



Chapter 10

Author: LINDSAY, EVERETT

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Chapter 10

Chronostratigraphy, Biochronology, Datum Events, Land Mammal Ages, Stage of Evolution, and Appearance Event Ordination

EVERETT LINDSAY¹

ABSTRACT

Chronostratigraphy and biochronology are the prime conceptual methods for relating biologic events to the geologic time scale. Chronostratigraphy is the dominant method applied in the oceanographic-marine realm, and biochronology is the dominant method for the terrestrial realm. These concepts were conceived in the early half of the 20th century, and major advances in both occurred during the latter half of the 20th century. Historical development of both chronostratigraphy and biochronology is briefly reviewed, and it is concluded that the early definition and application of biochronology is tainted by reference to and inference from biostratigraphy. It is proposed that biochronology be redefined as *the organization of geologic time according to the irreversible process of organic evolution*, following the characterization and application by Berggren and Van Couvering (1978, G.V. Cohee, M.F. Glaessner, and H.D. Hedberg [editors], Contributions to the geologic time scale: 39–55. Tulsa, OK: American Association of Petroleum Geologists). The new term “chronostratigraphic marker” is proposed and defined as *any chronologically significant event (biologic, isotopic, isotopic-ratio, or paleomagnetic), recorded in a stratigraphic sequence, that can be directly related to and/or tied to any other chronostratigraphic marker*. According to definitions given herein, a biochronologic event can become a chronostratigraphic marker, but only when tied to a discrete stratigraphic sequence and related to other stratigraphic sequences and/or chronostratigraphic markers.

The terms and concepts “datum event”, “land mammal age”, “stage of evolution”, and “appearance event ordination” are discussed and defined. A datum event is defined as *any chronostratigraphic marker*. Land mammal ages, along with European Neogene and Paleogene mammal units, are considered biochronologic entities; they are defined as *relatively short intervals of geologic time that can be recognized and distinguished from earlier and later such units (in a given region or province) by a characterizing assemblage of mammals*. Stage of evolution is a very basic biochronologic concept defined as *the chronologic ordering of faunal assemblages based on morphological (evolutionary) differences observed in members of a single, well-established phyletic lineage*. Appearance event ordination is a new tool of biochronology. It is defined as *ordering the appearance of fossil mammal genera by multivariate analysis, using overlapping (conjunctive) and nonoverlapping (disjunctive) range distributions in large sets of data*.

INTRODUCTION

The latter half of the 20th century has witnessed a tremendous burst of knowledge related to geochronology. This “progress” has

required numerous additions to and revisions of the geologic time scale, driven by new applications or new standards. For example, Gilluly et al. (1960: 99) in the second edition of their textbook *Principles of Geology* listed

¹ Professor Emeritus, Department of Geosciences, University of Arizona, Tucson, AZ 85721.

the age of the Earth as approximately 2.5 Ga. This age was based on potassium/argon (K/Ar) dating of volcanic rocks in southeastern Manitoba, as detailed in their textbook. Around the same time, the International Union of Geological Sciences (IUGS) was established, with a Commission on Stratigraphy to promote stability and uniformity in the "Standard Stratigraphic Scale," the forerunner of the geologic time scale. About 20 years later, Harland et al. (1982) published *A Geologic Time Scale*, updating and clarifying the calibrated framework for geochronology based on new constants for isotopic dating along with an early calibration of the geomagnetic polarity time scale (GPTS). Estimates of the age of the Earth almost doubled, to 4.6 Ga, during that 20-year interval.

The latter half of the 20th century also marked the development of stratigraphic guides as well-reasoned and widely used guidelines for terminology and practices in geology, especially as relating to geochronology and stratigraphy. The first attempt at a North American stratigraphic guide was published in 1933 as the "Ashley code" (Ashley et al., 1933). This was followed by a series of informal notes from practicing stratigraphers, which resulted in extensive discussion and culminated in a formal, revised stratigraphic code, published by the American Association of Petroleum Geologists, known as the North American Code of Stratigraphic Nomenclature (NACSN) (American Commission on Stratigraphic Nomenclature [ACSN], 1961, 1970 [revised version]). This code was intended as the final word in stratigraphic nomenclature and practice; it has been emended and amended repeatedly over 40 years, usually with beneficial results. Similar codes of stratigraphic nomenclature and practice were developed by geologists in other parts of the world, and in 1976 the first *International Stratigraphic Guide* (ISG-1) was published by the International Subcommittee on Stratigraphic Classification of the IUGS (Hedberg, 1976). In 1994 the second *International Stratigraphic Guide* (ISG-2), with a number of significant additions, was published by the same Subcommittee (Salvador, 1994). It is likely that more revisions and additions to

the codes of stratigraphic nomenclature will be required as our knowledge advances.

I stress these points because during more than five decades of development and codification of stratigraphic nomenclature, the primary unit of North American vertebrate chronology—the land mammal age (LMA)—has never been mentioned in any of these stratigraphic guides, nor has terrestrial stratigraphy (with the exception of pedostratigraphic [soil], allostratigraphic [alluvial], or glacial units) ever been discussed in any of the stratigraphic codes. The authors of these codes have implied that the principles of marine stratigraphy are directly applicable to terrestrial stratigraphy and that a single set of stratigraphic principles (and terminology) developed for marine deposits is directly applicable to the realms of both oceanic and terrestrial stratigraphy. I believe this reasoning is counterproductive. The terms and concepts developed and applied by vertebrate paleontologists for application in terrestrial stratigraphy and biochronology during the last five decades should not be ignored; they should be defined and discussed in the context of stratigraphic codes. Communication of this nature will surely promote better understanding among earth scientists and should help to clarify and support the application of biologic events for geochronology. This contribution is directed toward that lofty goal. First, however, a review of the history and principles of chronostratigraphy and biochronology is needed to set the stage for these arguments.

HISTORY AND PRINCIPLES OF CHRONOSTRATIGRAPHY

The chronostratigraphic concept was introduced by Schenck and Muller (1941) to resolve a problem stratigraphers had created by correlating bodies of rock (lithostratigraphic units) directly with units of time (chronologic units). For example, the concept of the Devonian Period was based on contorted rocks in southern England (Sedgwick and Murchison, 1839), but the characterization of Devonian life was based primarily on fossils and rocks from Germany (Berry, 1968). The Devonian rocks in Germany (where Schenck and Muller had worked) were more complete

and therefore were better suited for developing a comprehensive chronologic framework for the Devonian Period. Schenck and Muller invented a way to resolve correlation of Devonian sediments, whether in England, Germany, or any other global location, with a complete Devonian Period. They did this by proposing a new “chronostratigraphic” hierarchy (System, Series, and Stage) for the stratigraphic representation of equivalent chronologic intervals (Period, Epoch, and Age) of the Devonian. Schenck and Muller (1941) characterized the development of chronostratigraphic units, and their relationship to lithologic units, by a four-step procedure. First, the stratigrapher studies a continuous section of strata, collecting fossils and carefully noting their position in the stratigraphic sequence; second, the fossils are identified and their stratigraphic ranges are accurately determined; third, stratigraphic ranges of the fossils are analyzed, grouping the strata by fossil content (and the absence of some fossils in other parts of the section); fourth, similar sections and different facies are sampled in other areas to test the repetition of the stratigraphic sequence of fossils discovered in the third step. Schenck and Muller characterized the stratigraphic sequence of fossils determined in step 3 as a “provisional” time-stratigraphic unit, with its validation resulting from repeated testing (and verification) throughout the entire geologic province (i.e., step 4). This time-honored biostratigraphic procedure remains the foundation of chronostratigraphic practices, with the addition of new tools (e.g., radiometric, isotopic, and magnetostratigraphic data) to the biostratigraphic methods advocated by Schenck and Muller.

Schenck and Muller (1941: table 1) illustrated the chronostratigraphic units and corresponding chronologic units in separate columns next to one another, and they oriented the local or geographically restricted lithologic units perpendicular to the chronostratigraphic and chronologic columns (see fig. 10.1). This was done to emphasize the temporal relationship between chronostratigraphic and chronologic units, and the lack of temporal relationship between lithostratigraphic and chronologic units. Schenck and Muller also emphasized that the boundaries of lith-

Geologic-Time Units	Chrono-Stratigraphic Units	Rock-Stratigraphic Units
Era Period Epoch Age -----	----- System Series Stage Zone	Group Formation Member, etc. Bed, etc.

Fig. 10.1. Relationship between geologic time units, chronostratigraphic units, and rock-stratigraphic units (based on table 1 of Schenck and Muller, 1941).

ostratigraphic units might represent a hiatus and are frequently time-transgressive.

The unique features that distinguish chronostratigraphic and geochronologic units from lithologic, biostratigraphic, and similar units of earth history are: (1) *time units cannot overlap*, and (2) *time units must be complete, lacking any temporal gaps*. It is well established that rock units overlap, and detailed study of sediments indicates that virtually no thick record of sedimentation is continuous. The key to developing chronostratigraphic units, and differentiating them from rock units, is that *the boundaries of chronostratigraphic units are always isochronous*, whereas the boundaries of rock units are usually time-transgressive. To my knowledge, Schenck and Muller never stated this; apparently, the principle was developed later by Hedberg (1951) to clarify the nature of time-stratigraphic units relative to geologic time units. Both ISG-1 (Hedberg, 1976: 67, 95) and ISG-2 (Salvador, 1994: 78, 92) explicitly state that boundaries of chronostratigraphic units are isochronous.

This is the legacy that Schenck and Muller left us, the kernel of truth that has never been adequately emphasized in stratigraphic guides. This feature distinguishes rock from time-rock units; it is the primary reason that time-rock units represent units of time.

So, how do we demonstrate that boundaries of chronostratigraphic units are isochronous? With great difficulty! Stratigraphers had no tools for demonstrating a stratigraphic isochron prior to the invention of isotopic

geochronology and magnetostratigraphy more than 30 years ago. Before that time the concept of chronostratigraphic units was widely accepted, but isochronous boundaries of chronostratigraphic units were rarely challenged. For more than 100 years biostratigraphers made approximations of chronologic correlation by application of the Opeelian zone or its modern analogue, the concurrent-range zone. A guiding principle of an Opeelian or concurrent-range zone is to use overlapping ranges of several fossil taxa to identify the zone and its boundaries. By applying the overlapping ranges of several taxa, the presence of a significant hiatus within the zone is minimal, and the probability that a hiatus is located at the zonal boundary is greatly reduced. During the last 10 to 20 years the practice of applying overlapping ranges of several fossil taxa to define or identify chronostratigraphic zones has not been emphasized, and in modern stratigraphic guides (e.g., Salvador, 1994) neither Opeelian zones nor concurrent-range zones are required for establishing chronostratigraphic "chrons". In fact, ISG-2 lists concurrent-range zones as biostratigraphic rather than chronostratigraphic units.

The application of magnetostratigraphy to biostratigraphy has been a great boon to chronostratigraphy. Magnetostratigraphy, where applicable, is preferable to using Opeelian zones or concurrent-range zones because *all magnetic-polarity reversals are isochrons* in terms of geologic time. As the stratigraphic record has become much better documented, multiple biostratigraphic frames of reference (e.g., nannoplanktonic, planktonic foraminiferal, conodont, ammonite, palynologic, and mammalian zonations) and other methods (i.e., magnetostatigraphy and/or isotopic data) are often combined for chronologic correlation and the identification of temporal gaps in stratigraphic sections.

In many areas, the stratigraphic record is now robust, permitting application of multiple biostratigraphic, isotopic, magnetostratigraphic, and isotope fractionation data to a particular sequence of strata. Any physical event identified in these robust sequences is potentially a "chronostratigraphic marker", which can be defined as *any physical event recorded in the stratigraphic record whose*

biological, chemical, or physical properties yield chronological significance by direct association with any other chronostratigraphic marker. A chronostratigraphic marker can be based on superpositional, fossil, isotopic, or paleomagnetic data; these data enable us to identify the age of the stratal sequence or parts thereof, and multiple chronostratigraphic markers will yield a more accurate age and probably a better estimate for the duration of stratal accumulation and/or gaps in stratal accumulation. Chronostratigraphic markers have already contributed greatly to chronologic resolution in many intervals of geologic time.

What is of utmost importance for both biostratigraphy and chronostratigraphy is that the boundaries of units are not knowingly placed where there is a stratigraphic (and chronologic) gap. For example, the placement of the Pliocene/Pleistocene boundary has been challenged because biostratigraphers, with the help of magnetostratigraphy, have pointed out that latest Pliocene strata are not present below the global stratotype section and point (GSSP) or "golden spike" in the Vrica section of Calabria, Italy (Rio et al., 1991: see their fig. 6), which had been designated as the base of the Pleistocene (Pasini and Colalongo, 1994). Subsequent to 1991, Rio et al. (1998) identified and named a new unit, the Gelasian Stage, for the "underrepresented" latest Pliocene segment in the Italian Neogene sequence that predates the Calabrian Stage. The Gelasian Stage could have been designated either latest Pliocene or earliest Pleistocene based on its relative position. Morrison and Kukla (1998) argued for lowering the base of the Pleistocene to the base of the Gauss magnetic chron (base of chron C2An.3n), where more significant climatic indicators can be identified. Aubry et al. (1998) argued for keeping the base of the Pleistocene at the base of Calabrian Stage, in part because of historical precedents. The volume on the Pleistocene boundary, edited by J.A. Van Couvering (1997) especially the preface, provides background on the historical development and resolution of this important chronostratigraphic concept. Currently, the GSSP for the Pliocene-Pleistocene boundary is placed proximal and superjacent to sapropel layer

“e” in the Vrica section of Italy, and recognition of the boundary separating chrons C1r.2r/C2n in the Vrica section yields precise global correlation and calibration of that boundary.

HISTORY AND PRINCIPLES OF BIOCHRONOLOGY

Biochronology is an important concept for geochronology, but it has been compromised by a history of loose definition and diverse applications. In addition, biochronology has never been discussed in any stratigraphic code because of that loose and ambiguous application. Biochronology is important to vertebrate chronology because the primary temporal units developed and applied by vertebrate paleontologists for correlation in terrestrial deposits—land mammal ages (LMAs) and mammal Neogene (MN) and mammal Paleogene (MP) “zones”, for example—are all biochronologic entities.

The terms “biozone” and “biochron” were listed (article 22h) as subordinate synonyms for the preferred term “range zone” in the 1961 and 1970 NACSNs. This is the closest that any North American stratigraphic guide has come to presenting terms or concepts related to biochronology. In chapter 2 and again in chapter 8 (ISG-1) and chapter 10 (ISG-2), the *International Stratigraphic Guide* illustrates the relationship between categories and units of stratigraphic nomenclature, but biochronology and biochronologic units are not included. Figure 10.2, modified from table 1 in ISG-2 to exclude the ambiguous “Unconformity-bounded” category and “Synthem” unit-term, illustrates these categories and terms. Note that lithostratigraphic units have been oriented parallel to, rather than perpendicular to, the chronostratigraphic and geochronologic units, as proposed by Schenck and Muller (1941) (compare figs. 10.1 and 10.2).

The term “biochron” and the concept of biochronology originated with H.S. Williams (1901), who defined biochron as the total time represented by a biozone; the absolute duration of a fauna or flora or component parts of it. Williams was attempting to demonstrate the temporal component of a biostratigraphic unit (e.g., the chronostratigraphic

concept), and “biozone” was the term he selected. There was no precedent then for using the term “zone” for stratal concepts, the term “chron” for temporal concepts, or the term “bio-” for any form of life. The mixing of temporal entities (biochrons) and stratal entities (biozones) led to confusion.

The concept of biochronology was developed more thoroughly, however, by Teichert (1958), and many of our current ideas about biochronology stem from that influential paper. Isotopic dating was in its infancy when Teichert wrote about biostratigraphic and biochronologic concepts, and a major thrust of his 1958 presentation addressed the application of biostratigraphic methods (with little or no regard for isotopic, isotopic ratio, or magnetostratigraphic correlations) to develop chronostratigraphic units. Teichert (1958: 103) defined biochronology as “the dating of geologic events by biostratigraphic methods.” This definition and discussion, subsequent to the definition of chronostratigraphy by Schenck and Muller, has resulted in confusion because Teichert did not characterize biochronologic terms and concepts relative to chronostratigraphic terms and concepts. Hence, the chronologic equivalent of a biostratigraphic unit can be either a biochronologic unit (according to Teichert, 1958) or a chronostratigraphic unit (according to Schenck and Muller, 1941). The ACSN (1961) adopted the chronostratigraphic concept of Schenck and Muller and did not acknowledge the arguments of Teichert (1958).

The term “chronozone” (= the basic chronostratigraphic unit) was introduced in the 1970 NACSN, and later the term “chron” (= the geochronologic equivalent of a chronozone) was introduced in IGS-1 (1976). The term “biozone,” submerged in the 1961 NACSN (article 22h), was reintroduced in ISG-1 (Hedberg, 1976: 48) as a general term for any kind of biostratigraphic unit, with the note that biostratigraphic “biozones” should not be confused with chronostratigraphic “chronozones.” Throughout this approximately 15-year interval, the terms and concepts of biochron and biochronology, as interpreted by Williams (1901) and Teichert (1958), were virtually banished from mainstream stratigraphic literature as ambiguous.

Stratigraphic Categories	Principal Stratigraphic Unit-terms
Lithostratigraphic	Group Formation Member Bed(s), Flow(s)
Biostratigraphic	Biozones: Range zones Interval zones Lineage zones Assemblage zones Abundance zones Other kinds of biozones
Magnetostratigraphic polarity	Polarity zone
Other (informal) stratigraphic categories (mineralogic, stable isotope, environmental, seismic, etc.)	-zone (with appropriate prefix)

Equivalent Geochronologic Units

Chronostratigraphic	Eonothem Erathem System Series Stage Substage (Chronozone)	Eon Era Period Epoch Age Subage (or Age) (Chron)
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Fig. 10.2. Summary of categories and unit-terms in stratigraphic classification (modified from Salvador, 1994).

The term “biochronology” was resurrected when Berggren and Van Couvering (1974) popularized the concept in their review *The Late Neogene*. The concept received further impetus when Berggren and Van Couvering (1978) discussed biochronology and its relationship to biostratigraphy in *Contributions to the Geologic Time Scale*,

edited by Cohee et al. (1978). In their 1978 contribution, Berggren and Van Couvering characterized biochronology as *the organization of geologic time according to the irreversible process of organic evolution, compared to biostratigraphy as the organization of geologic time according to the iterative arrangement of strata by superposition of*

preserved fossils. Although not a definition, this characterization comes closer to a definition for their application of biochronology than any other. In other words, “the irreversible process of organic evolution” (Berggren and Van Couvering, 1978: 39) is the founding principle of biochronology.

In ISG-2 (1994) a glossary was introduced as a comprehensive guide to the initial definitions of stratigraphic terms. The ISG-2 glossary distinguished currently useful and acceptable terms (in large type) from useless, invalid, obsolete, ill-defined, or synonymous terms (in smaller type). “Biochron” (as defined by Williams) was listed as an acceptable term, whereas “biochronologic unit” and “biochronology” (as defined by Teichert) were listed as unacceptable terms in that glossary.

“Biochron” and “biochronology”, as proposed and characterized by Berggren and Van Couvering (1974, 1978), should be applied for the concepts and principles used in vertebrate chronology when ordering faunal assemblages based on features interpreted to result from organic evolution. I recommend that vertebrate paleontologists abandon the concepts of biochron and biochronology as defined by Williams (1901) and Teichert (1958), and when these terms are used, we should clarify whose definition is being followed. The alternative—to retain the terms “biochron” and “biochronology” in the sense Williams and Teichert—would require creation of *new* terms for the concepts characterized by Berggren and Van Couvering. I believe these terms are meaningful and useful; there should be no ambiguity if authors indicate whose concept for biochron and/or biochronology is followed.

In summary, the concept of “biochron” and “biochronology” should be redefined as “the organization of geologic time according to the irreversible process of evolution in the organic continuum” (Berggren and Van Couvering, 1978: 39). It is time for biochronology to be recognized as a reliable method for geochronology. Similarity and differences between chronostratigraphy and biochronology should be addressed in stratigraphic guides.

DATUM EVENTS

Berggren and Van Couvering (1974) emphasized the development of multiple biostratigraphic zonation scales (especially calcareous nannoplankton, radiolarians, and diatoms in the marine realm) and the application of these multiple zonations to attain a more secure chronologic framework. They emphasized the correlation of similar chronologic intervals in strata using different biostratigraphic markers (e.g., different zonation scales). They characterized the more secure (which often meant more abundant, or widespread, or better studied) biostratigraphic markers as biochronologic “datum events”, which they defined as “changes in the fossil record with extraordinary geographical limits” (Berggren and Van Couvering, 1974: ix, foreword). Their biostratigraphic markers, called datum events, represent *many* of the “chronostratigraphic markers” defined above.

The datum event concept was developed by Bandy (1963a, 1963b, 1964) for biostratigraphic markers in planktonic foraminifera (e.g., *Orbulina* datum and *Globorotalia menardii* datum) identified in marine deposits in southwestern France and the Philippine Islands. Bandy characterized these datum events as significant biostratigraphic markers with widespread (and assumed near-contemporaneous) distribution in deep-water deposits. The concept was applied widely, and its utility was expertly demonstrated in chapter 2 of Berggren and Van Couvering (1974). Datum events were applied almost exclusively to marine microplanktonic studies, as biostratigraphic markers, prior to the seminal publication of Berggren and Van Couvering (1974).

Moreover, Berggren and Van Couvering (1974) applied the concept of datum events to vertebrate paleontology, recognizing that “stage of evolution” had been widely applied and discussed by vertebrate paleontologists as a biochronologic concept (e.g., based on organic evolution) before and after the development of LMAs, citing Tedford (1970) as a reference. Berggren and Van Couvering (1974: see their fig. 11) were impressed that the resolution of mammalian chronology in many parts of the world (e.g.,

North America, Europe, Africa, and Asia) based on stage of evolution, isotopic dating, and paleomagnetism was comparable with the resolution of marine chronology based on similar isotopic dating, paleomagnetism, superposition, and biostratigraphic zonation. The message of Berggren and Van Couvering's (1974) *The Late Neogene* synthesis is that global correlations between marine and terrestrial deposits were attainable, and the terminology they employed to illustrate this unity included "biochronology" and "datum events".

In 1978 Berggren and Van Couvering expanded on their use of first appearance datum (FAD) and last appearance datum (LAD), which they characterized as "... features in the paleontologic record which mark the most widespread, easily identified, and rapidly propagated events". Many of these are biochronologic datum events, and are commonly "the [local] extinction or the immigration of a particular taxon" (Berggren and Van Couvering, 1978: 41). They cited the Old World *Hipparion* datum, which they had introduced in their 1974 presentation of vertebrate biochronology.

The *Hipparion* FAD is a very important European datum event; it marks the beginning of the Vallesian "Stage" and the MN 9 "zone." In both their 1974 and 1978 presentations Berggren and Van Couvering used the *Hipparion* FAD as a biochronological datum event; they were more concerned about the synchrony of the "event" throughout Eurasia than they were about application of this event as a biostratigraphic record. Chapters 2 and 3 of Berggren and Van Couvering (1974) create the impression that all of the datum events recognized in the marine record were based on biostratigraphy (i.e., chronostratigraphic datum events) rather than biochronology. They characterized "biostratigraphy" with correlation of local sections, and characterized "biochronology" with correlation of more distant biologic events, based partly on isotopic dating. These long-distance correlations were generally reliable, and although revised repeatedly, the framework presented by Berggren and Van Couvering in 1974 has been very useful.

The Old World *Hipparion* datum was thoroughly reviewed and updated by Woodburne

(1996), who concluded that (1) the dispersant horse that appeared in the Old World should be identified as *Hippotherium* von Meyer, 1829 (rather than *Hipparion* Christol, 1832), (2) the Höwenegg volcanic deposits (where Berggren and Van Couvering identified their "*Hipparion*" datum) have been restudied and are now dated isotopically as 10.3 Ma, (3) fossil material of *Hippotherium* at Eppelsheim in Germany is probably slightly more primitive than that from the Höwenegg locality, and (4) synchronous resolution of the Old World *Hippotherium* datum still seems reliable, falling consistently ca. 10.5 to 11 Ma. Steininger et al. (1996) reviewed the marine and terrestrial chronologic records in Europe and placed the *Hippotherium* FAD-Vallesian (MN 9) lower boundary at 11.2 Ma, based on correlations in the Vienna Basin (Rögl and Daxner-Höck, 1996) and Spain (Garces et al., 1996; Krijgsman et al., 1996). Thus, there remains some diachrony with the *Hippotherium* FAD, but the example for mammalian biochrons and faunal datum events (e.g., intercontinental FADs) selected by Berggren and Van Couvering (1974) some 20 years earlier was a good choice considering the magnitude of the correlation.

A more precise definition of faunal datum events is needed, however, and guidelines for applying these concepts in chronostratigraphy and biochronology are long overdue. These terms will be used more frequently in the future. In ISC-2 the term "datum level or datum plane" was defined as "The base or top of a range of fossils that can be correlated in sections over a wide area" (Salvador, 1994: 56, section 7.C.4, Biostratigraphic Horizon [Biohorizon], where FADs and LADs are discussed briefly). By implication, faunal datum events in ISC-2 are considered biostratigraphic entities.

Application of the term "datum event" in terrestrial stratigraphy and vertebrate chronology should be confined to those biologic events that are tied directly to a chronostratigraphic marker. By implication, these must be derived from biostratigraphic records. Similarly, application of datum events that are derived from biochronologic concepts (as applied initially for the *Hipparion* FAD by Berggren and Van Couvering, 1974) should be discouraged. Also, by implication, any bi-

ologic event derived from biochronologic concepts that can be tied to a stratigraphic section is potentially a chronostratigraphic marker. I suggest that two discrete types of biostratigraphic datum events be recognized: local datum events (e.g., lowest stratigraphic datum/highest stratigraphic datum) and wide-ranging datum events (e.g., FADs/LADs).

In his discussion of principles and practices in mammalian vertebrate paleontology, Woodburne (1996) did not adopt the same conceptual framework for FAD/LAD terminology as Berggren and Van Couvering (1974). He considered that FADs/LADs should be restricted to what I have called chronostratigraphic markers and avoided designation of any biochronologic events as chronostratigraphic markers. A cursory search through the stratigraphic literature suggests that most authors apply FAD/LAD terminology only to biologic events that I identify as chronostratigraphic markers, as defined above. These concepts should be expressed thoroughly in stratigraphic guides.

LAND MAMMAL AGES

Land mammal ages were developed by Wood et al. (1941) about the same time that chronostratigraphy was developed by Schenck and Muller (1941). LMAs were created in a report by a seven-member committee of the Paleontological Society headed by Horace E. Wood. The committee had been appointed in 1939 and charged with responsibility for presenting terminology and concepts in support of and consistent with the North American stratigraphic guide (the "Ashley code" [Ashley et al., 1933]) for use by vertebrate paleontologists in terrestrial stratigraphy. The Wood Committee was probably influenced by the article "Succession of North American Continental Pliocene Mammalian Faunas" by R. A. Stirton (1936), as well as by Osborn and Matthew's (1909) "Cenozoic Mammal Horizons of Western North America" and Matthew's (1924) "Correlation of the Tertiary Formations of the Great Plains." Stirton (1936) proposed three divisions of the Pliocene (as then understood), calling them "ages" and characterizing them by assemblages of mammals (primarily horses), noting first and last appearances plus well-represent-

ed taxa. Stirton did not name his Pliocene faunal divisions but listed 52 taxa for his Lower Pliocene, 57 taxa for his Middle Pliocene, and 38 taxa for his Upper Pliocene divisions. Many of these are still characteristic of the Clarendonian, Hemphillian, and Blancan North American land mammal ages. Stirton (1936: 166) noted, "Until the stratigraphic evidence becomes clear, it would seem better to consider the fossil assemblages in their biological rather than their geological aspect." When the Wood Committee report was published it was well received; it has served as a useful model for terrestrial chronology in North America and as a global framework for mammalian evolution.

The Wood Committee report divided the Cenozoic Era into 18 provincial ages plus one Pleistocene assemblage. Each provincial age was associated with one faunal "zone" bearing the name of a prominent mammal taxon represented in that zone. The name given for each provincial age was intended to be independent of rock stratigraphic terms, but most of the provincial ages were named after rock units. Each provincial age was characterized as a faunal association of mammals that lived during that age. The faunal association was characterized further by listing (1) "index fossils" restricted to that age, (2) "first appearances", or fossils appearing during that age, (3) "last appearances", or fossils disappearing during that age, and (4) "characteristic fossils", or fossils known from earlier or later ages but common in that age. There was no attempt to provide complete faunal lists for each provincial age but rather the goal was to select significant genera for each of the ages. The report included a glossary and a chart showing the distribution and chronologic correlation of many faunal assemblages known in North America. It is a credit to the members of the Wood Committee that their product, the North American land mammal ages (NALMAs), has served so well for 60 years with only slight modification.

Unfortunately, the Wood Committee report was never acknowledged or cited in any North American or international stratigraphic code. Stratigraphers and invertebrate paleontologists argue that the Wood Committee report is about mammals; it is not about stra-

ta. This is very true, but fossil mammals are derived from sediments, and we use the mammals to correlate those strata and place them into a global geochronologic framework. What is different about mammalian biochronology, and distinguishes it from chronostratigraphy, is that stage of evolution is an important *additional* principle (method) applied in mammalian biochronology.

In place of a “terrestrial stratigraphic guide”, vertebrate paleontologists have relied on irregular and informal reviews of their terms and practices. For instance, the term “provincial” has generally been dropped from the framework of NALMAs since the critique of Savage (1962). The current framework consists of 19 NALMAs: the Irvingtonian and Rancholabrean NALMAs were added by Savage (1951) in place of the unnamed Pleistocene mammal association proposed in 1941, and the Dragonian NALMA was demoted to the first subzone of the succeeding Torrejonian NALMA (Archibald et al., 1987). Epoch assignments for the 19 current NALMAs have changed significantly as the geologic time scale has been calibrated, but the ordering of the NALMAs has never changed.

Probably the most significant mistake committed by the Wood Committee was the lack of provision for periodic review and updating of terms and concepts. Reviews have proven very helpful, but they lack the authority of a stratigraphic guide. One notable review that has been especially helpful in clarifying our concept of NALMAs is “Principles and Practices of Mammalian Geochronology in North America” by R. H. Tedford (1970).

Tedford (1970) addressed the historical background leading up to the development of NALMAs. He noted that the first chronologic framework for mammalian evolution in North America was the “Life Zone concept,” developed by H. F. Osborn and W. D. Matthew (1909). As Tedford (1970: 670–673) emphasized, most of the early practices in North American vertebrate paleontology were based on sound biostratigraphic principles: fossils were characterized relative to the strata that produced them. The life zones of Osborn and Matthew (1909) were conceived as *belts of strata characterized by as-*

semblages of organic remains (e.g., the “faunizone” concept of Buckman, 1902). The scientific rigor of some of the early correlations might be called into question, but the basic concept was a *biostratigraphic* framework, with the development of practical units comparable to modern assemblage zones.

Later, as the paleontological record was gradually increased, the biostratigraphic foundation of life zones was de-emphasized and replaced by a biochronologic “faunal zone” concept. The first biochronologic framework for North American terrestrial deposits was Matthew’s (1924) paper on “Correlation of the Tertiary Formations of the Great Plains.” Tedford (1970: fig. 1) noted that Matthew (1924) applied the names of selected multituberculates for faunal zones of the Paleocene Epoch and the names of selected horse genera for the remaining faunal zones of the Cenozoic. Fossil horses were well studied at that time and widespread in North America. Matthew’s faunal zones were very practical and served as a useful chronologic frame of reference. Other faunal zones were proposed later, culminating in the NALMAs.

Thus, there was precedent in the historical development of NALMAs for the application of both biostratigraphic (e.g., the life zones of Osborn and Matthew) and biochronologic (e.g., the faunal zones of Matthew) concepts, as reflected in their names. Some NALMAs were named after strata (e.g., Arikarean, Bridgerian, Wasatchian), yet all NALMAs were characterized and identified by mammal genera, irrespective of the deposit from which they were derived, hence they were called land mammal ages.

So, what is a land mammal age (LMA)? Is it a biostratigraphic or a biochronologic entity? LMAs are clearly biochronologic entities, based on their application; vertebrate paleontologists have always considered the natural associations of fossil species as biological entities rather than clasts in strata. The features of life during LMAs (mammals, that is) are of primary concern; the features of the rocks that produced the record are of secondary concern. To be more specific, the Blancan land mammal age represents the mammalian life that inhabited North Ameri-

ca between 2 and 5 Ma (more or less); it does *not* represent all or some percentage of the rocks that were deposited in North America during that time. Each LMA is characterized by a selected group of mammal *taxa* (usually genera) that lived during that LMA and aid in distinguishing it from the group of mammal taxa that lived during preceding and following LMAs. What could be simpler? The LMAs are biochronologic entities.

How do we define a land mammal age? I suggest it be defined as *a relatively short interval of geologic time that can be recognized and distinguished from earlier and later such units (in a given region or province) by a characterizing assemblage of mammals.* The boundaries of a LMA should be defined by the appearance of one mammal that is morphologically distinctive, well represented, and widely distributed in that biogeographic region or province. The boundary-defining taxon is most conveniently an immigrant from another biogeographic region or province. These boundary definitions should be emended and amended as the need arises.

European Neogene (MN), Paleogene (MP), and Quaternary (MQ) mammal "zones" are also biochronologic units, and the boundary-defining taxa can probably be applied to these biochronologic units, although that is not the purpose here.

Note that the term "strata" is not included in the definition of a land mammal age. This does not mean that biostratigraphy and chronostratigraphy should be excluded from the development or refinement of LMAs. During the last 10 to 20 years, greater emphasis has been placed on the recognition of unit boundaries for all things geologic. This has resulted in greater resolution of geochronology, often incorporating new isotopic and paleomagnetic data. A primary thrust of the 1987 Woodburne volume dealt with the definition and recognition of the boundaries of LMAs. Vertebrate paleontologists should utilize all available stratigraphic, isotopic, and paleomagnetic data in developing, testing, and refining LMAs.

Three of the NALMAs (Clarkforkian, Wasatchian, and Clarendonian) have been proposed as chronostratigraphic stages (Savage, 1955, 1977; Rose, 1981), and more

could readily be recognized, if desirable. However, placing the Clarkforkian, Wasatchian, and Clarendonian into a chronostratigraphic as well as a biochronologic framework did not provide a significant increase in the resolution or security of those NALMAs, nor were they presented and discussed differently in their respective chapters (3, 4, 6) in the 1987 Woodburne volume (see discussion in chapter 2 therein). The biochronologic NALMAs can be as reliable and as useful as chronostratigraphic stages.

Woodburne (1987: 15) emphasized that the best way to resolve many problems in biochronology is to place the biochronologic framework into a biostratigraphic framework. He recommended that "mammalian stratigraphers continue to avail themselves of detailed analysis of the mammal-bearing stratigraphic record, search for replicable and unambiguously defined, as well as characterized, biostratigraphically based chronostratigraphic units, and pursue methods that ensure that use of traditional zoological binomial nomenclature serves both paleobiologist and chronostratigrapher."

STAGE OF EVOLUTION

Stage of evolution (SOE) is a biochronologic concept that has been a fundamental principle applied for vertebrates since the establishment of the LMAs. The SOE concept is highly regarded by vertebrate paleontologists but poorly understood by other geologists; it has rarely been mentioned, described, or defined. The earliest application of the SOE concept for vertebrate chronology was in Osborn and Matthew's methods of correlation (1909: 30): (1) percentages of common genera and species, (2) *similar stages of detailed evolution in related forms*, (3) simultaneous introduction of new forms by migration, (4) predominance or abundance of certain forms, (5) convergence and divergence of faunas in comparison with Europe and Asia, and (6) extinction of certain forms. Stage of evolution is clearly expressed as method 2.

Matthew, who developed the faunal zone concept, was more vague. He listed the following criteria for correlation (Matthew, 1924: 744): (1) direct superposition, (2)

stratigraphic continuity of lithologically similar strata, (3) correspondent relationships of widespread tectonic movements and other geologic evidence, and (4) faunal identity and relationships, with subheadings (a) faunas must be adequate and the identifications reliable, (b) certain genera and species appear to have wide geographic and limited geologic range, (c) while identities in fauna point usually to correspondence in age, differences may be due to different facies, (d) the first appearance and the extinction of certain races or groups is very commonly used, and (e) *probably the soundest evidence is that derived from the progressive structural modification of races and phyla*. Criterion 4e implies the SOE concept, but the term was not expressed until two pages later, where Matthew said, "Taking the stages in the evolution of the Equidae as our basis, the sequence of faunae may be divided into nine primary zones". I find it anomalous that Matthew would be so reticent in crediting SOE as a correlation concept. Perhaps between 1909 and 1924 there had been criticism regarding SOE as a criterion for correlation, or perhaps there had been some critical discussions between Osborn and Matthew, resulting in this change.

Stage of evolution is not mentioned in the 1941 Wood Committee report, nor in Tedford's (1970) review of principles and practices, nor in Berggren and Van Couvering's (1974) presentations regarding biochronology and mammals. Berggren and Van Couvering (1978: 40) approached a definition for the concept when they characterized biologic evolution as the basis of biochronology, and discussed biochronology as "the recognition of the fossils as having an evolutionary grade or 'age' which falls at a known point in the span of evolutionary time". SOE was mentioned but undefined by Savage in Evernden et al. (1964: 147): "The use of characterizing aggregates [of mammal genera] is a simple application of 'stage-of-evolution' or 'biogenetic' correlation and suffers from all the errors and lack of refinement that may accompany such a discipline". Savage (1977: 430–431) mentioned SOE again in his review of vertebrate stratigraphy and geochronology but failed to define it adequately: "We assert empirically that the platform of

evolutionary development—the *stage of evolution*—usually signified by a particular genus or species, may be used as [an] indicator for a discrete segment in a time scale" (italics added). Woodburne (1987: 10) pointed out that the SOE concept is buried under "Material Categories Based on Content or Physical Limits" in the North American stratigraphic code (NASC) (North American Commission on Stratigraphic Nomenclature, 1983: 849): "Biologic remains contained in, or forming, strata are uniquely important in stratigraphic practice. First, they provide the means of defining and recognizing material units based on fossil content (biostratigraphic units). Second, *the irreversibility of organic evolution makes it possible to partition enclosing strata temporally*" (italics added). Neither Woodburne nor the NASC discussed the SOE concept in more detail or defined it. Unfortunately, SOE is not mentioned in the comparison of North American and European mammal chronologies presented by Lindsay and Tedford (1989) either.

I believe that SOE is a very important concept in biochronology, especially in mammalian chronology. The concept has been applied repeatedly (and probably unconsciously) by vertebrate paleontologists in ordering the sequence of faunas they study. It has been especially valuable in ordering mammalian faunas when stratigraphic relationships are ambiguous or lacking, as in Australia (Stirton et al., 1961). The European MN zonation was conceived primarily on the SOE concept and remains the primary criterion for ordering faunas in European Cenozoic mammal faunas (Bruijn et al., 1992: 66).

In searching for a definition of the concept of stage of evolution, I went back to my own roots and found it discussed in R. A. Stirton's textbook *Time, Life, and Man*, written for the introductory paleontology course he taught at the University of California at Berkeley. Stirton (1963: 84) presented SOE as a biologic method for ordering events in Earth history, along with species identifications and the "percentage of modern species" method developed by Lyell. I assume that this concept was passed down, but not precisely defined, from teacher to student in the lineage from W. D. Matthew to R. A. Stirton to many oth-

er students, including D. E. Savage, R. H. Tedford, M. C. McKenna, M. O. Woodburne, and many others, including me. Stirton (1963) described SOE as a concept applicable to either an entire fauna or any group of animals. He emphasized that the method is dependent on our knowledge of evolution in the families, genera, and species involved, through time and space. And it is more precise and useful when knowledge of the phyletic evolution in different groups of organisms is well established. Stirton illustrated (1963: fig. 29) an example based on his own experience, the SOE in fossil beavers recorded in North America, showing fragmentary teeth of these rodents found in superposed sediments. Stirton used the SOE method most frequently and securely when discussing horse teeth. He liked to play a game with his students, asking them to give him isolated horse teeth behind his back or when he was blindfolded. He would then identify the horse teeth (often to species), impressing the students by naming the age and probable deposit the specimens came from, based on the "feel" of the teeth and his knowledge of horse evolution.

I will attempt to define SOE and provide more examples and illustration of the concept. Stage of evolution is *the chronological ordering of faunal assemblages based on morphological differences observed in members of one phyletic lineage recorded in different assemblages within the same deposit or basin or biogeographic region; advanced evolutionary stages are ranked higher in the order*. Ideally, this method is more secure when assemblages are well represented, when knowledge of the phyletic relationships in the lineage is well established, and when multiple lineages (e.g., horses and beavers) are available for comparison to support (or reject) the ranking. As with other terminology used in geology and paleontology, this definition should be emended and amended, as the need arises.

In my experience (with small mammals), the height of the crown in the dentition of well-known mammals *never decreases*; it remains the same or increases. In addition to the actual increase in crown height, other morphological features that complement the increase (such as the height of dentinal tracts,

the loss of roots in upper molars, and the development of cementum on the crown) are frequently used to differentiate SOE. Figure 10.3, copied from Fejfar and Heinrich (1989), illustrates these morphological changes in arvicoline rodents of Europe. These morphological changes are well documented and represent part of the biologic foundation for the MN units of European mammal chronology (Mein, 1975).

The history of European mammal chronology was reviewed by Lindsay and Tedford (1989). A solid European chronologic framework, incorporating marine stratigraphy and mammalian biochronology with radiometric and paleomagnetic data, was developed by Steininger et al. (1989) and later updated by Steininger et al. (1996).

APPEARANCE EVENT ORDINATION

Appearance event ordination (AEO) was proposed as a new method of biochronology by Alroy (1994, 1998), who compiled a data set of taxa from published faunal lists. The data were analyzed for faunal similarity, relying on the presence (= co-occurrence) of the same taxon within two or more of the faunal lists as an indicator of similarity. The earliest chronologic record of a given taxon should be in a faunal list with few co-occurrences of other taxa, and similarly the latest chronologic record for that taxon should also be in a faunal list with few co-occurrences of other taxa. As the number of faunal lists in the data set is increased the analysis becomes more complex, but the reliability of interpretations increases dramatically. Fortunately, large data sets can be analyzed rather quickly through multivariate ordination analysis using computer software. A serious flaw (or constraint) of this type of analysis is that taxonomic identifications in published faunal lists are subject to revision and/or error that may not be known to the AEO analyst. The same criticism could be raised for any type of taxonomic study, and it is likely that published faunal lists are more stable than unpublished data.

The AEO method was developed by Alroy (1992), who was searching for undetermined characteristics of faunal similarity, completeness, and taphonomic and ecologic bias in

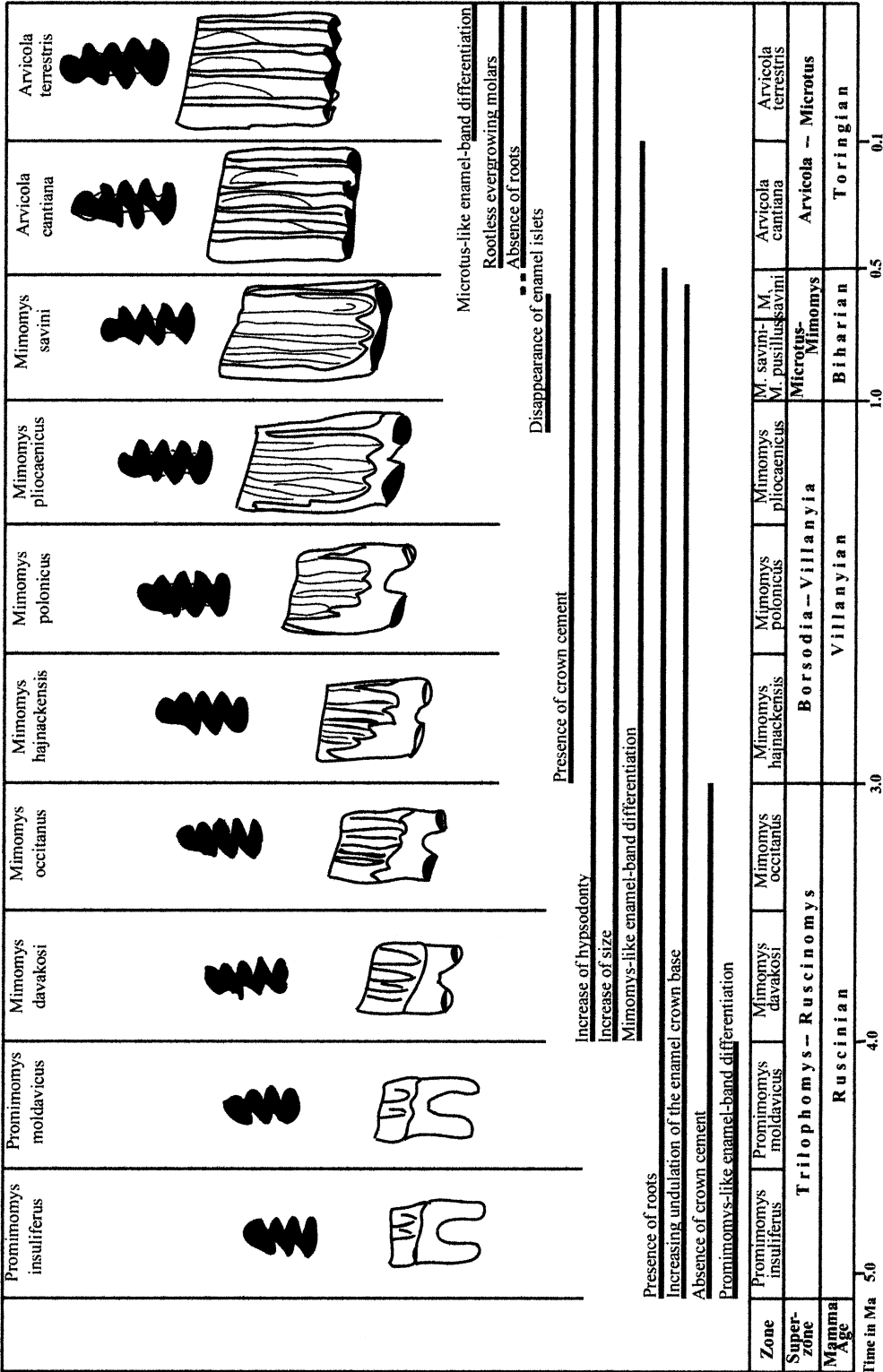


Fig. 10.3. Stages of evolution in first lower molars of European arvicoloid rodents (after Fejfar and Heinrich, 1989).

the fossil record. Alroy developed algorithms to analyze mammalian taxa whose stratigraphic ranges overlap (= conjunctive) and/or do not overlap (= disjunctive) the ranges of other taxa. That is, he assembled a data set of faunal lists from the literature and identified taxa recorded in more than one list. Taxa found on more than one faunal list were said to have overlapping (conjunctive) distributions. Conjunctive distributions of paired taxa were then analyzed in search of instances where the first occurrence (FO_A) of taxon A was prior to the last occurrence (LO_B) of taxon B; these were called F/L relationships (or statements of probability). In the real world, F/L relationships converge on the appearance event of taxon A (AE_A) if the actual record of taxon A precedes that of taxon B (e.g., AE_B). Assuming that everything else is constant, the number of conjunctive distributions increases as the number of faunal lists is increased, and at some point one can claim with confidence that one F/L statement represents the real appearance event of taxon A. A biochronologic tool was invented, or so it would seem.

Actually the analysis is much more complicated than described above, and the objective is to develop a conjunction index (CI), which equals the number of conjunctions recorded in the data set relative to the possible number of conjunctions. The conjunction data are then subjected to correspondence analysis (CA) in order to maximize the disjunction of taxonomic ranges. These values are summed for the taxa in each faunal list, then normalized, and the faunal lists are arranged according to their CA scores (Alroy, 1992). In a sense, the conjunction index of Alroy is similar to the method of overlapping biostratigraphic records applied in Oppelian and concurrent-range zones some 50 to 60 years earlier to recognize and eliminate stratigraphic gaps in the fossil record.

The AEO multivariate analysis can be a powerful biochronologic tool; it should be tested on additional data to learn more about its merits and limitations. I doubt whether AEO analysis will replace superposition, biostratigraphy, or stage of evolution as fundamental tools for understanding Earth history, but it provides a convenient test for evalu-

ating numerous problems in biochronology and chronostratigraphy.

CONCLUSIONS

This discussion of chronostratigraphy and biochronology has been directed toward similarities and differences in approach and assumptions. Any geologic or paleontologic term including the root "strat" should relate to stratified rock. Any geologic or paleontologic term including "chron" should relate to time or temporal interval. By consensus and codification, any geologic or paleontologic term with "zone" (or variation thereof) should relate to rocks. Therefore, the term "chronostratigraphy" should relate to the temporal interval or limit of stratified rocks, and "biochronology" should relate to the temporal relationship of life or parts thereof. Similarly, both "biostratigraphy" and "biozone" should relate to life in stratified rocks. Formal definition and characterization of these terms has been clarified over several decades through repeated applications in the literature and stratigraphic codes.

Unfortunately, the terms "biochron" and "biochronology" were applied prior to the formalization of stratigraphic terms and subsequent to the entrenchment of both terms in the geologic literature. This has resulted in ambiguous usage and general rejection of "biochron", "biozonation", and "biochronology" in geologic literature and stratigraphic codes. Berggren and Van Couvering (1974, 1978) later characterized the terms "biochron" and "biochronology" as the *sequencing of geologic events, based on organic evolution*. I recommend that the etymologically correct application of "biochron" and "biochronology" by Berggren and Van Couvering should be adopted, and earlier definitions and characterizations of those terms should be abandoned.

"Chronostratigraphy" should be characterized and defined as *the sequential ordering of geologic events, using biostratigraphic, isotopic-radiometric, and paleomagnetic data*. Also, "biochronology" should be characterized and defined as *the sequential ordering of biologic (and geologic) events using morphologic differences that result from organic evolution (when applied to Earth*

history). Both chronostratigraphy and biochronology are fundamental procedures (methods) for geochronology.

A unique feature of time is that *temporal units must not overlap and must be complete, lacking any temporal gaps*. These features should apply to all terms and concepts in both chronostratigraphy and biochronology. As methods for geochronology, in both chronostratigraphy and biochronology the boundaries of all units must be isochronous rather than time-transgressive.

The term “chronostratigraphic marker” is introduced as *any chronologically significant event, recorded in a stratified sequence, that can be related to any other chronostratigraphic marker*. Datum events (e.g., FADs) are (or should be) chronostratigraphic markers. However, an initial application (i.e., the Old World *Hippotherium* FAD) of a datum event to mammalian biochronology by Berggren and Van Couvering (1974) was not a chronostratigraphic marker because the stratigraphic record of *Hippotherium* was not well documented, nor was it tied to a reliable chronostratigraphic marker. Now, some 25 years later, the Old World *Hippotherium* FAD of Berggren and Van Couvering is much better resolved and can be applied as a reliable chronostratigraphic marker. Ideally, the boundaries of all chronostratigraphic and biochronologic units should be based on chronostratigraphic markers.

Land mammal ages have been characterized repeatedly during the last 50 years, but their precise limits or boundaries have been identified only recently. LMAs are biochronologic units; they *reflect a partial representation of the mammal life in a particular area for a discrete interval of time*. What is important for recognition and application of LMAs is that they can be readily distinguished from younger and older LMAs.

Stage of evolution is a fundamental and widely applied concept in biochronology. Horse evolution has been a prime example for SOE, preceding the origin of LMAs. Height of crown in mammal teeth is a common example of the application of SOEs; height of crown in small arvicolid rodents is illustrated herein. Crown height in mammals is unidirectional; that is, mammals with high-crowned teeth never evolve lower-crowned

teeth. Other examples for SOE can be found, and as the fossil record becomes more robust and better calibrated, many examples for SOE are sure to be found.

Appearance event ordination is a new tool of biochronology based on statistical analysis of faunal lists. Like other tools, it must be applied and tested to develop confidence in and learn limitations of the method.

Mammalian biochronology, like other disciplines of natural history, has come a long way during the last 60 years. Mammalian biochronology has a sturdy foundation, thanks to the contributions of many capable, dedicated, and productive researchers, like Dick Tedford.

ACKNOWLEDGMENTS

This study is dedicated to Dick Tedford in recognition of his outstanding contributions to mammalian biochronology and vertebrate paleontology. I was introduced to the Mud Hills in the Mojave Desert by Dick during the summer of 1964, when he was teaching at the University of California at Riverside and I was an inexperienced but eager graduate student. We had arranged a rendezvous by phone, to meet at the Big Boy Restaurant in Barstow early on a Monday morning in June. I arrived on Sunday evening, camped out north of Barstow, and drove into town on Monday morning and found a Big Boy Restaurant. Neither Dick nor I was aware that a second Big Boy Restaurant had opened in Barstow. Dick was waiting at the old Big Boy and I was waiting at the new one. By noon we figured out why our plans had gone awry, and found one another. We hurried out to the Mud Hills, where Dick pointed out in a couple of hours as much as he could about fossil sites, their location, and how to avoid getting stuck in the sand. Then he was off to Riverside for an important meeting. I am eternally grateful to Dick for this brief but informative introduction to my favorite fossil beds. Later, after that first field season, it was Dick Tedford who convinced my advisor, R.A. Stirton, that I should continue working in the Mud Hills. Dick has been a great source of inspiration and a focus of admiration throughout my professional career. I am truly honored for the opportunity to contrib-

ute to this memorial volume. Many thanks to Larry Flynn for his efforts in bringing this volume together; I am also grateful for the efforts of Larry and two anonymous reviewers for helping to make this contribution more succinct and clear.

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