure (bias of persistence by differential durability) and/or (b) produce more replicated taphonomic elements, of the same or of different composition and structure (bias of multiplication by differential redundancy). In general, the more different the architecture of stabilized, transformed or replicated elements of a taphonic population, the greater their variability, and the higher will be the number of environments in which the taphonic

population can be preserved. Populational alteration is important because it can promote intrataphonic trends, as well as channel the diversity and the differential preservation of populations of the same or of different taphon. The selective preservation by populational alteration has influenced in the formation of a great variety of taphonic associations, that can be included in two categories, in accordance with the prevailing effects of stabilization or replication processes. These two categories of taphonic associations correspond respectively to the so-called conservation and concentration fossil-lagerstätten (cf. [Seilacher et al.](#), 1985; [Seilacher](#), 1992).

Taphonic alteration

Taphons can be analyzed on the basis of their population composition (the composition of taphonic populations composing the taphon) or their elementary

composition (the composition of taphonomic elements composing the taphon) and their structural properties: size, density, diversity, geographic distribution and temporal structure of the taphon. Taphonic size is the total number of taphonomic elements composing a taphon. Taphonic density is the average of taphonomic elements of a particular taphon per unit of surface or volume in the area occupied by them. Taphonic diversity is the variety or dissimilarity of types of preservation state, taphomorphotypes or subtaphons of a taphon. It can be estimated by means of the taphonic richness and/or the taphonic evenness. Taphonic richness is the number of types of preservation state, taphomorphotypes or subtaphons of a taphon. Taphonic evenness is the similarity of types of preservation state, taphomorphotypes or subtaphons of a taphon in relative abundance.

Alteration of taphons can be due to destruction or modification of taphonomic elements (by upward causation), as well as by destruction or modification processes at taphonic level (taphonic alteration). *Taphonic alteration* means selective preservation of entities or evolutionary units (taphonic populations, taphons and taphoclades) due to supra-elementary actual properties conferring them different capacity (differential taphonic retention, differential taphonization and preservability) to interact with the respective external environments (Fig. 5).

Taphonic destruction, the disappearance of a taphon without producing new taphons, implies the disappearance of all the taphonomic elements, anatomical components or parts with a certain architecture representing one or more species and, accordingly, the corresponding supraspecific taxa. Destruction of taphons can result from

destruction of taphonomic elements. However, the selective destruction of taphons or the rate and degree of destruction of a taphon are not reducible to elementary characters if they depend on supra-elementary characters (e.g., population or taphonic size, density, diversity and geographic distribution).

Taphogenic taphonization and taphonic retention require the modification of taphonomic elements. However, relative values of these properties (differential taphogenic taphonization among taphons or selective taphonization, rate of taphonization or degree of taphonization of a taphon, as well as differential taphonic retention, rate of taphonic retention or degree of taphonic retention) usually are not reducible to elementary characters because they depend on supra-elementary structural characters such as population or taphonic size, density, diversity and geographic distribution.

In consequence, taphonic destruction and selective modification at the taphon level, as well as preservability, should be analyzed as properties dependent on supra-elementary characters, not reducible to elementary characters. Changes during fossilization by taphonic retention, taphonization or taphonic destruction related with some supra-elementary structural property represent a genuine taphonic alteration. Alteration of taphons due to supra-elementary properties, such as the geographic distribution of a taphon or the population density, should be distinguished from, and cannot be attributed to, elementary alteration. In the case of ammonites, selective preservation of ammonite shells of a certain species or genus correlated with structural differences at the taphon level, such as the different geographic distribution of each taphon, implies processes of taphonic alteration. Taphonic alteration implies

correlation between a supra-elementary character, being or not emergent, and the capacity to be preserved or the aptitude at the taphon level.

Taphonomic alteration also acts on taphons and, in such cases, tends to eliminate those of smaller preservability. Constraints due to the architecture (composition and structure) of taphonomic elements influence on the alteration of taphons and in the fossilization processes. However, characters increasing the durability and/or the redundancy of taphonomic elements do not necessarily increase the preservability, cause the taphonic retention and/or taphonization or prevent the destruction of taphons and taphoclades. To explain the fossilization processes and taphonomic trends it is necessary to keep in mind the different capacities of taphonomic elements (durability and redundancy), but also the different capacities of taphons (preservability, differential retention and differential taphonization). Elementary alteration and taphonic alteration should be treated as different processes that can act in opposite directions. Elementary alteration can act against taphons, worsening the architecture of taphonomic elements and reducing the longevity of taphons. In other cases, however, elementary alteration may contribute to increase the longevity of taphons (improving the architecture of taphonomic elements, for example) or it may not affect them. In consequence, elementary alteration can affect or not the taphons.

The present concept of taphonomic alteration assumes that every new specific taphon is produced and maintained due to some advantage on the remaining ones, whilst the less favoured forms are destroyed. However, taphonomic alteration

does not guarantee their preservation in any circumstance, and if the external environment undergoes rapid and deep changes, these alterations can exceed the preservation potential and result in the destruction of taphons. If the taphonic valence is defined as the result of the capacity of any taphon to be preserved in different environments, or the result of the activities developed by taphons, then the taphonic valence is the expression of the preservability that have had the different taphonic populations of one taphon when they have been in different environmental conditions. A taphon of weak taphonic valence has been able to resist only small variations of limiting environmental factors, and will be called stenoic. For the same reasons, those taphons that have been able to be preserved in very variable or different environments will be called euryoic. Taphons of high taphonic valence, euryoic taphons, will be able to present a wide geographic distribution and they will be eurycore, whereas the stenoic ones will probably occupy restricted geographical areas and will be stenocore. Taphonic valence allows characterizing taphons, but the concept of taphonic valence cannot explain the geographical distribution of taphonomic elements or taphons (Fernández-López, 1991b, 2000; De Renzi, 1995). Concepts of taphonomic effectiveness and of taphonic valence allow setting out problems referring to the factors of preservation of a taphon in an area or region. They are useful concepts to describe and treat problems related to preservability.

Main ways of taphonic alteration observable in the fossil record result from differential preservation by taphonic retention and taphonization. Secondary characters appeared by taphonic alteration and taphonic retention resulting from maximum stabilization or minimum

transformation represent supra-elementary changes of smaller magnitude, whereas characters resulting from taphonization by maximum transformation or by simple replication correspond to the taphonic modifications of highest magnitude. The magnitude of changes in the architecture (composition and structure) of taphonomic elements during fossilization is correlated with the magnitude of taphonization processes. Taphonic alteration will favour taphonic populations, taphons or taphoclades producing more novel taphons (bias of multiplication by differential taphonization) and/or generating preservable types under changing local conditions (bias of persistence by differential retention of taphons and subtaphons). As a general rule, the more different the variability of taphonic populations of a taphon or the variability of taphons of a taphoclade, the greater the number of environments in which the taphonomic group will be able to be preserved. The importance of taphonic alteration lies in its power to promote intertaphonic trends and to channel the diversity and the differential preservation between taphons of the same or of different taphoclade.

From the systemic and evolutionist point of view, presented and defended here, it is also possible to distinguish functional or alterative taphonomic factors from evolutionary taphonomic factors, taking into account their effects on taphonomic entities. Alterative or functional factors influence on functional properties of taphonomic elements and the geographical distribution of taphons, leading even to their disappearance, whereas evolutionary factors promote the appearance of evolutionary modifications, favouring the durability and/or redundancy of taphonomic elements as a

reaction to environmental changes. The variability of taphonomic entities changes due to the introduction of novelties and/or by taphonomic alteration of the existent variants. Alterative or functional taphonomic modifications take place by stabilization, transformation and/or replication of taphonomic elements, as well as by development, aggregation or disgregation of taphonomic entities. Evolutionary taphonomic modifications take place by taphonic retention and/or taphogenic taphonization of taphonomic groups. Novelties arisen in the organic evolution correspond to mutations and adaptations, whereas novelties appeared during fossilization originate from taphogenic production and taphonomic alteration. Functional properties of taphonomic entities depend on, or result from, structural properties. And the taphonomic role played by every taphonomic entity is the result of the interactions maintained with the external environment. But what determines the behaviour of each taphonomic entity is a complex of actual conditions resulting from the previously happened taphonomic modifications. Therefore, within taphonomic analyses and interpretations a distinction should be made between changes in composition and structure, changes in behaviour or function, and evolutionary modifications. Among evolutionary taphonomic modification, in turn, it is possible to discern between micro- and macroevolutionary taphonomic processes.

Taphocladal alteration

A taphoclade is a group of taphons of common (para)taxonomic origin (Fig. 6). Taphoclades can present genetically differentiated parts, called subtaphoclades, and constitute taphocladal groups. A subtaphoclade is a biogenically produced taphon and, as

Taphonomic alteration

appropriate, the ulterior phyletically derived taphons. Subtaphoclades can represent types of anatomical components or parts of past organisms. In turn, a taphocladal group is a group of taphoclades of common (para) taxonomic origin. Taphoclades and taphocladal groups can be of specific or supraspecific category, according to the (para)taxonomic level of reference. Every unit of these types, with the sole exception of the smallest one, includes subordinate units and (except for the largest) is in turn included in a higher order unit. 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. For example, the different taphons of the ammonite species *Trimarginia iberica* constitute a specific taphoclade, whereas the different taphoclades of the species of the genus *Trimarginia* constitute a specific taphocladal group. Taphoclades can be analysed on the basis of their taphonic composition and structural properties: size, density, diversity, geographical distribution and temporal structure. Taphocladal size is the number of taphonomic elements composing a taphoclade. Taphocladal density is the average number of taphonomic elements of a taphoclade per unit of surface or volume in the area occupied by them. Taphocladal diversity is the variety or dissimilarity of taphons composing a taphoclade. Taphocladal diversity can be estimated according to the taphocladal richness (i.e., the number of taphons) and/or the taphocladal evenness (i.e., the similarity of taphons in relative abundance). In describing and interpreting some taphoclades it can be also useful the concept of subtaphocladal diversity, understood as the variety or dissimilarity of subtaphoclades composing a taphoclade.

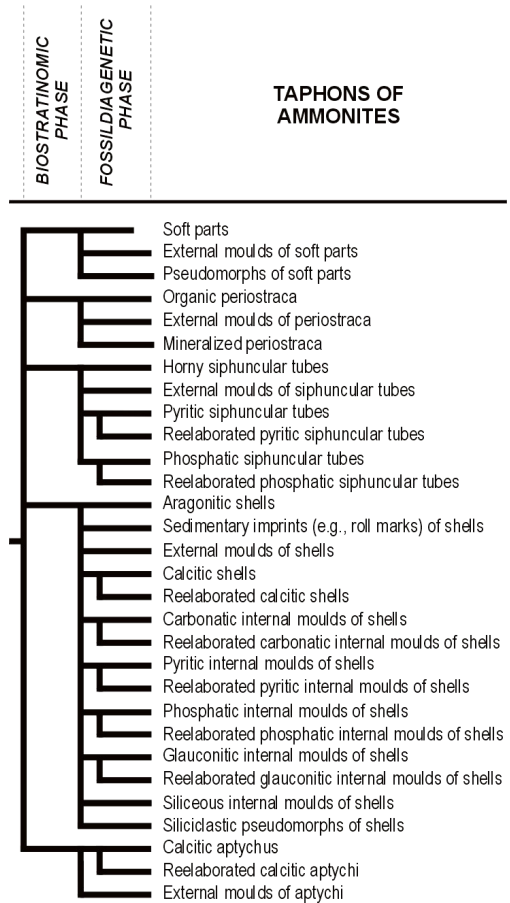


Figure 6. Schema of the taphoclade of the order Ammonitida (Triassic-Cretaceous). At the present time, more than 30 ammonite taphons are known, from pseudomorphs of soft parts or organic periostraca more or less carbonized until external moulds of aptychi. Taphons represented in this figure correspond to 5 subtaphoclades (i.e., soft-parts, periostraca, siphuncular tubes, shells and aptychi). These subtaphoclades and taphons represented in the figure constitute a paraphyletic group, because some subtaphoclades and taphons that correspond for example to anaptychi, stomach contents or ammonite coprolites observed in the fossil record are not included.

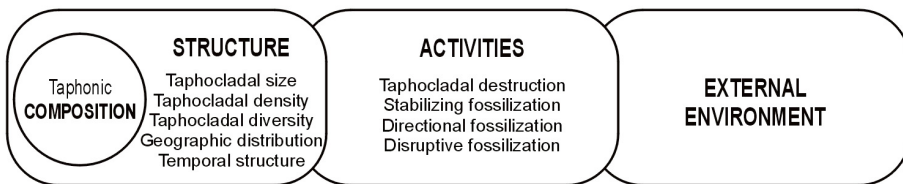
Every taphoclade has a taphonic composition, being constituted by taphons,

and some structural characters, which can influence on the capacity of preservation of the taphons that compose it or in the aptitude at the taphon level (differential taphonic retention and/or differential taphonization). *Taphocladal alteration* implies destruction or modification of taphoclades (Fig. 7). Taphocladal destruction means the disappearance of one or more taphoclades without producing new taphons. The taphocladal destruction implies the disappearance of all the taphonomic elements representing one or more species and, in such case, the corresponding supraspecific taxa. The taphonomic alteration by taphonic retention, taphonization or taphonic destruction related with some structural character of a taphoclade represents a process of taphocladal alteration. Examples of taphocladal alteration are those cases of selective preservation correlated with the area of distribution of the taphoclade or of the taphocladal group, and not with the particular distributions of the integrating elementary taphons. For example, the selective preservation of

taphoclades generated by each ammonite species or genus is conditioned by the area of distribution of the corresponding taphoclade, not by the particular geographic distribution of some of the integrating taphons. Taphocladal alteration will favour those taphons and taphoclades producing more elementary taphons (bias of multiplication by differential taphonization) and/or generating preservable types under changing local conditions (bias of persistence by differential retention of taphons and subtaphoclades). Taphocladal alteration can promote intrataphocladal trends, or else channel the diversity and the differential preservation among taphoclades of the same or a different taphocladal group.

From the theoretic and methodological point of view, it is useful to distinguish between alteration of taphonomic elements of the same or different taphon, and alteration of taphons of the same or different taphoclade. Alteration of taphonomic elements of the same or of different taphon is conditioned

CONSTRAINTS OF TAPHOCLADAL ALTERATION



RESULTS:

- 1) *Destruction of taphoclades (taxa without fossil record).*
- 2) *Maintenance of taphoclades (taxa with "unaltered fossils").*
- 3) *Modification and diversification of taphoclades (taxa with "varied fossils").*

Figure 7. Taphocladal alteration directly affects to taphoclades, causes macroevolutionary taphonomic modifications, and can modify or destroy all the taphonomic elements of a species or of a supraspecific taxon. The composition and structure of taphoclades impose conditions on the preservation potential of taphons and can channel stabilizing, directional or disruptive taphonomic trends, giving rise to "unaltered fossils" and "altered or varied fossils".

Taphonomic alteration

by the respective values of elementary destruction, durability and redundancy. Alteration of taphons of the same or of different taphoclade 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 (the differential success) of taphonomic elements. On the other hand, taphocladal alteration and macroevolutionary taphonomic changes are impelled by differential taphonic retention and taphonization (the differential success) of taphons. 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. During taphonomic alteration, some trends can harm to taphoclades although they favour the preservation of 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; therefore, they were favourable environments for the preservation of some ammonite taphons. 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 taphoclades during the early fossilization. Consequently, marine environments of high sedimentary rate were unfavourable for the preservation of ammonite taphoclades.

The concept of evolutionary taphonomic trend can be used in a wide sense to denote any supra-elementary change in a particular direction during fossilization. It is important to distinguish between (intra- or inter-)taphonic trends and (intra- or inter-) taphocladal trends. Intrataphonic trends result from changes in taphonic populations of the same taphon or taphonomic lineage. Intertaphonic trends are produced by changes in taphons of the same subtaphoclade or taphonomic phyletic group. Intra- and intertaphonic trends can be the result of processes of elementary destruction and/or differential replication, and they represent microevolutionary taphonomic processes. Taphocladal trends in turn are due to changes in subtaphoclades of the same taphoclade (intrataphocladal trends) or in taphoclades of the same taphocladal group (intertaphocladal trends). Taphocladal trends can be the result of biases of taphonization and/or taphonic destruction, and they represent macroevolutionary taphonomic processes. Taphonization biases or directional taphonization can generate trends in two different ways, depending on whether taphons with a certain architecture (*i.e.*, subtaphoclades or taphoclades) either multiply more frequently to become more common or multiply in a preferent direction. Taphocladal trends due to biases of taphonic destruction occur when taphons or lineages of a particular architecture (*i.e.*, subtaphoclades or taphoclades) disappear more rapidly and become scarcer.

From the evolutionary point of view, trends developed by taphocladal alteration can be due to the production and differential destruction of taphons, being caused by taphonization processes and taphonic destruction, not by transformation of taphonomic elements. Taphonomic trends at the taphocladal level can result from processes of taphonization and/or differential taphonic destruction, not from mere transformation of taphonomic elements. As components of taphocladal evolutionary trends, the role of taphons in such trends will be comparable to that of the taphonomic elements as units of change within a taphonic population or a taphon subjected to alteration. If taphons act as entities or units, then taphocladal evolutionary trends and general paths of fossilization processes can be due to processes of alteration of superior order (i.e., macroevolutionary processes) by differential taphonization and/or taphonic destruction, and they are not a consequence of intrataphonic modifications or of elementary alteration (stabilization, transformation, replication or destruction of elements). For example, the reelaborated, concretionary, internal moulds of ammonites of some stratigraphical intervals in the Jurassic of the Iberian Range represent the only persisting taphon among a varied group of taphons, and it is not the result of a progressive transformation of the originally produced ammonite remains.

The different values of taphocladal diversity can serve as a relative indicator of macroevolutionary success of each taphoclade of the same taphocladal group. Similarly, the number of taphons of each subtaphoclade can serve as a relative indicator of macroevolutionary success of each subtaphoclade of the same taphoclade.

The capacity that have had the taphoclades to perpetuate their characters, by taphonic retention and/or taphonization, as well as the effects or the results achieved by the preservability of their integrating taphons are represented by their effectiveness. *Taphocladal effectiveness* is the use carried out by the taphoclades, the use that they have made, of their taphonic retention and/or taphonization. The taphocladal effectiveness can be assessed keeping in mind the taphonic survival (that is to say, the proportion of taphons of a taphoclade persisting after an environmental change with respect to the number of taphons before the change) and the subtaphocladal survival (i.e., the proportion of subtaphoclades of a taphoclade persisting after an environmental change in relation to the number of subtaphoclades before the change). The concepts of taphocladal effectiveness, taphonic survival and subtaphocladal survival can be useful to describe and interpret the preservability of taphoclades.

Differential durability of taphonomic elements can be estimated by experimental methods and by observation in natural environments. However, 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. Taphonomic evolution means cumulative change in the properties of taphonic populations generated by taphonomic elements. The study of taphonomic evolution is necessarily historical, and ideas about what happened, and how, can only be inferred from the

remaining evidence (cf. Skelton, 1993: 511). Preservability of taphons and taphoclades can only be assessed and tested in a retrospective way keeping in mind the actual 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, even being abundant in supratidal environments and in continental facies (as reelaborated internal moulds) beyond the limits of tolerance of the originally produced taphonomic elements (i.e., the aragonitic shells).

From a determinist approach, macroevolutionary trends of fossilization processes can be attributed, after being tested, to some particular causes such as environmental changes, interactions between taphons or the appearance of evolutionary taphonomic novelties increasing the preservability of taphons and taphoclades. From a probabilistic approach, however, it is necessary to take into account that macroevolutionary trends in fossilization processes may have been randomly achieved. Anyway, the different ways of change, as well as the taphocladal trends and paths of fossilization processes, resulting from the taphocladal alteration, can be classified into three categories: stabilizing or normalizing fossilization, directional fossilization and disruptive fossilization.

Stabilizing or normalizing fossilization of a taphon or taphoclade, similarly as taphonic retention, does not mean temporary invariance of actual properties, but rather their composition and structure remaining with relatively similar values during fossilization. Stable

taphoclades, or the cases of stabilizing fossilization, correspond to the so-called "unaltered fossils", which have stayed apparently unchanged or showing minimum changes in their properties. Taphonomic elements without apparent changes, as some Quaternary frozen remains, or some Cenozoic remains included in asphalt or in peat-bog deposits, as well as the Recent mummified remains, should be understood as representatives of taphonomic groups with minimum taphonization degrees, rather than as unmodified taphonomic elements. "Unaltered fossils" are usually scarcer among the oldest taphons and, as a general rule, show relatively smaller changes in their primary characters. They usually present the maximum proportion of taphonomic characters in primitive state and the minimum proportion in derived state. Stable taphons or taphoclades, or "unaltered fossils", are taphonomic groups persistently staying with a low population, taphonic or taphocladal diversity. Longevity of taphons has not influenced this result, because the necessary condition is that the number of taphons stays low, without undergoing taphonization processes. Such taphonomic groups cannot be common, because low diversity values increase the probabilities of destruction of a taphoclade. In contrast, "altered or varied fossils" correspond to taphons or taphoclades that have reached, by taphonization, higher values of taphonic and taphocladal diversity than "unaltered fossils". Cases of directional fossilization comprise the fossils altered preferably in some sense, which represent taphons and taphoclades of a certain composition and structure. Disruptive fossilization comprises fossils altered simultaneously in several senses, giving rise to taphons and taphoclades of different composition and

structure. Such taphonomic groups are usually common, because high taphocladal diversity values and processes of taphonomic dispersion diminish the probabilities of destruction of a taphoclade.

Fossilization potential

Properties, activities and capacities of taphonomic entities should not be confused with other properties of the taphonomic systems, of the external environments of taphonomic alteration or of the sedimentary environments in which fossilization processes take place. Neither should they be mistaken with properties of the (palaeo) biological entities. In particular, the preservability or preservation potential of taphonic populations, taphons or taphoclares, should be distinguished from the fossilization potential of palaeobiological entities, different external environments or different sedimentary environments (cf. Schopf, 1978; Plotnick *et al.*, 1988; Mackensen *et al.*, 1990; Palmqvist, 1991; Hayes *et al.*, 1993; Fernández-López, 1995, 2000; Bromham *et al.*, 1998; Orr *et al.*, 1998; Goldstein and Watkins, 1999; Hesse *et al.*, 1999; Alba *et al.*, 2001; Blake, 2000; Conway Morris, 2000; Nowak *et al.*, 2000; Scout *et al.*, 2000; Morigi *et al.*, 2001; Seilacher *et al.*, 2001; Seilacher, 2002; Walker *et al.*, 2002; Cady *et al.*, 2003; Curran & Martin, 2003; Kowalewski & Flessa, 2003; Maeda *et al.*, 2003; Wani, 2003; Krause, 2004; Lazo, 2004; Waugh *et al.*, 2004; Zaton & Marynowski, 2004). The *fossilization potential* of a palaeobiological entity in a particular environment depends on palaeobiological factors (palaeoecological, palaeobiogeographical and evolutionary), productive factors and taphonomic factors.

On the other hand, the fossilization potential of a particular environment with respect to a particular taxonomic group can be understood as directly proportional to the production and import rates, and inversely proportional to the export and destruction rates, of taphonomic elements of this taxonomic group. For example, the fossilization potential of a Mesozoic epicontinental platform regarding the ammonite shells could reach maximum values in the distal and deep environments or in the proximal and shallow environments. Production of ammonite remains took place in general in open and deep marine platforms, but accumulation of these remains was carried out in the production place and also in other far away and shallow areas to those shells arrived by necroplanktic drift. In consequence, fossilization potential of an epicontinental platform regarding ammonite shells could reach maximum values in the distal and deep environments and also in the proximal and shallow environments. The abundance or the concentration of ammonite shells in epicontinental platform deposits cannot be used as a directly proportional bathymetric indicator of depth of the sedimentary environments. However, instead of the abundance or the concentration of taphonomic elements, it is possible to use other taphonomic properties of ammonite taphonic populations, taphons and taphoclares, such as the taphonomic clines (Fernández-López, 1995; Fernández-López & Meléndez, 1995).

The term taphocline denotes a continuous gradation in some character across the range of a taphon or a group of phyletically related taphons, associated with some environmental gradient, which allow interpret the corresponding palaeoenvironmental trend where the gradation has been formed.

Conclusions

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 distinguishing alteration processes at 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 of a same taphon. Taphonic alteration acts on taphons, eliminating those of smaller preservation potential. Taphocladal alteration implies destruction or modification of taphoclades. The architecture of taphonomic elements influences on the alteration of taphons and on the trends in fossilization processes. However, trends in processes of fossilization at different levels of the taphonomic hierarchy can work in opposite directions. The characters lowering durability and redundancy of taphonomic elements can cause taphonic retention and taphonization, increase preservation potential and prevent destruction of taphons and taphoclades. Accepting the existence of taphonomic modifications at different level of organization, evolutionary taphonomy provides a new method that increases the possibilities of analysis and synthesis in taphonomic researches.

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