TAPHONOMIC CONCEPTS FOR A THEORETICAL BIOCHRONOLOGY

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ABSTRACT

Taphonomy is a conceptual subsystem of palaeontology which strives to ascertain how the fossil record has been produced and what sort of modification it has undergone. Taphonomy has its own concepts that allow the fossil record to be dissociated conceptually from the geological or stratigraphical record. It is also possible to regard fossils (or recorded-entities of different organizational levels) and corresponding organisms (or palaeobiological entities) as being distinct in nature. The aim of taphonomical studies is the fossils, i.e. the recorded-entities, and not the strata that bear them or the palaeobiological entities they represent. Taphonomical data are necessary for palaeobiological interpretations, and are relevant in applied palaeontology. It is necessary, however, to develop a systematic approach to fossils that takes into account logical and epistemological assumptions used in biology and Palaeobiology. By identifying integrated systems with taphonomical-palaeobiological relationships, new problems in palaeontology can be raised and solved. In order to obtain a biochronological framework, it is only necessary to identify and classify systematically into units the different kinds of topologically successive recorded-entities. These concepts are neither incompatible nor contradictory to those in biostratigraphy and chronostratigraphy, and may serve to elucidate their fundamental basis.

Keywords: Biochronology, Stratigraphic classifications, Geochronological Scale, Geological Time, Fossil Record.

INTRODUCTION

The so-called theory of organic origin of fossils was developed during the 17th and 18th centuries (Rudwick, 1972). Since that time, the term fossil has been given many different meanings. The prevailing use of this term has been, up to the present, to designate the remains of past organisms, or else the traces of their activity, preserved in the rocks by means of natural processes. Fossils and fossilization have been regarded as states and processes undergone by organisms, their parts, or any kind of organic matter.

During the present century many palaeontological concepts concerning associations of fossils have been developed by means of analogical reasoning and on the basis of some concepts of biosociology: Abel (1911); Weigelt (1927, 1929); Deecke (1923); Wasmund (1926); Quenstedt (1927); Richter (1928, 1929); Efremov (1940, 1953); Davitashvili (1949); Müller (1951, 1963, 1979); Boucot (1953); Johnson (1960); Schäfer (1962); Chave (1964); Clark et al. (1967); Holtzman (1979); Janin (1983); Westrop (1986); Poplin (1986); Graham and Kay (1988).

Many other taphonomical terms have also been proposed by different authors in recent decades taking into account the meaning of ecological theory: Fagersstrom (1964); Craig (1966); Lawrence (1968, 1971, 1979); Rolfe and Brett (1969); Krassilov (1975); Kauffman and Scott (1976); Stanton (1976); Lasker (1976);
Figure 1. Two taphonomic patterns of fossilization currently used. According to the traditional model (left) fossilization consists of selective destruction of palaeobiological variability and implies loss of palaeobiological information. By using a systematic and evolutionary set up (right) fossilization consists of biogenic and taphogenic production of taphonomic variability, and the regulation of such variability by means of taphonomic alteration. According to this new set up, fossilization would only involve an increase of taphonomic information.

Rollins et al. (1979); Olson (1980); Retallack (1981); Dodd and Stanton (1981); Damuth (1982); Cummins et al. (1986); Badgley (1986); Martin and Wright (1988); Wilson (1988).

In addition to that, the great progress achieved in theory of systems and in information theory has allowed fossilization to be regarded as a matter of transmission of information from biosphere to lithosphere: Tasch (1965, 1969, 1973); Beerbower and Jordan (1969); Hanson (1980); Fernández-López (1984, 1988b); Behrensmeyer and Kidwell (1985).

However, during this century palaeontologist have conceded much more importance to palaeobiological and biostratigraphical problems than to those related to the "origin and nature of fossils". In the present state of knowledge it is important to remark that taphonomic data are necessary to carry out palaeobiological and biochronological interpretations and that they are also relevant in applied palaeontology (e.g. biostratigraphy, ecostratigraphy).

TAPHONOMIC MODELS OF FOSSILIZATION

The scarcity of unifying concepts and the lack of unanimity on what are the theoretical grounds of taphonomy are due, among other reasons, to the diversity of assumptions with which the study of fossils has been faced, as well as to divergence of objectives (cognitive and/or practical) of taphonomic works.

The most widely accepted concept of fossilization nowadays, either implicitly or explicitly, corresponds to the idea of palaeobiological modification and selective destruction (Fig. 1, left). According to this conception, fossilization means the transition from the living to the fossil state, and the process involves palaeobiological information loss, as a result of the action of different agents which have acted as successive filters and destroyed the less preservable remains. Taphonomy has so far been regarded as the study of postmortem processes. Many authors, though, have assumed that changes of state during fossilization have been undergone by palaeobiological entities belonging to different levels of organization (organisms, populations, communities, ecosystems, among others). Moreover, fossils have been accepted to be of organic nature. However, these suppositions and assumptions are neither justified by the so-called theory of organic origin of fossils, nor by the recent advances of the theory of organic evolution or by ecologic theory.
Taphonomical postulates

Fossils are not necessarily formed of organic matter and all of them lack the diagnostic features of biological entities such as, for instance, metabolism or viability (Fernández-López, 1989; Rolfe and Brett, 1969, p. 220). Therefore, fossils are not palaeobiological entities, although they bear palaeobiological information and have been produced by biological entities of the past. It is necessary to accept in palaeontology the postulate of production, according to which fossils, or the preserved entities, have been directly or indirectly generated by palaeobiological entities. More precisely, the term biogenic production denotes those palaeoecological-taphonomical processes through which preserved entities are generated by palaeobiological entities, whilst the term taphogenic production denotes the taphonomic processes through which preserved entities give rise to other preserved entities. A consequence of such a postulate of production is that if a preserved element is regarded as a reproduction or a replica of an organism of the past, then preserved elements and their corresponding producer organisms are entities of a distinct nature.

In order to delimit the domains of applicability of taphonomy and palaeobiology, the delimiting criteria must be congruent with the basic palaeontological assumptions employed. Once the existence of biological entities of different levels of organization (organisms, populations, communities, 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 of different levels of organization had been able to give rise to different preserved entities. The existence of hierarchically organized taphonomic systems is a logical assumption compatible with those used in ecological theory and in the theory of organic evolution. According to these assumptions, taphonomic systems are integrated by elemental preserved entities (that is preserved elements) or supraelemental preserved entities (such as taphonomic-populations and preserved-associations). This is the taphonomic postulate of emergence (Fernández-López, 1984, 1986, 1989).

A preserved element is a remain and/or trace which is (para)taxonomically meaningful and determinable. A preserved association may be understood as a group of interrelated elements and may be represented by its relational structure. These features of any supraelemental preserved entity will be the result of both the external influences and the interaction between its components. Any supraelemental preserved entity has a size (number of elements), density (mean of preserved elements by unit of surface or volume), diversity and evenness, geographic distribution and temporal structure. All these are features which determine the behaviour of any supraelemental preserved entity in relation to different environmental factors. Therefore, they are properties which make possible its analysis and the representation of its structure. These structural properties of preserved-associations should not be confused with textural properties of fossil-assemblages (Dodd and Stanton, 1981, p. 300; Shipman, 1981, p. 137) or with biotextures or facies of fossiliferous rock-bodies (Speyer and Brett, 1988; Brett and Bain, 1986; Kidwell et al., 1986; Seilacher et al., 1985; Kauffman, 1981, p. 329).

A third necessary postulate for any taphonomic research, the so-called postulate of modification, is that preserved entities are not inert and that every preserved entity is involved in some kind of process. Preservation is not the result of isolation of produced remains or of the inhibition of alternative 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 may be regarded as an extrinsic principle of regulation, which is able to fix the direction of an evolutive taphonomic process. 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 might favour as well the appearance of preservative modifications. Fossilization, therefore, means an increase in taphonomic information or in taphonomic order, which does not necessarily involve loss or decrease of palaeobiological information (Fernández-López, 1982, 1986, 1989a).

Figure 2. Different features, or spatial attributes, of palaeobiological entities in relation to preserved entities, taking into account their different frameworks of spatial reference.
Preservation states of fossils

Accumulation = laying on the bottom of biogenically produced remains or traces, (with or without transportation).
Resedimentation = displacement on the bottom, before their burial, of preserved elements (with or without transportation).
Reelaboration = exhumation and displacement on the bottom, after their burial, of preserved elements (with or without transportation).

Examples:
Palaeobiological entities
Accumulated elements
Resedimented elements
Reelaborated elements

Figure 3. Meaning, genetic relationships and examples of different states of preservation in which fossils may be found.

Model of taphonomic modification and differential retention

An alternative model to that traditionally used in taphonomy may be developed taking into account the postulates of production, emergence and modification: a model of taphonomic modification and differential retention (Fig. 1, right).

The postulates mentioned so far allow us to distinguish between organisms of the past and preserved elements present in the geological record. They may be used as well to distinguish between supraindividual palaeobiological entities (palaeobiological populations, communities of the past, etc.) and supraelemental preserved entities (taphonic-populations and preserved-associations). Preserved entities are organized systems which may have undergone evo- lutive processes and which may be integrated in more complex systems. Recorded-entities are the observable evidence of palaeobiological entities and are the result of fossilization processes acting on previously produced and preserved entities. Recorded entities are preserved entities in the present state of fossilization, whilst produced entities are preserved entities in the initial state of fossilization. Any recorded entity is bounded in space and time within the rock-bodies of the geological record. Preserved entities may be also regarded as bounded in space and time but, unlike the recorded entities, they may have disappeared or been destroyed during fossilization. Each of these sorts of entities (palaeobiological, produced, preserved and recorded) must be separated from obtained entities, which are those observed in the geological record.

Taphonomic and palaeobiological processes correspond to entities distinct in nature, although they may also be interrelated. Palaeobiological entities may have acted as alternative and/or preservative agents during fossilization, although they could not have acted as producers of preserved entities. Similarly, preserved entities may have acted as retroactive agents of biogenic production (either inhibitors or activa- tors) even though they might not persist as recorded entities.

Taphonomy must study both the structure and composition of preserved entities, as well as the processes of production and modification of such entities. Understood in that way, taphonomy is a conceptual subsystem of palaeontology which strives
to ascertain how the fossil record has been produced and what sort of modification it has undergone.

**TOWARDS A THEORETICAL BIOCHRONOLOGY**

One of the most interesting interdisciplinary subjects in taphonomy, palaeobiology and biostratigraphy is that of the time-space relationships between fossils, palaeobiological entities, and rock-bodies of the stratigraphical record.

**Allochthony and ademy in palaeontology**

The allochthonous vs. autochthonous character of fossils and the meaning of these terms have been treated by many authors. These terms are currently used arbitrarily and it is difficult to know the differences assigned to them, or those which distinguish them from other concepts such as *in situ*/*ex situ* and indigenous/exotic. Many of these problems may be solved if it is admitted that palaeobiological and preserved entities are of a distinct nature, and the different frameworks of spatial reference are not mistaken.

As shown in Figure 2, the autochthonous / allochthonous and *in situ*/*ex situ* character must be assigned to preserved entities. However, it is convenient to use some other terms to make explicit whether a preserved entity is inside (demic character) or outside (ademic character) the area occupied by the organisms of the same taxonomic group (cf. Fernández-López, 1990). Recorded entities may be in their original situation (*in situ*) or may have been transported to a new stratigraphic situation (*ex situ*). On the other hand, preserved entities may be in the same place or region where they were produced (autochthonous) or they may have been transported laterally to a different place or region than that of production (allochthonous). The *in situ* or the autochthonous character of a preserved entity does not guarantee that it is in the same place or region as the corresponding palaeobiological entity. Neither does the *ex situ* or allochthonous character of a preserved entity mean this is outside the living area of the corresponding palaeobiological entity.

From a palaeontological point of view, palaeobiological entities which are producers of remains and/or traces may be inferred in the area where they lived and where organisms of their (bio)species or (phylo)genus bred. In that case they are called *eudemic*, according to the proposition recently made by Callomon (1985, p. 63). Some palaeobiological entities may also be inferred in the area where organisms of their species or genus lived without breeding nor being transported (*miodemic*), or else in the area where they have been transported by external agents and where organisms of their species or genus did not breed (*parademic*). Moreover, some palaeobiological entities may be inferred outside the living area occupied by organisms of their taxonomic group (*ademic*). The miodemic character is typical of, but not exclusive to, migratory species with migrating capacity and ontogenic segregation. Eudemic or miodemic entities become parademic when they are transported by external agents to some other place within the living area, where organisms of the species or genus did not breed. A palaeobiological entity becomes ademic when it moves, or is transported by external agents, to some other environment under lethal conditions outside the area normally occupied by organisms of their taxonomic group. Allochthonous elements resulting from taphogenical production outside the living area occupied by the species or genus similarly represent ademic entities. In the same way, the allochthonous character of preserved elements does not preclude them from representing eudemic or miodemic palaeobiological entities. Ademic entities may be represented by both autochthonous and allochthonous elements.

**Preservation states of fossils**

From a taphonomical point of view, to accept that fossil remains are formed and/or traces of palaeobiological entities means accepting as well that fossilization might not involve preservation of matter but only of information. The term *accumulation* proposed by Éfremov (1950) may be used to designate the process of transference of information from biosphere to lithosphere, which may or may not be accompanied by matter and which does not necessarily involve sedimentation. Any recorded element has had to be accumulated inside or upon materials of the lithosphere, but it is not necessary for it to have been sedimented after being produced (Fig. 3). Two other taphonomic processes may affect the preserved elements after being accumulated, namely: resedimentation and reelaboration. Taphonomic resedimentation means the displacement along the floor, prior to the burial, of previously accumulated elements. The reelaboration (or taphonomic reworking) means the exhumation and displacement of preserved ele-

![Figure 4. Components and in-between relationships of (bio-) stratigraphical successions with respect to recorded and registrator successions.](image-url)
A **CHRONOBIOTHEMIC SCALE** is a conceptual scale, established through the temporally sequential order of palaeobiological entities.

**CHRONOBIOTHEMIC DIVISIONS**
- are abstractions, conceptual units.
- a CD is the time-interval of one or more species, defined by its initial and terminal evolutionary events (*). 

**CHRONOBIOTHEMIC UNITS**
- are historical referents (palaeobiological entities).
- a CU is an organism or an ensemble of organisms of the past, producers of remains or traces during a specific time-interval.

**CHRONOREGISTRATIC UNITS**
- are material units.
- a CU is a fossil or an ensemble of fossils biogenically produced during a specific time-interval; 
- is the evidence of a chronobiothemic unit.

A **CHRONOREGISTRATIC SCALE** is a material scale, established through the temporally sequential order of recorded entities.

A **BIOCHRONOLOGICAL SCALE** is a dual scale: two scales (chronoregistratic and chronobiothemic) fitted to each other.

Figure 5. Relationships between different categories of biochronological units allowing establishment of a biochronological scale.

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A **CHRONOSTRATIGRAPHIC** (or CHRONOSTRATIC) SCALE is a material scale, established through the temporally sequential order of rock bodies.

A **GEOCHRONOLOGIC SCALE** is a dual scale: two scales (chronostratigraphic and chronometric) fitted to each other.

Figure 6. Relationships between different categories of stratigraphic and (geo)chronometric units allowing establishment of a geochronological scale.

It is possible to set a sequential ordering of different classes of elements integrating the mixed associations. Such an ordering may be directly correlated with a time sequence of the process of fossilization, without having to use a priori biochronological reasoning. Different recorded entities of a particular place or region may be generally ranked by means of several relational statements which account for the causal relationships called time of production and fossilization. The relevant palaeontological data from which the time relationships between two or more palaeobiological entities can be inferred are not the stratigraphic relations between the rock-bodies in which their remains or traces are contained, but the topological relations between their corresponding recorded entities.

It is possible to test, by exclusively palaeontological data, if two recorded elements from the very same rock-body correspond or not to the same palaeobiological entity. In any case, the question of whether the biogenic production and the fossilization of two recorded entities were simultaneous or successive must previously be resolved in order to ascertain whether such recorded entities represent simultaneous or successive palaeobiological entities (Fernández-López, 1986, 1987, 1989b).

Taking into account the taphonomical data, it is possible to distinguish between: a) fossiflerous rock-bodies which are part of, or constitute, a stratigraphical succession (i.e. biostratigraphical succession); b) recorded-entities from stratigraphically successive levels (recorded succession); and c) topologically successive recorded-entities, each one of them belonging to a rock-body which may be the same as, or different from, the rock-body where the other entities are found (registratic succession, Fig. 4). At a regional scale, the corresponding registratic succession may also be estimated taking into account the different pairs of recorded associations which are
topologically successive and which have been observed in different localities (cf. Guex, 1987; Gradstein et al., 1985). It should, however, be noted that biostratigraphical and registratic orders may be different from each other and in relation to the corresponding order of palaeobiological succession (cf. Springer and Lilje, 1987; Lazarus and Protero, 1984). The distinction, then, between biostratigraphical, registratic and palaeobiological successions is methodologically necessary to test any ecosequence from the past or the directionality of any palaeobiological evolutionary process.

Biochronological and stratigraphical units

The stratigraphical record has traditionally been assumed to be more complete than the fossil record. However, at least in some cases, the opposite may also occur (McKinney, 1986, 1985; Holman, 1985; Behrensmeyer and Kidwell, 1982; Behrensmeyer, 1982, 1980). Both biostratigraphical and biochronological systems of classification are based on the fossil contents of rock-bodies. But stratigraphical units of such systems of classification must not be identified or established by means of reeledaborated fossils. This has led some authors to state that reworked fossils lack biochronological and biochronostratigraphical relevance, although they might be the “best preserved” fossils in the associations.

By means of palaeoecological-taphonomic estimations, however, and using the relational concept of biostratigraphical, registratic or palaeobiological succession, it is possible to obtain class concepts of succession and to establish, respectively, independent biostratigraphical, registratic or palaeobiothemic units (Fernández-López, 1986, 1987, 1988a). Each of these units must be tested by data relative to taphonomic modifications undergone by the corresponding recorded entities. Registratic and palaeobiotohe-
mic units are biochronological units (Fig. 5). Taxorecords are recorded entities which are (para)taxonomically determinable and which have been established with no account of their time of production and fossilization. Chronorecords are recorded entities which have been biogenically produced during a specific time interval. The palaeobiotematic units which are structurally equivalent to the registratic units are called taxobiothemes and chronobiothemes. Therefore, to obtain a biochronological framework of reference, it is required to identify and classify systematically into units the different classes of topologically successive recorded entities, without excluding the reelaborated elements.

Relationships between taxorecords and chronorecords are analogous to those existing between biozones and chronozones, or between biozones and standard zones (Fig. 6). Each Chronozone may be represented by more than one type of biozone and each chronorecord may be tested by different taxorecords, even in the same locality. But in a particular locality, region or basin there may be taxorecords which are correlated taxonomically and geographically.

Figure 8. Relationships between different scales of geological time, and their corresponding classifications, which may be justified by the geological record.
records or chronorecords with no equivalent stratigraphic unit (neither biozone nor chronozone, Fig. 7).

Consequences for evolutionary interpretations

This system of biochronological classification is congruent with the original definition proposed by Schindewolf (1950, p. 32) according to which palaeontological studies carried out to establish a chronology of time-succession of organisms, or else a time subdivision by means of fossils, should be called biochronology.

In order to obtain a biochronological scale, it should be noted that it is necessary to ascertain the temporally sequential order of palaeobiological and recorded entities; however, knowledge of the evolutionary modalities of corresponding taxonomic groups is not required. Furthermore, from the principle of continuity and irreversibility of organic evolution, the necessary and sufficient evolutive assumption to justify a palaeontological scale of temporal reference is that palaeobiological entities of different chrono-biothemic units are phylogenetically related or belong to the same monophyletic group. The evolutionary modalities, and the kinship relations, of the inferred palaeobiological entities may be treated with regard to a previously established biochronological framework of reference (Fernández-López, 1986, 1987).

Biochronological scales may serve to assess and evaluate the antiquity of the time relations between recorded entities of a different taxonomic group, and are also applicable to stratigraphic units formed by fossiliferous bodies of rock.

If biochronology is regarded in that way, the problem of describing organic evolution with respect to a stratigraphic scale which is itself based on an interpretation of organic evolution is resolved (cf. Haq and Worsley, 1982; Harper, 1981, 1980; Sanchí, 1979; Berggren and Van Couvérin, 1978; Harland, 1978; Eldredge and Gould, 1977). Biochronology becomes a conceptual system which is independent of, although compatible with, those of biostratigraphy and chronostratigraphy.

Some remarks on chronostratigraphy and geochronology

On what concerns the current principles of geochronology (Haq et al., 1988; Owen, 1987; Cowie et al., 1986; Snelling, 1985; Callomon, 1984; N.A.C.S.N., 1983; Odin, 1982; Harland et al., 1982, 1978; Hedberg, 1976) it should be noted that geochronological units are subdivisions of geological time, justified by the stratigraphical record and by the evidence of chronostratigraphical units (Fig. 8).

It may be stated that (bio)chronostratigraphic units are identifiable by biochronological criteria, but (bio)chronostratigraphical scales are not based on, or derived from, stratigraphical or biostratigraphical scales. But biochronological scales are not based on, or derived from, stratigraphical or biostratigraphical scales. The geological record has two components: the stratigraphical record and the fossil record. These may be dated and assessed, as long as the knowledge allows it, either with a chronometric scale, with a chronostratigraphical scale, or with a biochronological scale. Subdivisions of each of these scales are established by means of units belonging to a different system of classification. As a consequence it is possible, especially in Proterozoic materials, that a chronostratigraphical subdivision lacks an equivalent in the biochronological scale. But it may also happen, in Phanerozoic rock-bodies of a particular region or sedimentary basin, that chronostratigraphical subdivisions are less numerous and resolutive than biochronological subdivisions.

Unlike what has been repeatedly written, the stratigraphical record is not the only record of the passage of the geological time. Both chronostratigraphical and chronoregistratic units are meaningful in geological time. Furthermore, isotopic decay and organic evolution are the only two known phenomena that, as continuous and irreversible, make it possible to establish a geological time scale.

Chronostratigraphy is, nowadays, the most adequate conceptual system to justify the most complete and valid geological time scale. However, both the stratigraphical and the fossil record are discontinuous. The question now is not to find out which of those records is the less discontinuous, in order to use it as a material referent for the geological time scale; it is to obtain, from each of them, two systems of classification which may justify a more resolutive and adequate synthetic scale.

CONCLUSIONS

Taking into account some of the logical and epistemological assumptions currently employed in biology and Palaeobiology, it is necessary to use a systematic and evolutionary approach in taphonomy and biochronology, in order to make the different conceptual subsystems of palaeontology congruent.

The identification of integrated systems with palaeobiological-taphonomical relationships allows the setting up, and resolving, of new palaeontological problems. Particularly, the taphonomical distinction between palaeobiological entities, recorded-entities of the fossil record, and rock-bodies of the stratigraphical record, makes it possible to establish biochronological classifications and scales independent of, but compatible with, those of biostratigraphy and chronostratigraphy.

From a methodological point of view, this approach can increase the way in which taphonomical data are analyzed and synthesized, and can promote comparison of a broader array of palaeontological hypotheses, which are of interest in both life and earth sciences.

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