

Taphonomy

A Process Approach

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1 Introduction: the science of taphonomy

Nature is full of infinite causes that have never occurred in experience.
Leonardo da Vinci

1.1 The foundations of taphonomy¹

Taphonomy is the science of the “laws of burial” (from the Greek *taphos* + *nomos*). It is the study of the transition of organic remains from the biosphere into the lithosphere or the processes of “fossilization” from death to diagenesis. Although the term “taphonomy” was first coined by Efremov (1940), the science of taphonomy has been practiced for centuries (Cadée, 1991). Taphonomic investigations were first conducted by Leonardo da Vinci (1452–1519), who used observations on living and dead bivalves to infer that fossils found in nearby mountains had not been transported there by the Biblical Deluge, but had actually lived and died *in situ* (see excerpts from da Vinci’s notebooks in Bolles, 1997; see also Chapters 2, 3). Subsequent taphonomic inferences were made by none other than Steno, who concluded that so-called tonguestones or glossopetrae were actually shark’s teeth (Albritton, 1986); Robert Hooke, who compared the cellular structure of cork to that of petrified wood, thereby supporting Steno’s assertion that fossils were of organic origin and not the result of the “plastic virtue” of the surrounding rocks (Albritton, 1986); the vertebrate paleontologist and anatomist, Cuvier; Alcide d’Orbigny, who erected the first detailed biostratigraphic zonations; and Armand Gressly, who formulated the concept of “facies.”

Near the end of the nineteenth century and continuing into the twentieth, German paleontologists came to dominate the science (Cadée, 1991). Johannes Walther (1904, 1910) studied marine environments in the vicinity of Naples and the Jurassic Solnhofen, and Abel (1912, 1927, 1935), who published several books on taphonomy, carried out initial studies of “*fossil-Lagerstätten*” or “fossil

¹ This section is based on the excellent summaries of Behrensmeier and Kidwell (1985) and Cadée (1991).

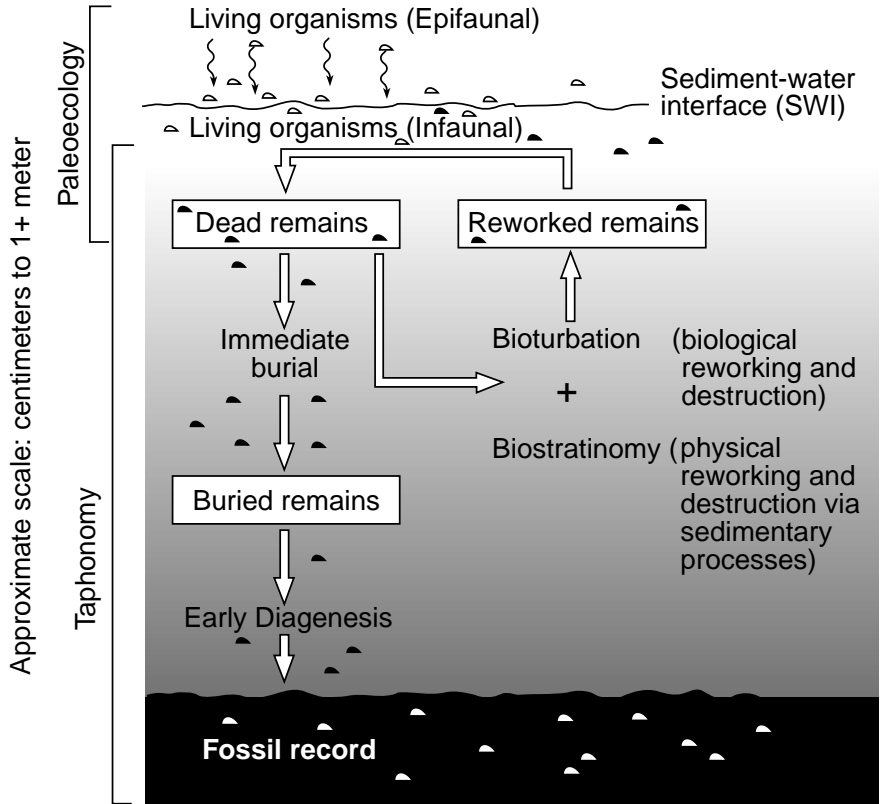


Figure 1.1. The processes of fossilization. Note the *dynamic* aspects of taphonomy, especially the recycling of fossils before final destruction or burial. Efremov (1940) included “fossil diagenesis,” or the chemical and mechanical alterations of fossils within sediment, as the final stage of taphonomy (Cadée, 1991), but diagenesis may begin as soon as hardparts enter the surface layer of sediment. (Based on Lawrence, 1968; Behrensmeyer and Kidwell, 1985; and Newton and Laporte 1989.)

mother lodes” of spectacularly preserved fossil biotas, which have received increasing attention (e.g., Seilacher, 1970, 1976; Whittington and Conway Morris, 1985; Allison and Briggs, 1991*a,b*; Chapter 6). Weigelt (1927; translated in 1989) is best known for his careful description of the decomposition, transport and burial of carcasses at the edge of a lake in the U.S. Gulf Coast after a severe “norther” in December, 1924, caused massive mortality of cattle and other vertebrates (he also described other vertebrates from modern and ancient deposits). Weigelt’s study was the first well-documented investigation of the *biostratinomy* (*biostratinomy*) or sedimentary history of fossils from necrolysis (death and decomposition; Figure 1.1) through final burial (most workers prefer the term *taphonomy*, perhaps because it is more inclusive and euphonious; cf. Figure 1.1).

Weigelt (1928) also studied the biostratigraphy of plants preserved in the Kupferschiefer (Upper Permian, Zechstein, Germany). Somewhat earlier, Chaney (1924) studied the correspondence between plant fossil assemblages and original vegetation, and Potonié (cited in Cadée, 1991) reviewed the formation of peats and coals. Taphonomic studies of fossil pollen were also beginning about this time (Cadée, 1991). Unfortunately, German investigations were largely ignored in other countries because of language difficulties and anti-German sentiment associated with the rise of the National Socialist party (Cadée, 1991). Consequently, taphonomy was not recognized as a distinct discipline outside of Europe until after World War II by such workers as Olson (1952), working on Permian vertebrates, and Johnson (1957, 1960, 1962), who studied modern and Pleistocene shallow marine invertebrates of the northern California coast (Behrensmeier and Kidwell, 1985).

Unlike the German taphonomists, who were concerned primarily with paleoenvironmental interpretation, Efremov, who was a vertebrate paleontologist, emphasized the incompleteness of the fossil record. As a result, to this day, taphonomy has come to be associated – even by many taphonomists – with the documentation of “information loss” and “bias” in the fossil record. Lawrence (1968), for example, compared modern and Oligocene oyster communities and concluded that 75% of the macroinvertebrates were not preserved. Numerous studies followed among a diversity of specialists, who largely worked independently of one another and who did not recognize taphonomy as a distinct discipline of the Earth sciences.

In an attempt to unify the discipline, Behrensmeier and Kidwell (1985, p. 105) defined taphonomy as “the study of processes of preservation and how they affect information in the fossil record.” As the science of taphonomy has emerged as a separate – albeit highly interdisciplinary – entity, especially in the past decade, its body of theory has become sufficient to begin predicting the utility of the fossil record in ecological and evolutionary studies (Chapter 7). For example, ancient river channel accumulations of bone and plant fossils are likely to represent regional, rather than local, samples of the biota, given the distances that the remains have been transported (Behrensmeier, 1982; Behrensmeier and Hook, 1992). In contrast, oxbows and other abandoned channels will likely fill with biota from the immediate vicinity and may record ecological succession from aquatic to terrestrial habitats (Behrensmeier, 1982; Behrensmeier and Hook, 1992). Although deltas may offer well-preserved fossil assemblages (because of rapid burial), their record will likely be highly discontinuous because of lobe-switching (Schindel, 1980, 1982); such a record may be adequate for studying

short-term ecological phenomena, but the record may prove too discontinuous to assess evolutionary lineages. Because of rapid sedimentation and subsidence (burial), active continental margins (e.g., California) may be characterized by taphonomically less complex shell beds than those of passive margins (Maryland coastal plain; Kidwell, 1988). Even along active margins, however, the degree of complexity and *fidelity* of shell beds to living communities will vary according to rates of uplift, erosion, and sedimentation (Meldahl and Cutler, 1992; Meldahl, 1993).

Behrensmeyer and Kidwell (1985) also emphasized the positive contributions of taphonomy to our understanding of the fossil record. For example, etching or breakage of shells contribute not only to information loss, but also to recognition of the biostratigraphic agents involved in the formation of fossil assemblages (such as waves, currents, predators and scavengers, hermit crabs, and birds), length of exposure of hardparts in the surface mixed layer (where early diagenetic phenomena are concentrated; Chapters 3, 4), rates of sedimentation, and pore water chemistry.

Typically, “time-averaging” of fossil assemblages results because rates of sedimentation are too slow to prevent mixing of “ecological” signals into accumulations of longer duration and lower temporal resolution (Chapters 4, 5). Although viewed negatively by most workers, time-averaging is actually an advantage, since short-term “noise” is damped and longer-term signals from a biological community are preserved (Behrensmeyer and Kidwell, 1985; Wilson, 1988*b*; Kidwell and Flessa, 1995); in fact, modern death assemblages from soft-bottom habitats are perhaps comparable to repeated (and expensive!) biological surveys in assessing the long-term dynamics of biological communities (Peterson, 1977; Kidwell and Bosence, 1991; Kidwell and Flessa, 1995).

Taphonomy has, however, only recently begun to assess “megabiases” in the fossil record (Behrensmeyer and Kidwell, 1985; Behrensmeyer and Hook, 1992), although Efremov (1940) was certainly aware of them (Chapters 8, 9). These include, but are not restricted to (1) the outcrop (sampling) area of particular environments, which reflects the influence of sea-level, continental configuration, and other climatic influences on patterns of sedimentation (Efremov, 1940; Signor, 1985); (2) cycles of preservation, which again appear to reflect the influence of plate tectonics, sea-level, and atmospheric CO₂ (e.g., Walker and Diehl, 1985; Martin, 1995*a*, 1996*a,b*); and (3) secular changes in the Earth’s biota, which have affected the cycling (through predation, scavenging, bioturbation) of biogeochemically important elements between – and their storage in – various reservoirs, as foreshadowed by Efremov’s (1940) definition of taphonomy (e.g.,

Vermeij, 1987; Boss and Wilkinson, 1991; Kidwell, 1991; Bambach, 1993; Martin, 1995*a*, 1996*a,b*; cf. Figure 1.1).

1.2 Methodology in historical sciences

“In a profession more observational and comparative than experimental, the ordering of diverse objects into sensible categories becomes a *sine qua non* of causal interpretation” because it represents a *causal ordering* (Gould, 1986). Taphonomy, and its sister disciplines of paleoecology, sedimentology, and stratigraphy, and geology itself for that matter, are historical sciences because, fundamentally, they are concerned with the history of Earth and its Life as they are recorded in the rocks. Other scientists regularly construct historical hypotheses based on observations arranged in stages, from the life histories of species and stars, to the development of atolls: similarly, taphonomists often refer to “taphonomic histories” and “pathways” of formation of fossil assemblages.

One may also infer history from single, *unique objects* by looking at anomalous features or imperfections (e.g., Lagerstätten; Chapter 6). Although each “singularity” is unique because of historical constraints, collections of singularities (fossil assemblages, especially Lagerstätten) may exhibit certain “nomothetic” (general or universal) relationships that can be predicted and tested (e.g., durations of time-averaging based on radiocarbon dates of hardparts from different depositional settings; Chapter 5).

By far and away the most common approach to interpreting the fossil record involves *upward scaling* from short-term observations to geological phenomena. The foundation of the Earth sciences, *and of all other sciences*, is the Principle of Uniformitarianism: “the present is the key to the past.” The origins of uniformitarianism are found in James Hutton’s *Theory of the Earth*, but uniformitarianism probably received its greatest impetus from Sir Charles Lyell’s incredibly influential *Principles of Geology, Being An Attempt to Explain the Former Changes of the Earth’s Surface, by Reference to Causes Now in Operation*, the first volume of which was published in 1830 and which went through 11 editions in ~50 years. Because of his religious outlook, Lyell was strongly committed to a steady-state view of the Earth (a view easily rationalized with a divine presence), and uniformitarianism was an attempt by him to deny any form of catastrophism or directionalism (progressionism) in the inorganic and organic worlds, such as that recognized by Cuvier and certain other early nineteenth century scientists (Bowler, 1976; Ruse, 1979); indeed, “jettison steady-statism, and you jeopardize . . . uniformitarianism” (Ruse, 1979, p. 79). The influence of Lyell –

and later Darwin (who read the *Principles* and subscribed to its tenets) – has been such that even to the present day, progressionism in the fossil record is viewed suspiciously as teleology: after all, “progress is not inevitable by the canons of natural selection” (Desmond, 1982, p. 101; see also Gould, 1996). Geochemical models are typically conceived, for example, under steady-state conditions primarily for the sake of simplicity (the shorter the interval considered the less likely conditions will change; cf. Chapters 8, 9; see also Bowler, 1976).

Lyell’s philosophical view consisted of two parts: the explanation of past geological phenomena by processes that (1) are *observable* today (“actualism”) and (2) are of the same *rate* as those observed today (uniformitarianism *sensu stricto*; Ruse, 1979).² Like many of his contemporaries (including Darwin), Lyell was probably influenced by the then (and still!) prevalent view of the astronomer Sir John Herschel’s *A Preliminary Discourse on the Study of Natural Philosophy* (1831), which espoused physics as the paradigm of a mature, quantitative science (Ruse, 1979). According to Herschel (1831), there are two kinds of laws: empirical (those that state relationships without stating their causes; e.g., Kepler’s laws) and *verae causae* or true causes (e.g., Newton’s laws of motion and gravitation, from which Kepler’s laws may be deduced; Ruse, 1979). According to Herschel (1831), *verae causae can only be determined by analogy (comparison) with our own experience*.

Lyell’s views were not without controversy, however (especially uniformitarianism *sensu stricto*), and were attacked by none other than Adam Sedgwick (who taught Darwin field geology in Wales shortly before his departure on H.M.S. *Beagle*) and the Reverend William Whewell (who also had extensive contact with Darwin) because phenomena that could not be observed (such as the intervention of a divine Creator) were automatically ruled out by Lyell (see Ruse, 1979, for further discussion).

Gould (1965; see also Lyman, 1994a³) also distinguished two types of uniformitarianism: methodological and substantive. According to methodological uniformitarianism, no unknown *processes* need be invoked if historical records can be explained by processes observed in the present (a form of Occam’s

²Both are referred to as uniformitarianism in England and the U.S.A., whereas in Russia uniformitarianism has meant “the specific Lyellian hypothesis . . . while actualism is a method” (Hooykaas, 1963, p. v).

³Lyman (1994a) gives a detailed – and often personal – view of the history and methodology of taphonomy, especially with respect to zooarcheology. The following discussion of methodology is based on his work, and also that of Salmon (1967), Gould (1986), Frodeman (1995), and Martin (1998a).

Razor); whereas, according to the substantive doctrine, *rates* of change have always been uniform and gradual and catastrophic changes are not caused by sudden changes in rates (cf. uniformitarianism *sensu stricto*). Methodological uniformitarianism is essentially identical to actualism and has been a mainstay of taphonomic research. Based on this tenet, modern fossil assemblages and their taphonomic settings, as well as field and laboratory experiments, can be used to make inferences about the processes – and their rates – that formed ancient assemblages; the actualistic method, then, involves argument by analogy (Lyman, 1994a). Although this approach began as early as da Vinci, it received tremendous support from German workers, among them Richter (1928), who founded the institute at Senckenberg am Meer in Wilhelmshaven (Germany) along the Wadden Sea, to study “aktuo-paläontologie” (Cadée, 1991). But the actualistic approach, at least in marine environments, probably received its greatest impetus from the translation (1972) of Schäfer’s (1962) actuopaleontological studies in the North Sea (Behrensmeyer and Kidwell, 1985; Cadée, 1991). Schäfer documented the death, decay, and disintegration of modern vertebrate and invertebrate remains; the traces of these and other animals (“Lebensspuren” or ichnofossils); and the transition from *biocoenosis* (living community) to *thanatocoenosis* or fossil (death) assemblage (“any group of fossils from a suitably restricted stratigraphic interval and geographic locality”; Fagerstrom, 1964). These terms had been used earlier by Wasmund (1926) in his study of lakes (see Kidwell and Bosence, 1991, their table 1, for review of the usage of these terms by different investigators; some workers have adopted the term *taphocoenosis* for a taphonomically modified thanatocoenosis).

It is in uniformity, however, where the rub lies. First, the *assumption* of uniformity cannot be tested because we cannot actually observe the past (Hubbert, 1967; Kitts, 1977); therefore, we are forced to assume an actualistic stance. And second, appeal to processes not observable in the present, especially unusual ones such as the classic view of “catastrophism,” is, strictly speaking, precluded (Kitts, 1977; Lyman, 1994a; see also Ruse, 1979). With regard to the first criticism, since we cannot demonstrate natural laws to be invariant in the past (even in “hard” – and largely ahistorical – sciences like chemistry and physics), conclusions are arrived at through the process of induction (Salmon, 1967; Lyman, 1994a). Unlike deduction, inductively derived conclusions contain inferences not present in the premises and can never be shown to be absolutely true (inductive arguments are therefore said to be ampliative); nevertheless, inductively derived generalizations are extremely useful as premises of deductive arguments (i.e., prediction) and are the basis of the hypothetico-deductive method of scientific inquiry

(Salmon, 1967). If inductively derived generalizations – or deductions based upon them – turn out to be incorrect, we seek new ones.

But logically, we cannot conclude that historical phenomena are explained by our actualistic generalizations if those generalizations were used to infer the historical phenomena in the first place. This represents *the* fundamental criticism of the process of scientific induction by the Scottish philosopher David Hume (“Hume’s paradox”): namely, how *does* one acquire knowledge of the unobserved (Salmon, 1967)? “If we attempt to rationally justify scientific induction by use of an inductively strong argument, we . . . [must] *assume* that scientific induction is reliable in order to prove that scientific induction is reliable; we are reduced to begging the question. Thus, we cannot use an inductively strong argument to rationally justify scientific induction” (Skyrms, 1966, p. 25; see also Salmon, 1967). Nevertheless, we use induction because the approach works and there is no alternative (Bridgman, 1959; Lyman, 1994a). We are, in effect, engaged in a pragmatic (some might say circular) form of reasoning that seems to work most of the time.

Unlike induction, deduction is non-ampliative: it “purchases . . . truth preservation by sacrificing any extension of content” (Salmon, 1967, p. 8). It is partly for this reason that scientists (unwittingly) subscribe to the principle of the “uniformity of nature”: such a principle is a “synthetic *a priori*” statement that, when part of the premises of an inductive argument – consciously or otherwise – attempts to make an inductive argument deductive in nature; synthetic statements are arrived at inductively, however, and their accuracy is indeterminate (Salmon, 1967). Moreover, Hume asked, how can we know *a priori* that Nature is uniform?

For this and a number of other reasons, Karl Popper – who has probably influenced scientific methodology more than any other philosopher this century – rejected induction, and proposed instead a *hypothetico*-deductive method that he claimed avoided the problems of induction by making statements (hypotheses) that could be falsified (Popper, 1959, and later works; see also Woodward and Goodstein, 1996). According to Popper, the more likely it is that a hypothesis can be falsified, the better it is. Hypotheses must run as great a risk as possible of being overturned, because the more falsifiable a hypothesis is, the more it tells us; therefore, the more falsifiable a hypothesis is, the more it excludes extraneous possibilities and the greater the risk it runs of being false (Salmon, 1967). This approach differs from that assumed by most scientists (who attribute it to Popper): that the more a hypothesis is corroborated by *positive* support, the more likely it is to be *confirmed*. Unfortunately, this often leaves too many hypotheses to explain the same phenomenon, and the “hypothetico-deductive theorist”

will likely choose the most probable one, whereas Popper would pick the least likely one because of the inverse relation between falsifiability and probability. According to Popper, a highly falsifiable hypothesis which is stringently and repeatedly tested and left unfalsified becomes “highly corroborated,” which is not the same thing as being confirmed. Popper considered his method to be strictly deductive; nevertheless, inductive argument still creeps in because without it conclusions (hypotheses) would only confirm the premises (observations), and science would “amount to [no] more than a mere collection of . . . observations and various reformulations thereof” (Salmon, 1967, p. 24).

Perhaps we can take some comfort in the fact that deduction may arrive at absurd conclusions if the premises are false. Understanding Nature by deduction from “indubitable” first principles grounded in *pure reason* was championed by rationalists such as Descartes and Leibniz, who wanted to reason *to* nature not *from* it (Ruse, 1979), and “who were impressed by the power of the mathematics they had helped to create” but “which failed to account for . . . observational and experimental aspect[s]” (Salmon, 1967, pp. 1–2). An early typical example of deductive reasoning was to accept the Judeo-Christian god as the Creator of the universe and its occupants, and to deduce what were thought to be the necessary consequences, such as that the creation occurred only a few thousand years ago, all species are immutable, and so on (Moore, 1993). Empiricist philosophers such as Sir Francis Bacon (1561–1626) found this approach repugnant, and emphasized that one should begin with data based on observation and experiment, not faith (Moore, 1993; see also Martin, 1998*a*). Not surprisingly, given the times, James Hutton – like Isaac Newton before him – believed that natural phenomena demonstrated the existence of a divine plan; according to Greene (1982), Hutton’s approach was more deductive than inductive. In taphonomy, one example of such a deduction, which would seem to be obvious based on reason alone, is that small bones should vastly outnumber larger ones in a vertebrate fossil assemblage because small animals vastly outnumber larger ones in living populations (“*Law of Numbers*”; see also Kidwell and Flessa, 1995; Chapter 2). Although *intuitively* this prediction makes perfect sense, it is exactly the opposite of observations made on mammalian remains of Amboseli Basin (East Africa) by Behrensmeyer and Boaz (1980).

With regard to the second criticism of the assumption of uniformity, modern usage of the principle does accept that the rates and intensities of processes have varied during the Earth’s history (even Hutton accepted this; Albritton, 1986). When historical phenomena cannot be explained using the actualistic approach we must concede that either our knowledge of modern processes is incomplete

or that there are processes that we have not yet observed or that are no longer operative in the modern realm (e.g., “megabiases”; cf. substantive uniformitarianism). Ironically, it was rationalists such as Descartes who argued that since our senses (or in modern terms, our scale of observation) often deceive us, only deductive arguments are valid.

The problem of scale strikes at the heart of actualism and is why historical sciences are so important (Martin, 1998*a*). If we do not observe a process over the typical span of a grant proposal of 3–5 years or a scientific career of several decades, much less a human life span of say 70 years, does that mean that the process does not occur? How many times has human civilization, which has spanned thousands of years, recorded the collision of an extraterrestrial body with the Earth (the closest in recent memory was the Tunguska event in Siberia in 1908), much less the impact of a comet with Jupiter’s atmosphere? Because we observe streams to erode gradually downward, are we always justified in extrapolating these rates to all river valleys? The Lake Missoula floods argue otherwise (Parfit, 1995). Mass extinctions may have occurred over considerable spans of geological time and may be preceded by gradual climate change that would be undetectable over many human generations but which nevertheless culminates in biological catastrophe in the fossil record (e.g., Martin, 1998*a*).

In the case of fossilization, even if we observe, for example, certain features on shells or bones to be produced at certain rates in laboratory or field experiments, we cannot blindly extrapolate those rates to the past. Similar features of fossils may have been produced at rates different from those observed in modern analogs and experiments (Behrensmeyer, 1982; Kotler *et al.*, 1992). Moreover, taphonomic features of a fossil or an assemblage that may appear to be diagnostic of a particular taphonomic agent may arise for different reasons (*equifinality* of Lyman, 1994*a*); i.e., the same features may result from different taphonomic pathways or histories.

Nevertheless, “data derived from actualistic research are . . . commonly used as a source of empirical generalizations or *formal analogies* rather than to build *relational analogies* and postulate diagnostic criteria” (Lyman, 1994*a*, p. 69). In formal analogies, two or more objects are said to be similar because they share certain attributes; such analogies are weak because the properties may have arisen by chance (Hodder, 1982). For example, just because two shells possess a similar *taphonomic grade* (surface appearance) does not mean that they have identical taphonomic histories: young shells, for example, may *appear* to be quite old and old shells may appear to be quite young (Flessa *et al.*, 1993; Kidwell, 1993*a*; Martin *et al.*, 1996; Chapter 5), so that shells of similar appearance may actually have quite different taphonomic histories (contrary to intuition; cf. Brandt, 1989).

In relational analogies, attributes are interdependent and causally related (Hodder, 1982). In the case of shell grade and age, shell grade is not a function of shell age itself, but of the shell's residence time near the sediment–water interface (SWI; cf. Figure 1.1) and accompanying exposure to bioeroders and dissolution before final burial (Flessa *et al.*, 1993; Cutler, 1995; Martin *et al.*, 1996). Exposure at the SWI is in turn a function of factors such as rates of sedimentation and bioturbation and reworking by storms (e.g., Meldahl, 1987; Flessa *et al.*, 1993). Thus, relational analogies can either weaken or strengthen formal analogies and result from *context*, which in this case is the taphonomic (depositional) setting.

Thus, taphonomic histories may be quite complex, and even deceptive, and the term “taphonomy” is itself a misnomer, as Efremov (1940) was no doubt aware (Cadée, 1991). In historical sciences we do not necessarily seek laws that “apply to all parts of space and time without restriction” (Salmon, 1967, p. 5) so much as principles or “rules of thumb” that can guide us, although not necessarily unerringly, in interpreting the history of fossil assemblages (Weigelt, 1989, also used the term “law” but in a much more restrictive sense, and it is clear from his discussion that his “laws” are really principles).

1.3 Laws, rules, and hierarchy

So-called laws, and even principles, are constrained by context or history (Olson, 1980; Allen and Starr, 1982; Martin, 1998*a*). If we interpret the past strictly in terms of anthropocentric laws, we will never truly understand what the fossil record has to tell us (Martin, 1998*a*; cf. Chapter 11). The Principle of Superposition, for example, states that younger sedimentary rocks lie on top of older ones, but not if they have been overturned by folding. Our inferences about ancient sediment and soils are based on the laws of physics and chemistry, but the exact chemical conditions that pertained to the formation of a particular fossil assemblage depend upon the contextual relations of bedrock, climate (arid, wet), type and amount of vegetation (especially in the case of soil), rates of weathering, intensity of bioturbation (including trampling), and so on.

Much of nature consists of hierarchies, which consist of discrete levels called “holons.” Each holon has three aspects: (1) its interior, which consists of (2) its parts (which may in turn be separate holons with their own parts), and (3) its surrounding environment (which may be another holon surrounded by its environment). Thus, holons are both parts and wholes simultaneously (Salthe, 1985). A taxonomic holon, for example, is a level that contains other objects (e.g., the species of a genus) and is in turn subsumed by a higher taxon (a

family of genera in the taxonomic hierarchy). If the holon is repeatedly recognized using different techniques, then it is robust (Salthe, 1985, delves into these topics from a philosophical approach; Allen and Starr, 1982, suggest multivariate statistical methods that can be used to detect holons; see also Ahl and Allen, 1996). A holon also exhibits spatiotemporal continuity: whatever it is that we recognize, it is sufficiently stable to persist over some area and last for some recognizable interval of time.

Holons have a history, and they have unique properties that have been determined in part by unique configurations of historical contingency. Hierarchy works by recognizing differences (history); it is what Salthe (1985) calls an *idiographic* approach, which emphasizes particularities. On the other hand, reductionist science works by using observational regularities or similarities (laws) discovered by comparing measurements (Salthe, 1985); reductionism is a nomothetic approach because it seeks general or universal laws. The processes (and their rates) studied using idiographic and nomothetic approaches may not interact directly (Salthe, 1985), thereby isolating the disciplines from one another.

Hierarchies may also be viewed as systems of constraint. When examining a holon we must consider the holon immediately above and that immediately below (which forms the constituent parts of the holon in question; i.e., integration). Higher (larger) holons tend to constrain the behavior of their constituent lower holons because the higher holons provide the environment (boundary conditions) within which lower holons must operate; conversely, lower holons provide the “initiating conditions” or “possibilities,” which, depending upon the boundary conditions, may or may not be realized. The greater the number of boundary conditions, the fewer the possibilities that are realized. Higher-level constraints produce boundaries that are historical in nature, whereas lower-level processes act in a more “lawful” manner (Salthe, 1985). The dynamics of lower levels are rate-dependent because they are dependent upon laws, which are “inexorable ... incorporeal ... and universal,” but they are constrained by rules at higher levels, which are independent of lower level rates because they are “arbitrary, ... structure-dependent, ... [and] ... local. In other words, we can never alter or evade laws of nature; we can always evade and change rules” (Pattee, 1978, in Allen and Starr, 1982, p. 42). History certainly has.

1.4 Rules of taphonomy

Considering that the taphonomy of fossil assemblages has been investigated for at least 500 years, taphonomists ought to have developed some empirical

generalizations – principles or rules – by now. Wilson (1988*b*) lists a number of them, which I have modified or supplemented

- (1) Organisms are more likely to be preserved if they have hardparts.
- (2) Preservation is greatly enhanced by rapid burial, especially in fine-grained sediment (low turbulence) or in the absence of decay and scavenging.
- (3) During the transition from biocoenosis to thanatocoenosis, disarticulation and chemical alteration resulting from decay, abrasion, transportation, predation, scavenging, or dissolution cause loss of information about species abundances and community diversity and structure.
- (4) Fossil assemblages consist of (a) *autochthonous* remains, which represent organisms that lived in the community and may have been preserved in life positions; (b) *paraautochthonous* remains, which are autochthonous components that have been moved (disarticulated, reoriented, concentrated) from their original position by bioturbators, predators, or scavengers, but not transported from another community; and (c) *allochthonous* or foreign remains that have been derived from other communities (Kidwell *et al.*, 1986).
- (5) Taphonomic loss, especially through dissolution and bioerosion, is typically most severe in shallow-water marine environments. Perhaps this “rule” also results from the attention these environments have received from “actuopaleontologists” because of their greater accessibility: salt-marshes, for example, are largely characterized by autochthonous remains (Scott and Medioli, 1980*b*; Behrensmeyer and Hook, 1992; Chapter 10), whereas complete unmixed deep-sea marine records are by no means the norm, despite the “optimistic assessments” of many biostratigraphers and paleoceanographers (Schiffelbein, 1984).
- (6) Information loss in terrestrial and fluvial biotas results largely from transport, disarticulation, sorting, and breakage by water, predators, scavengers, and trampling.
- (7) Bioturbation and physical reworking also cause time-averaging (temporal mixing) of different communities and may lead to *increased* diversity and variation in morphological features of fossil lineages. Temporal mixing often goes unrecognized in fossil assemblages.
- (8) Thus, false First and Last Appearance Datums (FADs and LADs) may result from bioturbation and physical reworking. False LADs are most serious because bioturbation and reworking preferentially mix sediment upward.

- (9) Nevertheless, information *gain* about taphonomic settings and long-term community dynamics may result from the actions of taphonomic agents (this point remains largely unappreciated by those outside the field).
- (10) Furthermore, catastrophic burial or smothering (*obrution*) may result in Lagerstätten that serve as “snapshots” of population dynamics. These “fossil censuses” may not, however, be truly representative of the long-term dynamics of the population, and so multiple snapshots of a fossil biota probably better represent the temporal variation in populations.

As Cadée (1991, p. 16) notes, after half a century of intensive investigation, much of it concentrated in the past decade or two, the number of taphonomic rules “seems rather meager” (see also Olson, 1980). But given the nature of laws and the role of history, this is to be expected (section 1.3; see also Chapter 11). Although we must begin with the assumption of the uniformity of Nature, any application of principles or rules must be done in a *comparative* (case-by-case) manner because each historical entity bears the imprint of the unique (or nearly so) circumstances that led up to it (Olson, 1980; Martin, 1998a).

Not surprisingly, most of these generalizations deal with information loss, lack any true predictive ability, and in hindsight, seem like so much common sense or intuition. But these rules, along with numerous corroborative studies, have served as a foundation for inductive *models* (“an intellectual construct for organizing experience”; Allen and Starr, 1982) and classifications, both of which may be considered “working hypotheses” and which hold the greatest promise for deductive or predictive approaches.

1.5 Models and classifications of fossil assemblages

In this section, I discuss several classifications and models of formation of marine fossil assemblages that emphasize *environmental gradients* of taphonomic processes. The review of these models serves as a foundation for much of the rest of this book: similar classifications and models of fossil vertebrate and plant assemblage formation are explored in succeeding chapters. These sorts of models are of heuristic value because they demonstrate that, although fossil assemblage formation is complex, the character and utility of fossil assemblages can be predicted. Although at first glance the models emphasize information loss, they demonstrate how much paleoenvironmental information can be *gained* through careful analysis of taphonomic pathways and agents (Behrensmeier and Kidwell, 1985; Wilson, 1988b), and how any and all criteria – paleontological, sedimentological, and stratigraphic

– should be brought to bear in paleoenvironmental interpretation. Some of the models also demonstrate the value of *comparing* fossil assemblages of greatly different ages but of similar preservational histories.

1.5.1 Johnson's models of assemblage formation

Johnson's (1960) models of assemblage formation are among the first – if not the very first – to emphasize taphonomic gradients, and other models of marine assemblage formation can be viewed as outgrowths of his work. Johnson (1960) plotted three theoretical *taphonomic modes* of formation of fossil concentrations (especially for bivalves) according to “exposure effects” (a function of residence time at the SWI) versus “transportation effects” (energy + shell import; Figure 1.2). A taphonomic mode is a “recurring pattern of preservation of organic remains in a particular sedimentary context, accompanied by characteristic taphonomic features” (Behrensmeier, 1988, p. 183). Each assemblage mode is characterized by certain taphonomic criteria (Figure 1.2). Model I represents a *census assemblage* which is rapidly buried so that there is little or no chance of transportation: remains are largely autochthonous and some may still be in life position. Model II represents a *low-energy assemblage (within-habitat time-averaged)* dominated by parautochthonous hardparts that mostly exhibit some degree of wear and movement through such agents as waves, currents, and bioturbation. Model III also consists largely of parautochthonous remains, but includes allochthonous hardparts as well, and represents a *high-energy* version of Model II. Although not

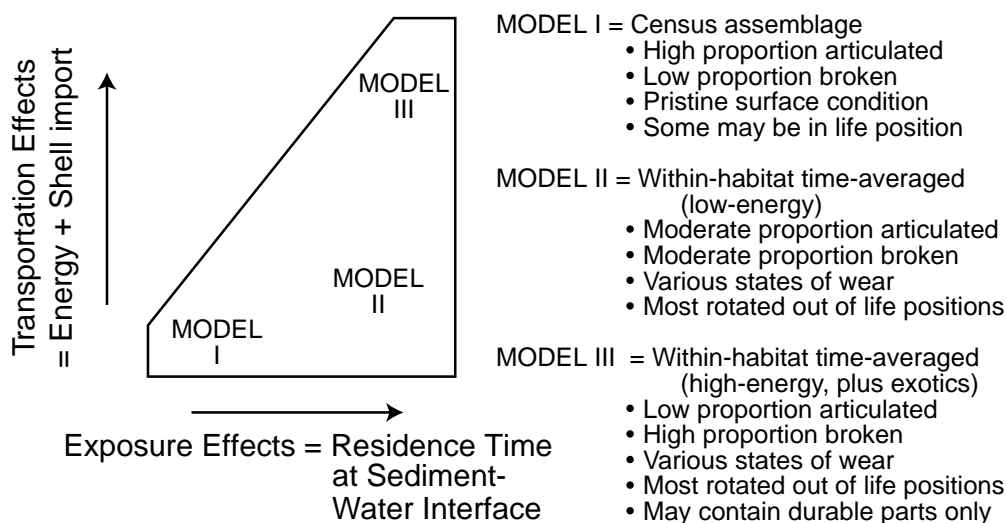


Figure 1.2. Plot of Johnson's (1960) models of fossil assemblage formation according to transportation versus exposure effects. (Redrawn from Kidwell, 1993a, after Johnson, 1960.)

stated explicitly, these models are in effect “end-members” and all gradations of assemblages conceivably occur between these extremes, as indicated by Johnson’s (1960) initial evaluation of the Millerton Formation (Pleistocene, Tomales Bay, California). Johnson’s approach to analyzing fossil assemblages has exerted a tremendous influence on subsequent taphonomic models, such as those that follow.

1.5.2 Biostratinomic classification

Kidwell *et al.* (1986) developed a *descriptive* nomenclature and a *genetic* classification for level (soft)-bottom fossil concentrations along modern and ancient onshore–offshore bathymetric transects. The descriptive procedure uses four features – taxonomic composition, bioclastic packing (biofabric), geometry, and internal structure – that can be used in the field to assess the genetic significance of biostratinomic factors (Figure 1.3), and is intended to “facilitate systematic characterization of local sections in terms of their skeletal concentrations, which are at present underexploited in the differentiation and mapping of sedimentary facies” (p. 236). According to *taxonomic composition*, concentrations may be monotypic or polytypic according to whether they consist of one or more types of skeleton; these terms apply to any taxonomic category appropriate to a study (monotypic accumulations may, for example, be said to consist of bivalves, oysters,

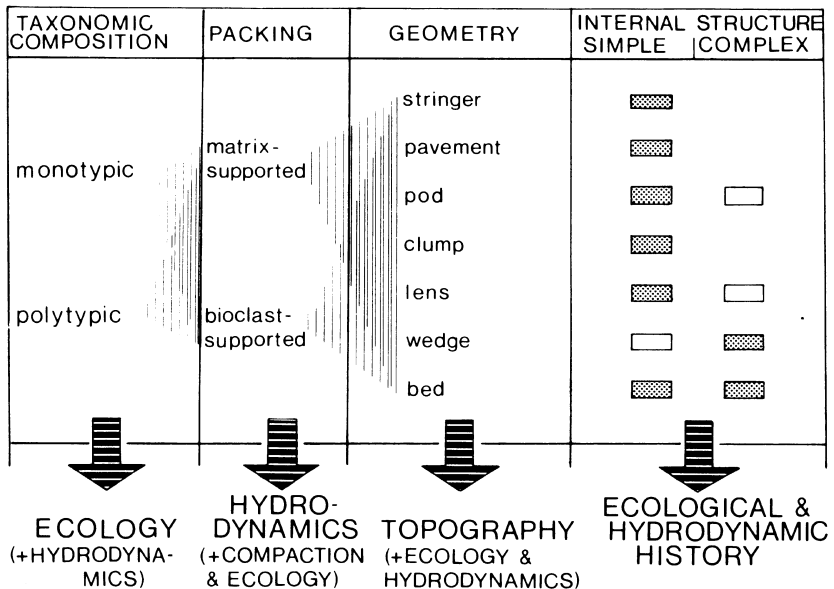


Figure 1.3. Procedure for describing skeletal concentrations proposed by Kidwell *et al.* (1986). (Reprinted with permission of SEPM [Society for Sedimentary Geology].)

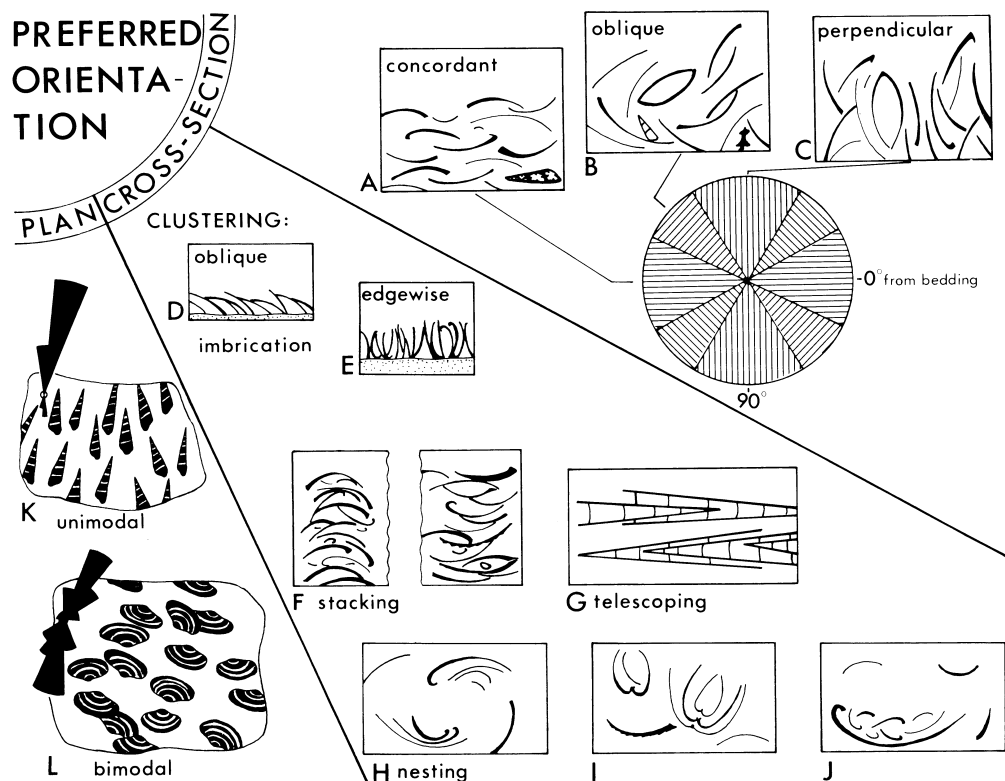


Figure 1.4. Terminology for hardpart orientation and biofabric. (Kidwell *et al.*, 1986; reprinted with permission of SEPM.)

or *Crassostrea virginica*), but the lower the taxonomic level, the greater the ecological or hydrodynamic significance of monotypy.

Biofabric refers to the three-dimensional arrangement of skeletal remains, including orientation, sorting by size and shape, and close-packing, which may range anywhere between matrix and bioclast-supported (Figure 1.3). Biofabric depends mainly on hydrodynamics but may also reflect ecology (life position), necrology (decay), predation, scavenging, bioturbation, and rotation and disarticulation during compaction. Kidwell *et al.* (1986) proposed descriptive terms for hardpart orientation and biofabric (Figure 1.4).

The *geometry* of a fossil deposit depends on a number of factors (Figures 1.3, 1.5), among them antecedent topography (including burrows and crevices); mode of life of the hardpart producers (e.g., whether they lived in clumps, such as oysters or archaeocyathids), biological activity (e.g., bioturbation, selective deposit feeding); and physical processes that produce syngenetic topography (shell lags, channels, etc.).

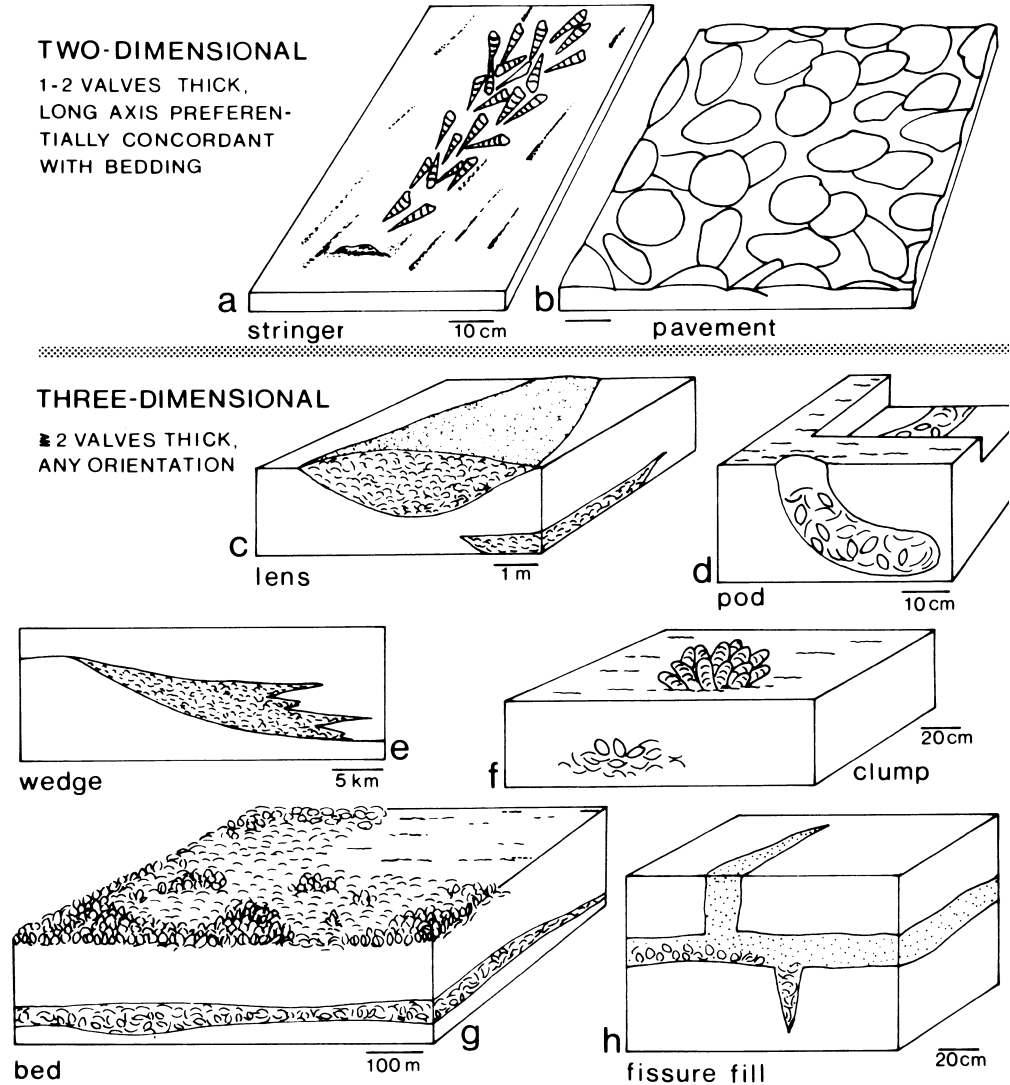


Figure 1.5. Geometry of skeletal accumulations. (Kidwell *et al.*, 1986; reprinted with permission of SEPM.)

The fourth criterion is that of *internal structure* of assemblages. *Simple* concentrations are internally homogeneous or exhibit some monotonic trend, such as upward fining of matrix or bioclasts (e.g., shelly turbidites, “tempestites” or storm deposits). *Complex* concentrations, on the other hand, include assemblages that consist of alternating horizons of articulated and disarticulated hardparts or concentrations that consist of lateral or vertical amalgamations of smaller-scale concentrations. Stringers and pavements are almost always simple, whereas both simple and complex internal structures occur in thicker beds (Figure 1.3).

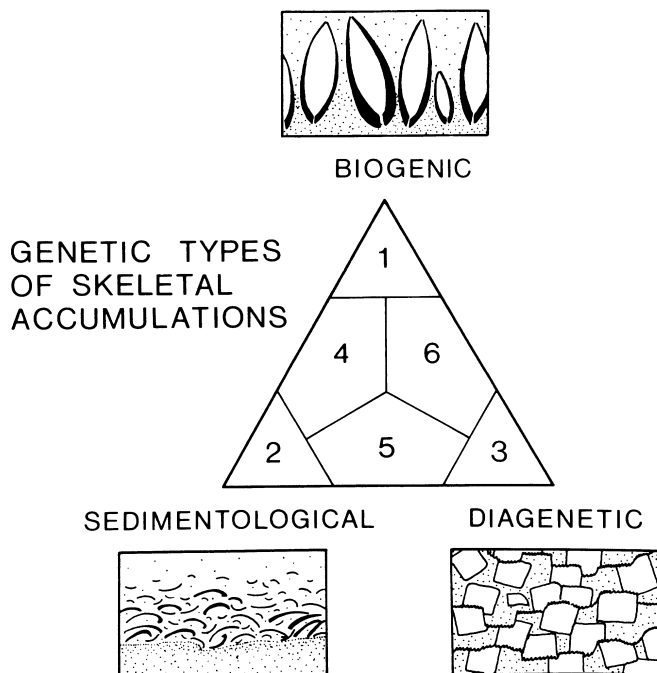


Figure 1.6. Genetic classification of hardpart concentrations consisting of endmember (1–3) and mixed assemblages (4–6). (Kidwell *et al.*, 1986; reprinted with permission of SEPM.)

The genetic classification is represented by a ternary diagram of lithological, biological, and diagenetic end-members (1–3; Figure 1.6) that includes three mixed concentration types (4–6). Any of the six assemblages may be autochthonous, parautochthonous, or allochthonous. *Intrinsic biogenic* concentrations are produced by the gregarious behavior of organisms in life through, for example, preferential colonization of sites already occupied by adults (e.g., brachiopods, vermetid gastropods, oysters) or their remains in death, and are usually autochthonous or parautochthonous. *Extrinsic biogenic* concentrations result from the interactions of organisms with other skeletonized organisms or their hardparts, and are typically parautochthonous or allochthonous; such assemblages include subsurface layers produced by Conveyor Belt (“head-down”) Deposit Feeders (CDFs; van Straaten, 1952; Rhoads and Stanley, 1965; Cadée, 1976; Meldahl, 1987; Boudreau, 1997), shell-filled shallow excavations produced by skates and rays (Gregory *et al.*, 1979; Fürsich and Flessa, 1987), accumulations produced by birds (Teichert and Serventy, 1947; Lindberg and Kellogg, 1982; Meldahl and Flessa, 1990), and *Diopatra* burrows lined by shells (Schäfer, 1972). In either case, live–dead interactions can change the physical nature of the

substratum and influence the structure of benthic communities via *taphonomic feedback* (Kidwell and Jablonski, 1983; Kidwell, 1986b).

Sedimentological concentrations result primarily from hydraulic processes of hardpart concentration. Such accumulations include (1) winnowed, parautochthonous fair-weather or storm lags (cf. model II of Johnson, 1960); (2) gradual accumulations of autochthonous–parautochthonous hardparts during intervals of low net sedimentation (cf. model II of Johnson, 1960); and (3) transport of allochthonous hardparts into otherwise autochthonous–parautochthonous assemblages (model III of Johnson, 1960).

Diagenetic concentrations result from physical and chemical processes that significantly concentrate shells after burial, including compaction (Fürsich and Kauffman, 1984), selective pressure solution, which concentrates fossils along stylolites in limestones, or the destruction of hardparts in adjacent beds (Fürsich, 1982; Haszeldine, 1984).

Mixed concentrations result from the interaction of two or more end-members, one of which may strongly overprint the other. Oyster biostromes formed by gregarious settlement or pavements of wave or tidal current-oriented shells of the high-spired gastropod *Turritella* (unimodal or telescoped orientations of Figure 1.4) may be further concentrated by hydraulic sorting (Figure 1.6, area 4). In some cases, hydraulic reworking may be sufficient to obliterate any evidence of biogenic accumulation, but if the reworked shells are judged to be strictly allochthonous, the accumulation is classified as sedimentological rather than overprinted biogenic; such overprinting may be indicated by lenses of hydraulically oriented specimens of species that are also found in surrounding or adjacent biogenic accumulations. Early cementation of hydraulically sorted shell pavements or of concretions following mass mortality (Brett and Baird, 1986) results in mixed assemblages of types 5 and 6, respectively.

Kidwell *et al.* (1986) suggested that the ternary genetic classification was applicable to environmental gradients across many soft-bottom environments (Figure 1.7), such as those preserved in the Miocene Calvert, Choptank, and St Mary's Formations of Maryland; Triassic Muschelkalk (Aigner, 1982a, 1985); and Pliocene Purisima Formation of California (Norris, 1986). Intertidal and supratidal flats are characterized by both biogenic accumulations (e.g., oyster bars, subsurface CDF-generated shell beds, ray pits, bird nests, hermit crab-generated concentrations) and winnowed lags. Biogenic accumulations also occur in lagoons, but sedimentological concentrations are likely to be represented by storm washovers and flood deposits. Similarly, beaches and shallow subtidal shoals consist almost entirely of sedimentological concentrations formed through