

Actualistic Taphonomy: Death, Decay, and Disintegration in Contemporary Settings

MICHAŁ KOWALEWSKI

*Department of Geosciences, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061,
Email: michalk@vt.edu*

MICHAEL LABARBERA

Department of Organismal Biology and Anatomy, The University of Chicago, 1027 East 57th St., Chicago, IL 60637

PALAIOS, 2004, V. 19, p. 423–427

INTRODUCTION

When Leonardo da Vinci contended that fossil shells of Monferrato (Lombardy, Italy) were not left there by the biblical deluge, he argued the point by observing that neither live bivalves nor their empty shells possibly could have traveled 250 miles from the Adriatic to Monferrato in 40 days (MacCurdy, 1938; Cadée, 1990). Five centuries later, the approach pioneered by the Tuscan scholar has become a discipline in its own right: it will be referred to here as Actualistic Taphonomy. Taphonomy denotes the study of fossilization processes: a search for principles governing the transition of organismal remains from the biosphere to the lithosphere (Efremov, 1940). Actualistic denotes the study of present-day patterns and processes in search for clues helpful in investigating their historical records. Practitioners of Actualistic Taphonomy collect observations on death, decay, and burial of organisms in contemporary settings to aid and guide interpretations of diverse data offered by the fossil record.

This special issue of PALAIOS includes eight case studies representing a diverse cross-section of the research themes of modern actualistic taphonomy. All projects have been conducted in the same study area (San Juan Islands, Washington State, USA), and represent the efforts of students who attended a 5-week field course offered in summer 2002 at Friday Harbor Laboratories of the University of Washington (Fig. 1). The fact that the eight projects offer such a diverse spectrum of research themes despite the similarity in geographic setting and logistics is an excellent demonstration of the remarkable intellectual breadth of actualistic taphonomy.

Hopefully this volume will offer a useful reference for all those who are interested in fossilization processes or who need to assess the quality of the fossil record to carry out their research. In this brief introduction, highlights are provided for the major research themes and methodological approaches of actualistic taphonomy that are represented in this volume. Also, a brief synopsis of each of the case studies is included below.

ACTUALISTIC TAPHONOMY: RESEARCH THEMES

Taphonomic research can be subdivided in various

ways, depending on one's classifying criteria and on what research aspects are viewed as fundamental. The research themes defined here (see Table 1) have been erected here specifically in the context of the research represented in this volume: they reflect our subjective view of what aspects of taphonomy deserve theme status. This is certainly not the only way to subdivide taphonomy—indeed, others may contend that this is neither the most exhaustive nor the most effective classificatory system. The classification below and Table 1 both serve primarily to guide readers through the projects published in this issue while making explicit intellectual threads that link these diverse studies.

The eight studies presented in this issue encompass five distinct research themes: (1) necrolysis, (2) biostratinomy, (3) comparative taphonomy, (4) fidelity, and (5) methodology of taphonomy (see Table 1 for definitions). Necrolysis is the primary focus of the experimental study on angiosperm leaves (Gupta and Pancost, 2004). Biostratinomy is the main theme of experimental projects on mollusks (Lazo, 2004) and brachiopods (Messina and LaBarbera, 2004). Other projects included in this volume that touch on this theme include the studies on bulk-sampled benthic invertebrates (Hannisdal, 2004), biogenic vertebrate accumulations (Terry, 2004), and brachiopod life and death assemblages (Tomašových, 2004). Comparative taphonomy is the primary focus of the comparative field-experimental study on mollusks (Lazo, 2004) and the methodological study comparing benthic invertebrate assemblages sampled across a depth gradient (Rothfus, 2004). Other projects included here that contain aspects of comparative taphonomy include the necrolysis of angiosperm leaves (Gupta and Pancost, 2004), the sieve effects on invertebrate bulk samples (Hannisdal, 2004), and the experimental research on brachiopod shells (Messina and LaBarbera, 2004). Fidelity assessment is the main goal of the studies on brachiopod morphometrics (Krause, 2004), anatomical composition of vertebrate bone assemblages (Terry, 2004), and the size-frequency distributions of brachiopod life and death assemblages (Tomašových, 2004). Methodological issues are the focus of two studies—one dealing with bulk-sampled benthic shelly assemblages and the assessment of the biasing effects of operator error (Rothfus, 2004), the other examining the effects of sieving on quantitative data used to study comparative taphonomic patterns (Hannisdal, 2004).

Three research themes included in this classification (post-burial taphonomy, time-averaging, and computer



FIGURE 1—Diverse taphonomic research settings available around the San Juan Islands. (A) A sample of live and dead invertebrates obtained by dredging off the coast of San Juan Island (photograph by Adam Tomašových). (B) The well-sorted sand tidal flats of False Bay, San Juan Island; a few miles southwest of Friday Harbor Laboratories (photograph by Jennifer Stempien). Note tidal channel in the upper left of the photo. (C) The intertidal inlet of Argyle Creek (San Juan Island). A mixture of subtidal and intertidal animals can be observed readily in this unusual, but very accessible habitat (photograph by Jennifer Stempien). Puget Sound is located to the left of this image, Argyle Lagoon to the right.

simulations; see Table 1) are not the primary focus of any of the studies in this theme issue. However, some of the studies touch on time-averaging (Krause, 2004; Terry, 2004; Tomašových, 2004) and some (especially Hannisdal, 2004; Tomašových, 2004) may be of relevance to those who are interested in computer simulations. Not surprisingly, perhaps, given the exclusively actualistic focus of this issue, research on post-burial taphonomy is not represented here.

RESEARCH STRATEGIES

There are basically three ways to acquire data that are directly relevant to actualistic taphonomic research, one observational and two experimental in approach. First, data can be acquired in the field by making direct observations on, and/or collecting samples of organisms and their remains in modern environments. Second, data can be collected by conducting field experiments (“let nature take its course”) based on various specimen-deployment and/or specimen-marking strategies. Finally, data may be collected in the laboratory setting (variables isolated and controlled) by conducting experiments on models or on specimens. Individual studies may integrate these strategies by combining experimental and field data into a single analysis.

Obviously, the applicability of each strategy varies somewhat depending on the research theme. For example, direct estimates of fidelity are most accessible in a field

setting and typically involve bulk sampling. Conversely, compaction processes (an aspect of post-burial taphonomy) may be simulated in the laboratory, but can hardly be studied in modern depositional settings. Nevertheless, all three approaches are applicable for virtually all themes of actualistic taphonomy (see Table 1). The studies included in this theme issue support this claim, as all three approaches are represented here, and some of the studies combine multiple approaches.

Laboratory experiments are the primary focus of projects on leaf necrolysis (Gupta and Pancost, 2004) and brachiopod shell movement (Messina and LaBarbera, 2004). Also, analysis of operator error (Rothfus, 2004) is based primarily on data that, by definition, can only be collected in a laboratory setting. Field experiments are an important part of the study on brachiopod shell biostratigraphy (Messina and LaBarbera, 2004). Field data are a primary focus of the majority of projects presented in this issue, including marine benthic shell assemblages (Hannisdal, 2004; Rothfus, 2004), brachiopod shell and specimen samples (Krause, 2004; Tomašových, 2004), bivalve specimen samples (Lazo, 2004), and terrestrial vertebrates (Terry, 2004).

Regardless of their origin, nearly all studies presented here focus on quantitative variables or quantified categorical data that can be treated in a statistically rigorous manner. The only (understandable) exception is the study on leaf necrolysis (Gupta and Pancost, 2004), which pri-

TABLE 1—Main themes of research of actualistic taphonomy and their representation in this special issue; *** = denotes primary research strategy, which serves as a principal venue for extensive investigations and often provides the best type of data (i.e., predominately direct, or otherwise useful, estimates of taphonomic parameters); ** = denotes important research strategy, which may serve as a primary venue for investigations and often provides high-quality data, including direct or otherwise useful estimates of taphonomic parameters; * = denotes secondary research strategy, which rarely serves as a primary venue for investigations and typically provides supplementary, indirect estimates of taphonomic parameters.

Research Themes of Actualistic Taphonomy	Brief Explanation	Actualistic Research Strategies			Selected Literature Examples	This issue	
		Laboratory experiments	Field experiments	Field observations in modern environments		Primary focus	Secondary relevance
Necrolysis and Soft-Tissue Preservation	Study of decay and decay-related processes, including soft-tissue mineralization	***	***	***	Allison, 1988; Briggs and Kear, 1994	Gupta and Pancost	—
Biostratigraphy	Study of pre-burial processes (disintegration, breakage, biological/chemical/physical alterations, weathering, transport, bioturbation, reworking, burial, etc.)	***	***	***	LaBarbera, 1977; Behrensmeyer, 1978	Lazo; Messina and LaBarbera	Hannisdal; Terry; Tomašových
Post-burial Taphonomy	Study of post-burial processes (compaction, dissolution, diagenesis, metamorphism, outcrop weathering, collection biases, etc.)	**	*	*	Flessa et al., 1992; Allison and Pye, 1994	—	—
Comparative Taphonomy and Taphofacies	Comparative study of taphonomic patterns and processes; in particular, explicit application of taphonomic data in paleoenvironmental and facies interpretations	*	**	***	Meldahl and Flessa, 1990; Best & Kidwell, 2000	Lazo; Rothfus	Gupta and Pancost; Hannisdal; Messina and LaBarbera
Fidelity and Biases	Study of the quality of data provided by the fossil record, including fidelity of anatomical, biogeochemical, ecological, and evolutionary data, as well as stratigraphic and secular megabiases	*	*	***	Schopf, 1978; Kidwell, 2001	Krause; Terry; Tomašových	Lazo
Time-averaging	Study of the spatial and temporal resolutions of fossil assemblages, including both direct estimates (e.g., ¹⁴ C dating) and various indirect proxies	*	*	***	Flessa et al., 1993; Carroll et al., 2003	—	Krause; Terry; Tomašových
Methodology of Taphonomy	Study of sampling techniques, sample-processing strategies, and analytical methods applied to taphonomic data	***	***	***	Kowalewski et al., 1995; Kidwell et al., 2001	Hannisdal; Rothfus	All studies
Computer Simulations Applied to Actualistic Data	Study of taphonomic processes and patterns via computer simulations, including both data-free models and data-based simulations	***	***	***	Behrensmeyer and Chapman, 1993; Olszewski, 1999	—	Hannisdal; Tomašových

marily focused on chemical and morphological aspects of soft-tissue decomposition.

BRIEF SYNOPSES OF THE FRIDAY HARBOR PROJECTS

The eight projects included here (Table 2) cover a wide range of environments—from inland forests to offshore

subtidal benthic habitats 100 m deep. Also, they target diverse organisms, including vascular plants (angiosperms), vertebrates, and multiple groups of invertebrates (brachiopods, gastropods, and bivalves). Here, each of those projects is discussed briefly in the order in which they appear in this issue.

Gupta and Pancost report detailed chemical and morphological observations on decay and decomposition of an-

TABLE 2—Summary of actualistic taphonomic studies included in this volume. The studies are arranged according to primary research theme.

Study	Primary Research Theme (see also Table 1)	Other Research Themes (see also Table 1)	Main Research Strategies	Targeted Organisms	Quantitative Data/Analysis
<i>Research Reports</i>					
Gupta and Pancost	Necrolysis	Comparative Taphonomy	Laboratory Experiments	Angiosperms	No
Messina and LaBarbera	Biostratinomy	Comparative Taphonomy	Laboratory & Field Experiments	Brachiopods	Yes
Lazo	Comparative Taphonomy	Biostratinomy, Fidelity	Field Data	Mollusks	Yes
Krause	Fidelity	Time-averaging	Field Data	Brachiopods	Yes
Tomašových	Fidelity	Time-averaging, Biostratinomy	Field Data	Brachiopods	Yes
Terry	Fidelity	Biostratinomy	Field Data	Vertebrates	Yes
<i>Research Letters</i>					
Hannisdal	Taphonomic Methods	Comparative Taphonomy, Biostratinomy	Field Data	Brachiopods/Mollusks	Yes
Rothfus	Taphonomic Methods	Comparative Taphonomy	Laboratory Experiments	Brachiopods/Mollusks	Yes

giosperm leaves. Thanks to a careful experimental design, the study also provides important insights into differences in decay patterns between freshwater and marine settings.

Messina and LaBarbera report on the transport characteristics of articulate brachiopod shells in both lab and field settings, with particular attention to their behavior on unconsolidated substrates.

Lazo exploits the unusual field opportunity—provided by a single species of bivalve that occurs both epifaunally and infaunally—to quantify differences in taphonomic alteration patterns between conspecifics that differ in their mode of life. This is a first rigorous analysis that assesses the importance of mode of life while controlling for biology; typically, epifaunal and infaunal taphonomic patterns are assessed using different suites of species.

Krause employs geometric morphometric techniques to compare the morphospace of live brachiopods with the morphospace defined by samples of brachiopod shells taken from a time-averaged death assemblage. This is the first rigorous study evaluating the morphological fidelity of time-averaged brachiopod shell accumulations, and one of the first studies of that type, in general.

Tomašových provides outstanding documentation of size-frequency patterns in the living populations and time-averaged death assemblages of brachiopods. Particularly noteworthy is the inclusion of very small (early juvenile) size classes of brachiopods that rarely have been included in previous actualistic and/or paleontological quantitative studies. In general, despite the common usage of size distributions in paleoecological studies of brachiopods, very few actualistic taphonomic projects have been conducted on this issue to date.

Terry documents the early phases in the formation of vertebrate bone assemblages resulting from predation by carnivorous birds (owls). Owl pellets are an important source of fossil data on many small mammals. Whereas previous taphonomic research emphasized the biasing processes that occur during digestion and pellet formation, this project provides the first description of degrada-

tion of pellets in natural settings after they are expelled from the owl.

Hannisdal uses bulk samples of marine benthic shelly assemblages to assess quantitatively the consequences of sieving that eliminates finer fractions of skeletal material. Although primarily of methodological relevance, this study also should be of interest to anyone interested in comparative taphonomy (especially, taphofacies analysis).

Rothfus documents the importance of operator disagreement in taphonomic analysis. Taphonomists often have expressed concerns about highly subjective and arbitrary scoring of specimens in terms of their taphonomic characteristics. This study provides a first numerical evaluation of the consequences of operator error for precision and accuracy of estimates such as taphonomic grades that are often used to quantify preservational state of skeletal remains.

It is hoped that these short descriptions help the reader appreciate the overall breadth and specific focus of the projects included in this volume. However, the major conclusions of the projects quite deliberately have not been revealed. These conclusions belong to their authors, and the readers need to go beyond those introductory pages to learn more. It will be well worth the effort!

CLOSING REMARKS

Although the study of fossilization processes encompasses a great diversity of topics and methods, the actualistic approach remains the most active and arguably the most critical area of research within taphonomy. Modern depositional environments and laboratory settings continue to be an inspiring and remarkably fertile source of diverse taphonomic data, often advancing fundamentally the understanding of fossilization processes and the perception of the nature of biological information preserved in the sedimentary record. Friday Harbor Laboratories have a long tradition as a potent playground for important taphonomic research (e.g., Schopf, 1978; Kidwell and LaBarbera, 1993). The thematic and methodological

wealth of this special issue offers a convincing advertisement of the dynamic status of actualistic taphonomy and a forceful demonstration of the enormous opportunities that are continuously provided by contemporary settings that surround us.

ACKNOWLEDGEMENTS

We sincerely and fervently thank all the students who attended the Friday Harbor Course on taphonomy and made this special issue possible. Their dedicated work and their enthusiasm are the primary reason for the success of our field course, as documented in this volume. We also thank the staff and faculty of Friday Harbor Laboratories for the generous financial support, unwavering intellectual help, and continuous logistic backing. We thank Chris Maples, Sara Marcus, and numerous reviewers for the hard editorial work that greatly improved the final product presented below.

REFERENCES

- ALLISON, P.A., 1988, The role of anoxia in the decay and mineralization of proteinaceous macro-fossils: *Paleobiology*, v. 14, p. 139–154.
- ALLISON, P.A., and PYE, K., 1994, Early diagenetic mineralization and fossil preservation in modern carbonate concretions: *PALAIOS*, v. 9, p. 561–575.
- BEHRENSMEYER, A.K., 1978, Taphonomic and ecologic information from bone weathering: *Paleobiology*, v. 4, p. 150–162.
- BEHRENSMEYER, A.K., and CHAPMAN, R.E., 1993, Models and simulations of time-averaging in terrestrial vertebrate accumulations: in Kidwell, S.M., and Behrensmeier, A.K., eds., *Taphonomic Approaches to Time Resolution in Fossil Assemblages*: Paleontological Society, Knoxville, Short Courses in Paleontology no. 6, p. 125–149.
- BEST, M.M.R., and KIDWELL, S.M., 2000, Bivalve taphonomy in tropical mixed siliciclastic-carbonate settings; I, Environmental variation in shell condition: *Paleobiology*, v. 26, p. 80–102.
- BRIGGS, D.E.G., and KEAR, A.J., 1994, Decay and mineralization of shrimps: *PALAIOS*, v. 9, p. 431–456.
- CADÉE, G.C., 1990, The history of taphonomy: in Donovan S.K., ed., *The Processes of Fossilization*: Belhaven Press, London, p. 3–21.
- CARROLL, M., KOWALEWSKI, M., SIMÕES, M.G., and GOODFRIEND, G.A., 2003, Quantitative estimates of time-averaging in brachiopod shell accumulations from a modern tropical shelf: *Paleobiology*, v. 29, p. 382–403.
- FLESSA, K.W., KOWALEWSKI, M., and WALKER, S.E., 1992, Post-collection taphonomy: shell destruction and the Chevrolet: *PALAIOS*, v. 7, p. 555–556.
- FLESSA, K.W., CUTLER, A.H., and MELDAHL, K.H., 1993, Time and taphonomy: Quantitative estimates of time-averaging and stratigraphic disorder in a shallow marine habitat: *Paleobiology*, v. 19, p. 266–286.
- GUPTA, N.S., and PANCOST, R.D., 2004, Biomolecular and physical taphonomy of angiosperm leaf during early decay: implications for fossilization: *PALAIOS*, v. 19, p. 428–440.
- HANNISDAL, B., 2004, Clams and brachiopods: chips that pass out of sight: *PALAIOS*, v. 19, p. 507–513.
- KIDWELL, S.M., 2001, Preservation of species abundance in marine death assemblages: *Science*, v. 294, p. 1091–1094.
- KIDWELL, S.M., and LABARBERA, M., 1993, Experimental taphonomy: *PALAIOS*, v. 8, p. 217–218.
- KIDWELL, S.M., ROTHFUS, T.A., and BEST, M.M.R., 2001, Sensitivity of taphonomic signatures to sample size, sieve size, damage scoring system, and target taxa: *PALAIOS*, v. 16, p. 26–52.
- KOWALEWSKI, M., FLESSA, K.W., and HALLMAN, D.P., 1995, Ternary taphograms: Triangular diagrams applied to taphonomic analysis: *PALAIOS*, v. 10, p. 478–483.
- KRAUSE, R.A., JR., 2004, An assessment of morphological fidelity in the sub-fossil record of a terebratulide brachiopod: *PALAIOS*, v. 19, p. 460–476.
- LABARBERA, M., 1977, Brachiopod orientation to water movement; 1, Theory, laboratory behavior, and field orientations: *Paleobiology*, v. 3, p. 270–287.
- LAZO, D.G., 2004, Bivalve taphonomy: testing the effect of life habits on the shell condition of the Littleneck Clam *Protothaca (Protothaca) staminea* (Mollusca: Bivalvia): *PALAIOS*, v. 19, p. 451–459.
- MACCURDY, E., 1938, *The Notebooks of Leonardo da Vinci* (2 vols): Jonathan Cape, London, 1247 p.
- MELDAHL, K.H., and FLESSA, K.W., 1990, Taphonomic pathways and comparative biofacies and taphofacies in a Recent intertidal/shallow shelf environment: *Lethaia*, v. 23, p. 43–60.
- MESSINA, C., and LABARBERA, M., 2004, Hydrodynamic behavior of brachiopod shells: experimental estimates and field observations: *PALAIOS*, v. 19, p. 441–450.
- OLSZEWSKI, T., 1999, Taking advantage of time-averaging: *Paleobiology*, v. 25, p. 226–238.
- ROTHFUS, T.A., 2004, How many taphonomists spoil the data? Multiple operators in taphofacies studies: *PALAIOS*, v. 19 p. 514–519.
- SCHOPF, T.J.M., 1978, Fossilization potential of an intertidal fauna: Friday Harbor, Washington: *Paleobiology*, v. 4, p. 261–269.
- TERRY, R.C., 2004 Owl pellet taphonomy: a preliminary study of the post-regulation taphonomic history of pellets in a temperate forest: *PALAIOS*, v. 19 p. 497–506.
- TOMAŠOVÝCH, A., 2004, Postmortem durability and population dynamics affecting the fidelity of brachiopod size-frequency distributions: *PALAIOS*, v. 19 p. 477–496.

ACCEPTED MAY 28, 2004

