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Classical Confidence Intervals and Bayesian Probability Estimates for Ends of Local Taxon Ranges[1]

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The observed local range of a fossil taxon in a stratigraphic section is almost certainly a truncated version of the true local range. True endpoints are parameters that may be estimated using only the assumption that fossil finds are distributed randomly between them. If thickness is rescaled so that true endpoints lie at 0 and 1, the joint distribution of gap lengths between fossil finds is given by the Dirichlet distribution. Observed ends of the range are maximum likelihood estimators of true endpoints, but they are biased seriously. Extension of the observed range at each end by a distance equal to the average gap length yields unbiased point estimators. Classical statistics can generate confidence intervals for ends of the taxon range; but with Bayesian inference, the probability that true endpoints lie in a certain region can be stated. For a 95% confidence level (classical) or a 95% probability (Bayesian), the range extensions exceed the observed range if the range is established on less than six finds; if only two finds are used, such range extensions are an order of magnitude longer than the observed range. Evidently the standard biostratigraphic practice that identifies zonal boundaries as horizons rather than confidence intervals may not be justified at the resolution of typical fossiliferous sections.

KEY WORDS: Dirichlet distribution, range extension, biostratigraphy, extinction.

1. INTRODUCTION

The highest and lowest finds of a particular fossil in a sedimentary stratigraphic section are most important: they routinely are used to define ends of the local range of that taxon for correlation purposes, and to approximate migration and extinction events. Some intervals of sedimentary rock within a local taxon range will have yielded fossils of that taxon, but usually other intervals lie between the fossiliferous horizons and still appear to be barren, or are unsampled. Such barren intervals result from a failure of either the preservation process or the collection process, but they obviously belong in the taxon range (Hazel, 1977).

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If similar barren intervals occur just beyond the highest and lowest finds, however, they will be excluded from the taxon range, and erroneously treated as if deposited before or after the local sojourn of the taxon.

Clearly, observed ends of a taxon range zone include an uncertainty imposed by the sampling strategy and another that results from vagaries of the preservation process. Where possible, these uncertainties should be stated explicitly by, for example, addition of confidence intervals to the ends of the range. Following Edwards (1982), the probability of reworking, borehole caving, and malpractice (contamination of samples, misidentification of taxa) is taken to be extremely small. Thus true ends of the local sojourn of the taxon correspond to horizons in the stratigraphic section that lie beyond the ends of the observed taxon range.

Paul (1982; also McKinney, 1986; Springer and Lilje, 1988) has pointed out that barren intervals within the range (''gaps'') carry information about the discrepancy between observed and true ends of the local taxon range: the gaps and the discrepancy both result from failures in preservation and collection processes. From this, confidence intervals may be established for endpoints of ranges; the assumption is that finds of a taxon are distributed randomly within its range (in a sense to be made precise in Section 3).

Shaw (1964), Paul (1982), Signor and Lipps (1982), McKinney (1986), Springer and Lilje (1988), and many others have used the simplifying assumption that fossils are distributed randomly. Paul (1982) and Springer and Lilje (1988) suggested tests for this assumption and, more significantly, showed that taxa and stratigraphic sections exist for which it is acceptable. Tests for randomness are relatively straightforward and are not discussed here. Even when the assumption of randomness is untested, an understanding of how confidence intervals depend on range length and number of fossiliferous horizons within the range can provide a baseline.

The analysis here takes account of the fact that limits of the local sojourn are unobserved, but fixed, evolutionary or migration events. They are not random variables, but parameters that limit the interval in which finds of the taxon may be distributed randomly. Consequently, the classical statistical approach to the problem proposed by Springer and Lilje (1988) must be corrected. A second consequence is that classical statistics cannot assign probabilities to the position of true ends of the range. The following sections show how to set up confidence intervals in the classical statistical framework, and how to use Bayesian inference to establish probability intervals.

2. AN EXAMPLE: LATE CRETACEOUS AMMONITE RANGES

The range of late Cretaceous ammonites reported by Macellari (1986, Fig. 5) from Seymour Island in Antarctica will be used to illustrate methods as they are developed below. Macellari reports the position of ammonite finds within taxon ranges, and only those ranges with three or more finds will be considered (Fig. 1). Several lines of evidence indicate that the assumption of random fossil distribution may be reasonable for this example. Lithology of the Cretaceous section on Seymour Island is monotonously fine grained (Macellari, 1986; Sadler, 1989), and ammonites at the surface are obvious. The Antarctic conditions imposed a uniformity on the collecting strategy: uncertain weather and a short field season required that fossils be collected during measurement of stratigraphic sections, and frozen ground prohibited excavation of fossils below the surface.

The gap length distributions within 13 ranges were tested for exponentiality and for absence of serial correlation. As will be made clear in the next section, these are appropriate procedures for testing of randomness (i.e., that fossil occurrence can be modeled by a Poisson process). If randomness is accepted, the Dirichlet theory for statistical inference purposes must be used (Sections 3 and 4).

Only taxon 5 has a serial correlation coefficient above 0.15. Least-squares regression of the means on the standard deviation of gap length gave over taxa a slope of 1.05, close to the value of 1.00 for an exponential distribution, although the regression is influenced strongly by one point. Furthermore, as in Springer and Lilje's (1988) examples, means were generally a little larger than

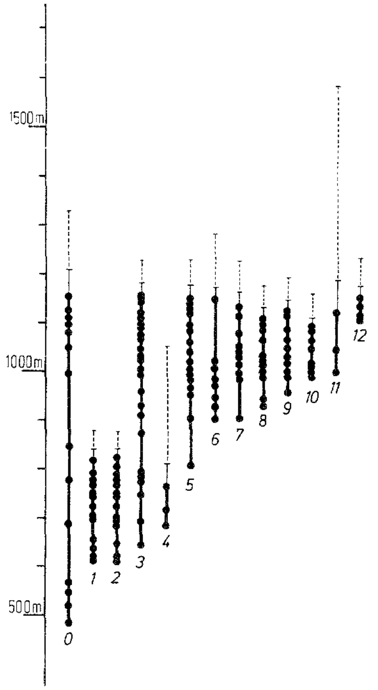

Fig. 1. Ammonite ranges in late Cretaceous strata of Seymour Island, Antarctic Peninsula. Observed local ranges (heavy vertical lines) and finds (filled circles) after Macellari (1986, Fig. 5). Light vertical lines: upper range extension to unbiased point estimator. Dashed vertical lines: upper range extension to 95% confidence interval. Taxa are numbered for ease of subsequent reference: 0 = *Diplomoceras lambi*; 1 = *Maorites seymourianus*; 2 = *Kitchinites darwini*; 3 = *Grossouvrites gemmatus*; 4 = *Maorites weddelliensis*; 5 = *M. densicostatus* morphotype-alpha; 6 = *Kitchinites laurae*; 7 = *Anagaudryceras seymouriense*; 8 = *Maorites densicostatus* morphotype-gamma; 9 = *Pachydiscus riccardi*; 10 = *Maorites densicostatus* morphotype-beta; 11 = *Pseudophyllites loryi*; 12 = *Pachydiscus ultimus*.

standard deviations. Gap lengths for ammonite data roughly follow an exponential distribution truncated below 8.5 m. This is approximately the limit of resolution of Macellari's (1986) published illustration. Note that a limit to the resolution of field data should always be expected: fossils have finite size and, when close together, usually will be recorded as one site. Thus, a truncated distribution should be anticipated when testing for randomness in published data.

After Macellari's (1986) landmark study, Sadler (1989) mapped rocks near the upper limit of ammonite ranges as part of a test of extinction hypotheses. The mapping, which included rocks between Macellari's measured sections, increased the efficiency of ammonite collection near the top of their ranges, and, perhaps not surprisingly, discovered ammonites above their previously observed limits. The significance of the highest ammonites is controversial (Huber, 1986; Sadler, 1989), but their presence warrants analysis of confidence intervals that might have been placed on Macellari's ammonite data.

3. PRELIMINARIES

The assumption of randomness of fossil distribution applies to the process which generates the fossil record, rather than the record itself. A Poisson process (see, for example, Ross, 1985) is a valid model for location of fossils if (i) Number of finds in an interval of the section follows the same Poisson probability distribution for all intervals of a given length; and (ii) Numbers of finds in two disjoint intervals are independent. A find is a fossiliferous horizon observed to contain the taxon in question. Note that gaps (successive differences) between finds have independent exponential distributions

$$f_X(x) = \lambda e^{-\lambda x}, \qquad x > 0 \tag{1}$$

where parameter λ is the reciprocal of the expected gap length. (As is customary, upper case letters are used here to denote random variables, and lower case letters denote their realized values.) The number of finds in a fixed interval is a Poisson random variable n whose mean is λ times the interval length. Conditional on n, the n finds are independently uniformly distributed on the interval.

The situation to be considered (Fig. 2) has parameters θ_1 and θ_2 which represent local origination/immigration and extinction/emigration of the species in question. The observed data consist of locations of n finds, assumed to represent a random sample from a uniform distribution on (θ_1, θ_2). This paper is concerned with the estimation and testing of hypotheses about the unknown parameters.

Let Y, Z denote locations of first and last finds. These random variables are respectively the minimum and maximum of the n uniform variables. They are sufficient statistics (Hogg and Craig, 1978, p. 364) in the sense that all the information about θ_1, θ_2 in the n observations is contained in them. For con-

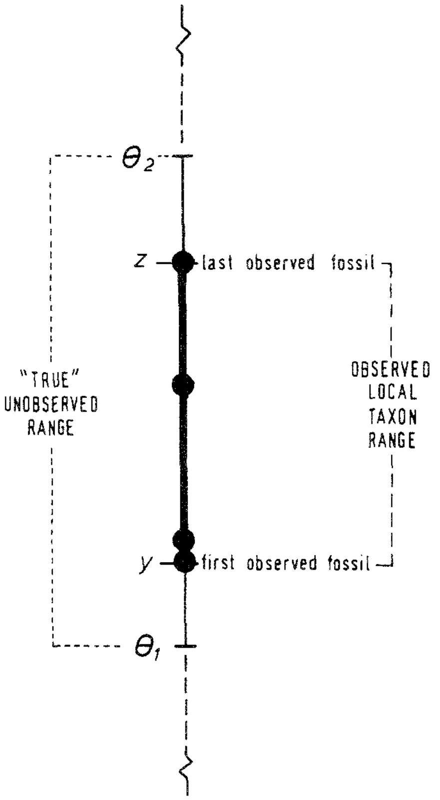

Fig. 2. The relationship between fossil finds (filled circles), ends of observed local range (y and z), and true ends of range (θ_1 and θ_2). Vertical scale is height above an arbitrary datum in the stratigraphic section.

venience, the special case where $\theta_1 = 0$ and $\theta_2 = 1$ will be mentioned often. For this standard uniform distribution,

$$P(Y \geq y, Z \leq z) = (z - y)^n, \qquad 0 < y < z < 1 \tag{2}$$

and hence, by differentiation, the joint density of Y, Z is

$$f_{Y,Z}(y, z) = \begin{cases} n(n-1)(z-y)^{n-2} & \text{for } 0 < y < z < 1 \\ 0 & \text{otherwise} \end{cases} \tag{3}$$

Marginal densities are

$$f_Y(y) = n(1 - y)^{n-1} \qquad 0 < y < 1$$

and

$$f_Z(z) = nz^{n-1} \qquad 0 < z < 1 \tag{4}$$

Springer and Lilje (1987) previously have considered the problem of inference about θ_1 and θ_2 based on the observed pattern of finds. They usefully noted the analogy between the distribution of n finds between θ_1 and θ_2 and the "broken stick model." In the latter, a stick of length $(\theta_2 - \theta_1)$ is broken at n randomly chosen points; the result is $n + 1$ pieces, the length of the first and last being $(y - \theta_1)$ and $(\theta_2 - z)$. Their paper rests on the claim that the distribution of sizes of the two pieces is exponential, as in (1). This claim is tempting but, unfortunately, incorrect. According to the Poisson process, gaps are indeed independent and exponentially distributed but, once one *conditions* on the event that n observations are in the range (θ_1, θ_2), the property is lost. This is clear immediately from the fact that exponential variables have an infinite range, whereas gap lengths in the broken stick model are constrained to be less than $(\theta_2 - \theta_1)$. In particular, in the simple case $n = 1$, gap lengths are obviously uniformly distributed on $(0, \theta_2 - \theta_1)$. In the case of n points, and with a rescaling so that $\theta_1 = 0$ and $\theta_2 = 1$, the joint distribution of the gap lengths under the broken stick model is known as the Dirichlet distribution (Hogg and Craig, 1978, p. 310).

A further point, rather subtle but relevant to developments in the next section of this paper, also should be noted. This is that once endpoints y and z are taken to be observed data, lengths $(\theta_2 - z)$ and $(y - \theta_1)$ cannot be taken as random at all, at least within the framework of classical statistics. Thus, in that context, to speak of the distribution of these lengths would be improper; only "confidence intervals" for the parameters can be discussed properly. Methods for constructing such intervals will be developed shortly. If endpoints θ_1 and θ_2 are discussed as random quantities with probabilities of lying in various intervals, discussion is in the realm of Bayesian statistical inference.

4. ENDPOINTS OF A SINGLE TAXON RANGE

Unbiased estimators and confidence intervals will now be developed for endpoints of taxon range, based on the distance and the number of finds between first and last occurrences.

4.1. Point Estimation

Maximum likelihood estimators of θ_1 and θ_2 are respectively y and z. These, however, are evidently biased, because $Y > \theta_1$, $Z < \theta_2$ with probability 1. To obtain unbiased estimators, note that in the uniform $(0, 1)$ case, from Eq. (4),

$$\begin{aligned} E(Y) &= 1/(n + 1) \\ E(Z) &= n/(n + 1) \end{aligned} \tag{5}$$

where $E(\cdot)$ denotes the expected value. Hence, with a linear transformation of y, z to make them uniform on (θ_1, θ_2),

$$\begin{aligned} E(Y) &= (\theta_2 + n\theta_1)/(n + 1) \\ E(Z) &= (\theta_1 + n\theta_2)/(n + 1) \end{aligned} \tag{6}$$

Rearrangement of Eq. (6) yields

$$E[(nY - Z)/(n - 1)] = \theta_1$$
$$E[(nZ - Y)/(n - 1)] = \theta_2 \qquad (7)$$

Thus, the quantities

$$\tilde{\theta}_1 = (ny - z)/(n - 1)$$
$$\tilde{\theta}_2 = (nz - y)/(n - 1) \qquad (8)$$

are unbiased estimators of θ_1 and θ_2. Standard theory (Hogg and Craig, 1978, p. 341) shows that they have the minimum variance of all unbiased estimators. At first sight, an estimator of θ_2 (range top) involving y (lowest occurrence) may seem surprising, but this is in fact proper: without knowledge of y, no information exists on the scale factor and θ_2 cannot be estimated sensibly.

Standard errors of the estimators (8) may be useful. The variance of $\tilde{\theta}_1$ is

$$\frac{1}{(n-1)^2}\left[n^2 \operatorname{Var} Y + \operatorname{Var} Z - 2n \operatorname{Cov}(Y, Z)\right] \qquad (9)$$

Variances and covariance in Eq. (9) can be obtained from integration of Eqs. (3) and (4). After simplification,

$$\operatorname{Var}(\tilde{\theta}_1) = (\theta_2 - \theta_1)^2 \frac{n}{(n-1)(n+1)(n+2)} \qquad (10)$$

The variance of $\tilde{\theta}_2$ is the same. To use Eq. (10) in practice, an estimate of the unknown range $(\theta_2 - \theta_1)$ must be substituted. The obvious choice is $\tilde{\theta}_2 - \tilde{\theta}_1$, which is

$$(z - y)(n + 1)/(n - 1) \qquad (11)$$

Note that Eqs. (8) and (10) cannot be used to provide confidence intervals in the usual way, because $\tilde{\theta}_1$, $\tilde{\theta}_2$ are not distributed approximately normally, even when n is large.

4.2. Confidence Intervals

Confidence intervals for endpoints can be determined in numerous ways, but the most natural and convenient seem to be those of form

$$y - \alpha(z - y) < \theta_1 < y \qquad (12)$$

or

$$z < \theta_2 < z + \alpha(z - y) \qquad (13)$$

for suitably chosen α. Inequality (12) asserts that the origination point of the species is lower than the first observed fossil by no more than a fraction α of the observed range. It is crucial that the probability $p(\alpha)$ that the inequalities hold be independent of the parameters, and thus depend only on α. To verify independence, θ_1 may be subtracted from all the variables and parameters, thus making the lower endpoint zero; then division throughout by $(\theta_2 - \theta_1)$ results in an upper endpoint of 1. Neither operation affects the probability. The next step is to find $p(\alpha)$ in the $(0, 1)$ case, and thus relate α to the confidence level of the intervals.

Consider first the single-parameter case. Let

$$p_1 = P[Y - \alpha(Z - Y) < 0 < Y] \tag{14}$$

as in Eq. (12) with $\theta_1 = 0$. The right-hand inequality is certain to hold, and needs no further consideration. Direct integration of Eq. (3) over the appropriate subset of the unit square would give p_1, but a simpler argument is available. Note that

$$p_1 = P\left(Y < \frac{\alpha}{1 + \alpha} Z\right) \tag{15}$$

Conditional on $Z = z$, one of the n observations must equal z, and the other $(n - 1)$ observations are uniformly distributed on $(0, z)$. Hence $1 - p_1$ is the probability that the minimum, and thus all $(n - 1)$, of these values are between $[\alpha/(1 + \alpha)]\,z$ and z. This probability is

$$\left\{1 - [\alpha/(1 + \alpha)]\right\}^{n-1}$$

and so

$$p_1 = 1 - (1 + \alpha)^{-(n-1)} \tag{16}$$

The result can be obtained by an alternative derivation, which shortly will prove useful. Let $V_1, V_2, \cdots$ be independent exponential random variables with means all equal to 1. Let

$$T = V_2 + \cdots + V_n$$

Consider the quantity

$$P(V_1 > \alpha T)$$

Conditional on $T = t$, the probability is $e^{-\alpha t}$. Hence, the unconditional probability is the expectation of $e^{-\alpha t}$ over the distribution of T. This is the moment generating function, with argument $(-\alpha)$, of the sum of $n - 1$ independent exponential variables, and hence is given by

$$(1 + \alpha)^{-(n-1)}$$

(Hogg and Craig, 1978, pp. 104–106). Observe that ratios of sums of the exponential variables are independent of their sum, and hence probabilities of events involving these ratios are unchanged if conditioned on the value of $(V_1 + \cdots + V_{n+1})$. In particular, that value may be taken to be 1 without loss of generality. But in this case, $V_2, \cdots, V_n$ may be taken as gaps between finds, and V_1, V_{n+1} as intervals $(0, y)$ and $(z, 1)$ respectively. Thus $P(V_1 > \alpha t)$ is just $1 - p_1$, and result (16) is established.

Now consider the two-parameter problem. First compute

$$P[Y - \alpha(Z - Y) < 0, Z + \alpha(Z - Y) > 1] \tag{17}$$

which can be found by some rather tedious integration. It is, however, much simpler to consider the exponential variables $V_1, \cdots, V_{n+1}$. This requires

$$P(V_1 > \alpha T, V_{n+1} > \alpha T)$$

Conditional on $T = t$, this is $(\exp(-\alpha t))^2 = \exp(-2\alpha t)$. Arguing as previously, the unconditional probability (17) is

$$(1 + 2\alpha)^{-(n-1)} \tag{18}$$

The event of interest for the confidence interval is

$$[Y - \alpha(Z - Y) < 0, Z + \alpha(Z - Y) > 1]$$

which has probability

$$p_2 = 1 - P[Y - \alpha(Z - Y) > 0] - P[Z + \alpha(Z - Y) < 1] \\ + (1 + 2\alpha)^{-(n-1)}$$

in view of Eqs. (17) and (18). From Eqs. (14) and (16),

$$p_2 = 1 - 2(1 + \alpha)^{-(n-1)} + (1 + 2\alpha)^{-(n-1)} \tag{19}$$

To use these results, a confidence level p_1 or p_2 is specified and Eqs. (16) or (19) are solved for the corresponding unique value of α. Equation (16) can be inverted to give

$$\alpha = (1 - p_1)^{-1/(n-1)} - 1 \tag{20}$$

and for Eq. (19) it is easy to find an α by trial to give a specified p_2. Values of α for various values of n at confidence levels 80 and 95% have been calculated (Table 1). For a two-parameter example, if $y = 20$, $z = 30$, $n = 50$, the statements

$$30 < \theta_2 < 30 + (0.078 \times 10)$$

$$20 - (0.078 \times 10) < \theta_1 < 20$$

have jointly a 95% level of confidence. Confidence intervals for the extinction points of ammonites observed on Seymour Island (Fig. 1) are derived from Table 1, one-parameter case.

Table 1. α Values for One or Two Parameter Cases for Various Values of n

Number of finds	Confidence = 80%		Confidence = 95%	
	One parameter	Two parameter	One parameter	Two parameter
2	4.000	6.316	19.000	28.830
3	1.236	1.857	3.472	4.832
4	0.710	1.044	1.714	2.299
5	0.495	0.721	1.115	1.465
6	0.380	0.550	0.821	1.064
7	0.308	0.442	0.648	0.832
8	0.258	0.370	0.534	0.682
9	0.223	0.318	0.454	0.577
10	0.196	0.279	0.394	0.500
11	0.175	0.248	0.349	0.441
12	0.158	0.224	0.313	0.394
13	0.144	0.204	0.284	0.356
14	0.132	0.187	0.259	0.325
15	0.122	0.172	0.239	0.300
16	0.113	0.160	0.221	0.277
17	0.106	0.150	0.206	0.257
18	0.100	0.140	0.193	0.241
19	0.093	0.132	0.181	0.226
20	0.088	0.125	0.171	0.213
21	0.084	0.118	0.162	0.201
22	0.080	0.112	0.153	0.191
23	0.076	0.107	0.146	0.181
24	0.072	0.102	0.139	0.173
25	0.069	0.098	0.133	0.165
30	0.056	0.079	0.109	0.131
35	0.048	0.068	0.092	0.114
40	0.042	0.059	0.080	0.099
45	0.037	0.052	0.070	0.087
50	0.033	0.047	0.063	0.078
60	0.027	0.039	0.052	0.064
70	0.024	0.033	0.044	0.055
80	0.021	0.029	0.039	0.048
90	0.018	0.026	0.034	0.042
100	0.016	0.023	0.030	0.038
∞	0.000	0.000	0.000	0.000

Note that the joint interval does not have to be symmetric in the two endpoints;

$$\theta_1 > y - \alpha(z - y)$$

$$\theta_2 < z + \beta(z - y)$$

may easily be shown to be a $100p_2\%$ confidence interval provided that

$$1 - (1 + \alpha)^{-(n-1)} - (1 + \beta)^{-(n-1)} + (1 + \alpha + \beta)^{-(n-1)} = p_2 \quad (21)$$

The choice $\alpha = \beta$, as in Eq. (19), does, however, minimize the total length $(\alpha + \beta)(z - y)$ of intervals subject to Eq. (20); this can be verified quickly with the help of Lagrange multipliers.

4.3. Bayesian Estimation

To speak of the probability that endpoints θ_1, θ_2 lie in a certain region is tempting. This is improper in the context of frequentist statistics, where θ's are regarded as unknown constants, but can be discussed legitimately in the framework of Bayesian inference (for an introductory treatment see, for example, Lindley, 1980). Here, a Bayesian approach to the estimation problem is sketched.

For the prior distribution of (θ_1, θ_2), representing knowledge about the parameters before observing any data, one might take

$$\pi(\theta_1, \theta_2) = \begin{cases} 2 & \text{if } 0 < \theta_1 < \theta_2 < 1 \\ 0 & \text{otherwise} \end{cases} \quad (22)$$

This is one representation of complete prior ignorance about the parameters, save that they lie in a certain interval that is scaled to be (0, 1). Other choices of prior knowledge are, of course, possible. For example, if species are currently extant, range of θ_1 and θ_2 could be taken to be $(0, \infty)$ instead of (0, 1). In this case, several choices of prior knowledge could be reasonably said to reflect ignorance. Alternatively, a prior knowledge may be chosen to incorporate a researcher's hunches about which values of the endpoint are more likely.

Conditional on θ_1, θ_2, the joint distribution of the data $\underline{x}$ is taken again to be independent and uniform on (θ_1, θ_2), and thus has density

$$f(\underline{x} \mid \theta_1, \theta_2) = \begin{cases} (\theta_2 - \theta_1)^{-n} & \text{if } 0 < \theta_1 < y < z < \theta_2 \\ 0 & \text{otherwise} \end{cases} \quad (23)$$

Assume that $n > 2$; the case $n = 2$ would require a separate treatment. The joint density of the data and parameters is the product of Eqs. (22) and (23):

$$f(\underline{x}, \theta_1, \theta_2) = \begin{cases} 2/(\theta_2 - \theta_1)^n & \text{if } 0 < \theta_1 < y < z < \theta_2 < 1 \\ 0 & \text{otherwise} \end{cases} \quad (24)$$

The marginal density of $\underline{x}$ is obtained by integration of Eq. (24) with respect to θ_1 and θ_2, ranges being respectively 0 to y and z to 1. This results in

$$f(\underline{x}) = 2u_n/[(n-1)(n-2)], \qquad 0 < y < z < 1 \quad (25)$$

where

$$u_n = (z - y)^{-n+2} - (1 - y)^{-n+2} - z^{-n+2} + 1$$

From Eqs. (24) and (25), the conditional density of θ_1, θ_2 given the data is

$$g(\theta_1, \theta_2 | \underline{x}) = (n - 1)(n - 2)(\theta_2 - \theta_1)^{-n}/u_n,$$
$$0 < \theta_1 < y < z < \theta_2 < 1$$

Finally, the posterior density of θ_2 is

$$h(\theta_2 | \underline{x}) = \int_0^y g(\theta_1, \theta_2 | \underline{x})\, d\theta_1, \qquad 0 < y < z < \theta_2 < 1$$

or

$$h(\theta_2 | \underline{x}) = \begin{cases} (n - 2)\left[(\theta_2 - y)^{-n+1} - \theta_2^{-n+1}\right]/u_n & \text{if } z < \theta_2 < 1 \\ 0 & \text{otherwise} \end{cases} \tag{26}$$

Equation (26) gives the distribution of extinction time given the data and assuming prior distribution (22). As may have been expected, the density decreases with θ_2 from its maximum at z. With a quadratic loss function, the Bayes point estimator of θ_2 is the mean of Eq. (26), which can be shown to be

$$\frac{(n - 2)\,u_{n-1}}{(n - 3)\,u_n} + y\left[(z - y)^{-n+2} - (1 - y)^{-n+2}\right]/u_n \tag{27}$$

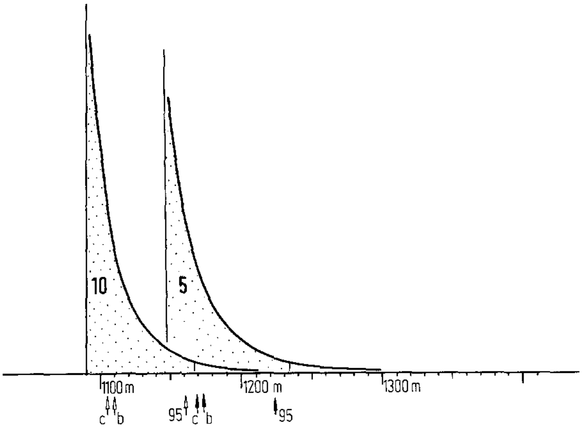

Fig. 3. Posterior distribution of upper endpoint θ_2 (extinction) in the Bayesian analysis for taxa 5 and 10. Shaded area: 95%. Also indicated are classical unbiased estimators (c), endpoints of classical 95% confidence interval (95) and posterior mean [b: Bayesian point estimates—see Eq. (4.22)]. Open arrows: taxon 10; closed arrows: taxon 5.

A probability interval for θ_2 can be constructed directly from quantiles of the posterior distribution. The distributions for ammonite taxa 5 and 10, the posterior means, calculated from Eq. (27), which provide Bayesian point estimates for θ_2, and the 95% probability intervals are shown (Fig. 3). For comparison, the classical point estimators and confidence intervals are indicated.

5. SEQUENCE OF ENDPOINTS FOR TWO OR MORE TAXON RANGES

Using the above ideas on confidence intervals for endpoints of single taxon ranges, confidence in the preserved sequence of the first and last appearances of several taxa also may be quantified. Of particular interest to the current search for evidence of mass extinctions is a format in which a confidence level is specified, and the question is asked whether the record is consistent with coincident upper endpoints. Other questions, such as that of whether true ranges of several taxa overlap, can be treated in much the same way.

Suppose that fossils of two different taxa have been found. For the first taxon let θ_1, θ_2, y, and z be defined as previously, and let a prime on these quantities denote the second taxon. Write r and r' for ranges $(z - y)$ and $(z' - y')$, where r is the value of a random variable R. A simple unbiased estimator of $(\theta_2 - \theta_2')$ is $(\tilde{\theta}_2 - \tilde{\theta}_2')$, as defined in (4). The confidence interval approach can be extended to provide confidence bounds for $(\theta_2 - \theta_2')$. As has been shown above,

$$P(Z < \theta_2 < Z + \alpha R) = p_1 \tag{28}$$

for a suitable value of α defined by Eq. (16) to give a desired value of p_1. Similarly,

$$P(Z' < \theta_2' < Z' + \alpha' R') = p_1 \tag{29}$$

for a suitable α'. (Unless the number of finds is equal, α and α' will be different.) Assuming that sampling procedures for the two taxa are independent, the events referred to in Eqs. (28) and (29) are independent. Thus, the probability that both occur is p_1^2. This will exceed a specified level $(1 - \gamma)$ if $p_1 = 1 - \gamma/2$. (For example, a choice of $p_1 = 0.975$ ensures a confidence level of at least 95%.) Now if both events in Eqs. (28) and (29) do occur,

$$(Z - Z') - \alpha' R' < (\theta_2 - \theta_2') < (Z - Z') + \alpha R \tag{30}$$

and thus, when sample values are substituted in Eq. (30), a confidence interval for $(\theta_2 - \theta_2')$ with level at least $(1 - \gamma)$ has been established. (Note that switching of primed and unprimed symbols in Eq. (30) gives the same result.) Further, by setting up the null hypothesis

$$H_0\colon \theta_2 = \theta_2'$$

and accepting H_0 if and only if the confidence interval contains zero, a hypothesis test with significance level at most γ has been defined. The test in this sense is conservative, and is not the only possible approach, but it is simple to use, and expression (30) is easy to interpret.

As an example, return to the ammonite data and consider the 16 finds of taxon 5 and the 8 finds of taxon 10. The observed finds occur in the intervals 800–1147 and 979–1091 m, respectively. Thus the ranges are

$$R = 1147 - 800 = 347$$

$$R' = 1091 - 979 = 112$$

Unbiased estimates (8) for the tops θ_2, θ_2' are

$$\tilde{\theta}_2 = (16 \times 1147 - 800)/(16 - 1) = 1170$$

$$\tilde{\theta}_2' = (8 \times 1091 - 979)/(8 - 1) = 1107$$

giving the unbiased estimate 1170 − 1107 = 63 m for $(\theta_2 - \theta_2')$. Using Table 1,

$$(1147 - 1091) - 0.534 \times 112 < \theta_2 - \theta_2' < (1147 - 1091) + 0.221 \times 347$$

i.e.,

$$-3.8 < \theta_2 - \theta_2' < 132.7$$

can be asserted with confidence greater than 90%. Thus, the hypothesis of co-extinction would be accepted (if just barely) at the 10% level.

The above method easily generalizes to the k-species case. For a test of specified significance level γ, set each of the k quantities $p_1, p_1', \cdots$ to $(1 - \gamma/k)$. The k inequalities such as Eq. (28) will hold simultaneously for every pair of taxa with probability at least $1 - \gamma$. Thus a test procedure is to accept the simultaneous extinction hypothesis provided that all $k(k - 1)/2$ confidence intervals Eq. (30) contain zero. Again, other approaches are possible but this seems to be one of the simplest.

As an example, consider a test of the hypothesis that ammonite taxa 3, 5, and 10 became extinct simultaneously. For a significance level of 5%, the confidence level of each species-pair is $(1 - 0.05/3)$. From Eq. (30), the intervals are

Species 3 to species 5: −108.3 to 99.2
Species 3 to species 10: −32.5 to 115.2
Species 5 to species 10: −32.5 to 164.3

Because all three intervals contain 0, the hypothesis is not rejected. By contrast, with $\gamma = 0.2$, analogous calculations show that the hypothesis should be rejected, as the top for species 10 appears lower than the others.

In a Bayesian treatment of the two-species problem, θ_2 and θ_2' would be regarded as independent random variables with distributions given by Eq. (26). By convolving the densities, the density of $(\theta_2 - \theta_2')$ is obtained. This is inconvenient to express algebraically, but numerical integration is straightforward. A prediction interval for $(\theta_2 - \theta_2')$ is obtained from suitable quantiles of the distribution. The plausibility of simultaneous extinction can be assessed by observing the location of the value zero in the distribution. If zero occurs below, say, the 0.025 quantile or above the 0.975 quantile, the hypothesis might be rejected.

In the case of the example just considered, for taxa 5 and 10, the posterior distribution of $(\theta_2 - \theta_2')$ (Fig. 4) has a mean at 60 m; this is the Bayesian point estimate if the loss function is quadratic. Because all the parameters and variables are taken to lie in (0, 1500), the range of $(\theta_2 - \theta_2')$ is from -353 ($= 1147 - 1500$) to 409 ($= 1500 - 1091$). A 95% prediction interval for $(\theta_2 - \theta_2')$ is from -24 to 150 m. The corresponding quantities from classical theory also are shown: the unbiased estimate of $(\theta_2 - \theta_2')$ is 63 m, and a 95% confidence interval is from -22 to 153 m. Both classical and Bayesian estimates and intervals are in good agreement.

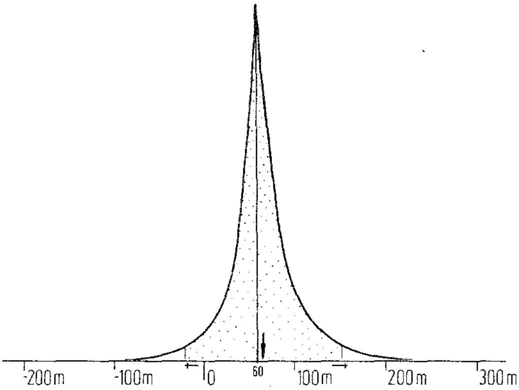

Fig. 4. Bayesian posterior distribution of $(\theta_2 - \theta_2')$, the difference between true extinction points for taxon 5 and taxon 10. Vertical line is the mean: this is the Bayesian point estimate of $(\theta_2 - \theta_2')$, assuming squared error loss. Shaded area: 95% prediction intervals. Also indicated are classical point estimate (arrow) and 95% confidence interval (crosses) for $(\theta_2 - \theta_2')$.

6. CONCLUSION

As is widely appreciated, the observed local range of a fossil taxon in a stratigraphic section is probably a truncated version of the true local range. Consequently, the fossil record does not always preserve the true sequence of migration and evolution events. Simple methods to attach confidence intervals to the ends of observed ranges, and thus deal with the inaccuracy, have been demonstrated. The lengths of extensions are a function of the chosen confidence level, number of finds, and length of observed range. For the traditional 95% confidence level, range extensions become longer than the observed range if the latter is established on less than 6 finds (Table 1). If a taxon is found at only two horizons in a section, drawing a local range seems inadvisable because 95% confidence intervals are more than 10 times longer than the observed range. Ammonite ranges analyzed here were established by careful collection in an unusually fossiliferous and uniform section. Nevertheless, some substantial range extensions were calculated. This example suggests that standard biostratigraphic practice, which identifies zonal boundaries or extinction events as horizons, routinely makes interpretations at greater precision than local data can justify.

Several methods of time correlation (summarized in Edwards, 1982) seek to eliminate the inaccuracy of observed local ranges by combination of data from several independent sections. Confidence intervals described here can be established independently, taxon by taxon and section by section; thus they may be used to evaluate individual sections *before* the application of these correlation procedures.

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