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How Many Species?

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ABSTRACT: – Simpson's query (Evol., 1952) as to the number of species during earth's history is addressed once again. Some possible mechanistic contraints are put on the problem to distinguish the effects on species evolution from punctuate forces (geological selection pressure generated by buoyancy and tectonic processes) and from near continuous point mutation forces (selection pressure put on the gene pool from the local environment). That is, the long time scaling rate for the life process (its appearance and disappearance) perhaps can be accounted for feasibly by rather straightforward geophysical-geochemical processes.

Introduction

Information has become available in the past few years, see Raup (1), Vail et al. (2), to warrant a return to the inquiry begun by Simpson in 1952 (3) as to the total amount of biological speciation during earth's history, for the entire period of existence of life. By arguing the plausibility of a particular geophysical model for driving speciation, these data permit putting constraints on the problem of producing and eliminating species in terms of a specific physical mechanism, the periodic stirring of sediment in streams and bodies of water related to river erosion and the isostatic and dynamic movement and rebalance of continents and margins by buoyancy forces and by plate tectonic processes. This tends to separate the problem of punctuate evolution of taxa higher than species (e.g., orders, classes) from the point mutation evolution of species and breeds by a more continuous local selection pressure.

Emergence and extinction of species

A recent data set exhibited by Raup (1) graphically presents an accounting for the appearance and disappearance of new biological "pseudocohorts", groups of families, at near uniform intervals during the past 600 million years (My) – using as a data base information on 2316 marine animal families, whose clustering becomes noted in the fossil-bearing stratigraphic record, and which then subsequently become gradually extinct. These newly accounted for evolutionary clusters are shown as appearing on the average every 8 My, i.e., about 70–80 such pseudocohorts in 600 My, with each pseudocohort therefore consisting on the average of about 30 or so families.

The extinction curve for each newly appearing grouping unit in (1) is presented as the variation of the remnant fraction of the total number of families of the newly accounted for cohort with time. The monotonic extinction of each pseudocohort of families is grossly but not smoothly exponential, disappearing on the average in perhaps 300 My. More precisely, these extinction curves, although tracking grossly along exponential decay curves, consist of ramps of extinction (diminution in the number fraction of member families) alternating with nearly flat steps of little loss in the remaining cohort fraction (Fig 1). The ramps of extinction are rapid, with descents in less than 10 My; the steps are about 25–40 My in duration; each pseudocohort extinction exhibits about 10 or so vaguely equal steps, beginning first with a ramp of descent. The extinction curves for the various pseudocohorts nest so that each of their flat (little or no extinction) regions stack above each other in the same time interval (periods of rapid extinction or of little extinction are forced to be isochronous, since they are associated either with a common stratigraphic or changing stratigraphic unit).

The assumption will be made that some such 'rapid' appearance and slow extinction curves as characteristic 'sawtooths' of birth (appearance of some such cohort unit) and death (substantial extinction of that cohort unit) of cohorts: (a) have marked the evolutionary process during the 600 My Phanerozoic Era; (b) have been associated with the specific continental erosion and tectonic processes not only for the Phanerozoic Era but

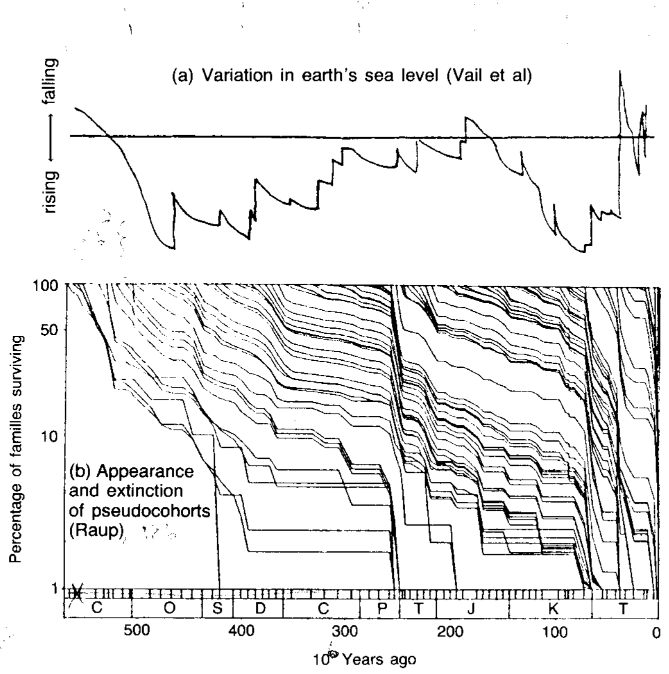

Fig 1 Variation in earth's sea level (data from Vail et al.) with appearance and disappearance of pseudocohorts of marine families (data from Raup). Figures adjusted to same time scale

for the past 2,500 My of sea level regulation by these processes; and (c) that speciation even during the Archean Era, from the origins of life (as prokaryotes) 3,800 Mya (million years ago) to 2,500 Mya did not differ much in character, since life appears to be nearly contemporaneous with the appearance of the first sedimentary rocks known (Isua), from 3,800 Mya (16). The major geophysical-geochemical characteristic marking that earlier epoch was the existence of a reducing rather than an oxidizing atmosphere which affected the character of the life forms, but not necessarily their general process of chemical evolutionary emergence (as a source for our point of view, we would be tempted to offer Hart (4) for the kind of current physical model accounts of the chemical nature of the early atmosphere that are at hand; and Margulis (5) as a source depicting the diversity of early chemical evolution of life, whose operational characteristics seem to have been considerably shielded from the toxic effects of contact with the early atmosphere).

It is here assumed that one can interpret the data set on pseudocohorts that Raup has referenced as representing the 'sudden' appearance of perhaps 30 different or related families (i.e., cohort as an aggregate of families; pseudo presumably indicating that they may or may not be closely related phylogenetically), on the average, and their extinction over the 300 My time scale of the individual extinction curves. 'Sudden', one could presume, might represent a time scale of perhaps not more than a My or so, small compared to each of the initial, less than 10 My, extinction ramps; also it is presumed that the time for essentially total extinction of these cohort families is about 300 My. *Alternatively,* one can interpret these pseudocohorts as representing the cumulant count of all families (new and old) that are found as one moves along statigraphically in time and encounters new families, in which case 'sudden' would merely have to mean in a time appreciably less than 300 My. We surmise from reviewers' comments that they interpret Raup's record to be merely the sheaf of families to be found in the stratigraphic record at any particular time, rather than any model of a coherently appearing cluster of families. Thus the latter interpretation of 'sudden', less than 300 My is likely more relevant. As we will point out later on, Simpson's studies can be the source of localization more nearly to less than 100 My. Whichever interpretation for the appearance of pseudocohorts of families is correct will not substantially affect the essential character of the argument being offered. That would only be affected if all the extinction curves were smooth, which is one basic point which Raup appears to be disputing.

In my attempt at modeling species appearance and extinction, I would like to overlook any one particular density spectrum or branching tree of speciation associated with that more or less 'sudden' cohort appearance and its subsequent stepwise extinction. Thus I am willing, at this point, to imagine models as extreme as the emergence of only one founder species representative of a new phylum with its further diversification at uniform rates or lumped rates into an entire tree of taxa; *or* the emergence of one or more founder species representing new classes from different phyla with their further diversification into lower taxon units; *or,* similarly, emergence of founder species representing new orders, or families, with their further diversification into lower taxon units. These diverse kinds of tree structures (evolutionary diversification of species among different kinds of taxon clusterings) can be imagined as represented by taxon distributions associated with each of Raup's extinction curves. One can presumably say that Raup's data perhaps represents one preponderant picture of taxon ramification (a tree representing emergence of about 30 families at once, or distributed over an extensive period of time like 100 My). Noting that we are passing over this very important problem at this point in the discussion, we can now bring in some geological information that perhaps bears on the problem of species formation or extinction (also see Fig 1).

Rise and Fall of Sea/Land

Vail and colleagues (2) have mapped out worldwide sea level changes and shown them to consist of rapid falls in level (less than 1 My), alternating with slower exponential rises in sea level. In an earlier NASA study (Iberall, Cardon (6)), erosion of continents was modeled and shown to be accounted for by two processes, one of chemical and one of mechanical erosion. Associating this erosion study with Vail's sea level fluctuation study (2) and using geological arguments that view the regulation of sea level as a conflict between the production of sediment by erosion and the isostatic rebalancing of the plates that float upon mantle and which bear these eroding continents (see Wood (7), and (6)), it was possible to isolate three time scaled processes within the Vail et al. data (2): a long 300–600 My 'fundamental' process, likely driven by thermal convective rolls and plumes in the upper mantle; and two shorter associated processes: a 25–40 My process likely associated with the time scale for erosion of localized, but both horizontally and vertically mobile, continental plates and their isostatic rebalance; and – at the tail of such adjustments – a more rapid 3–8 My process likely associated with the adjustment of plates due to the local sedimentary unbalance at the margin of continents, e.g., as plate subductions. Thus, in this modeling, rise and fall of sea level is associated with specific erosion processes of continental plates and their isostatic and dynamic rebalancing due to density derived and convectively driven force systems.

With the availability of the biological data set in Raup, it is possible to grossly compare the two data sets and note the comparability of their statistics (Fig 1). Highlighting the compatibility of the geological-biological fossil record – after all, as reviewers point out, it is a biostratigraphic record – makes it possible to suggest that the two more rapid plate tectonic processes might be responsible for the evolutionary appearance of living cohorts (and the subsequent evolution of their speciation tree) and their slower disappearance.

In Iberall (8), evidence was assembled to indicate that the long 600 My process was a slow smooth worldwide turnover of continental plates; scaled at 600 My intervals, plate turnover can account for the total 3,800 My record of sedimentary erosion that comprises the geological column (the total of all sedimentary deposits found on earth). This model, it was suggested, was compatible with the geological notion (see Gass and Wright (9)) that the earth's crust was essentially all made by 2500 Mya, and thereafter only periodically reworked by subduction, metamorphism at depth, turnover, and subsequent erosion. The drive would be the thermal convective cell rolls in the mantle. The 'smoothness' of that process would have little to do with speciation, except to move – aggregating and separating – continents. But, of course, the process also provides a gentle shifting and turning over of the solid state 'atmosphere' (the crust), and the liquid-state 'atmosphere' (the oceans) on the earth's surface.

The geological characteristics of the two faster processes – of marginal plate adjustments with a great deal of stirring of local shelf sediments every 8 My or so; of continental erosion that results in a more gentle deposition of sediments but with abrupt plate adjustments of continents every 40 My or so – are very plausibly to be associated with and of more concern to biological speciation.

The 25–40 My process represents the slow erosion of continents by rivers, the slow exponential adjustment of the floating continental plates to erosional products piling up on the continental shelf, and the slow correlated change in sea level. This medium range process, if associated with speciation at the taxon level of species, has essentially no effect on species disappearance at the taxon level of families. That is, family 'cohorts' (i.e., founder species prototypic of taxa at biological levels higher than families, such as orders, or classes) do not disappear by any general large scale process. Rather, as these cohorts diversify during the more gentle erosion process, species and breeds appear and adapt locally by point mutations and by local selection pressure that is developed by both the physical and ecological environments. The process just described is the slow smooth 'uniformitarian' character of Darwinian evolution, and is the one currently challenged by punctuate evolution.

On the other hand, the rapid adjustment of plates (and sea level), and the not quite as fast 3–8 My margin adjustments both involve tremendous rapid movements and stirrings of sediments. The obvious location of these processes are at continental margins, at the triple interface of atmosphere, ocean, land and sedimentary shelf. But such interfaces also occur within continents, particularly at the interfaces of all large bodies of water, when abrupt continental shifts take place. These processes both promote species extinction, e.g., of those species that are overwhelmed, and a fairly regular process of appearance of new founder or ur-species (the appearance of organisms that constitute the new cohort taxon, which will then begin to speciate further. No claim can be made here as to whether the speciation takes place uniformly of clumped). The latter process does not take place at all triple face margins. It likely appears at places where the stirring of sediment is appreciable, but also where species in such niches have been significantly decimated by earlier events.

Further, it is premised that such new cohort speciation every 8 My or so (species newly appearing at prototypic taxon levels such as families, orders, or classes) is occuring not markedly different from the initial appearance of life (which of course was in initially more chancy process. See Iberall, Soodak (10) for a discussion of the nature of the initial startup process, which we conjectured had to take place as a de novo chemistry in a 100 My slot. The driving processes, we surmise, have always been a chemistry driven by alternations of wet-dry, warm-cold, light-dark, a variable flow field within a shielded environment, and the availability of inorganic and organic catalysts). That is, new life forms are created or recreated from whatever remnant materials are available (now, of course, always involving genetic material. Because of the higher organized level of chemical material, for all periods past an initial startup, the subsequent biochemical process of producing new

Speciation level	Current scale of units	Feasible unit scales through 3,800 My history	
ecosystems	1	1	
kingdoms	10 (1)	1.4×10 (1)	1.9×10 (1)
phyla	10 (2)	1.9×10 (2)	3.7×10 (2)
classes	10 (3)	2.7×10 (3)	7.2×10 (3)
orders	10 (4)	3.0×10 (4)	9.0×10 (4)
families	10 (5)	5.1×10 (5)	2.7×10 (6)
genera	10 (6)	7.1×10 (6)	5.2×10 (7)
species	10 (7)	10 (8)	10 (9)

(Note: Parentheses in the table denote powers of 10)

Tab 1 The nominal scaling for current and total feasible biological taxa

cohorts could take place in the narrower slot of only millions of years instead of our conjecture of an initial startup of life chemistry in perhaps 100 My. In (10), we suggested that the near serial startup of about 9 geophysical processes formed a crowded agenda within a 4,600–3,800 My time frame, leaving not much more than 100 My for the startup of a life chemistry associated with the deposition of the first sedimentary material to be produced by weathering of more primitive continents. Such a complex chemistry, we conjectured, emerged in association with sedimentary-mediated catalysis at the well-stirred triple face of sedimentary solids, chemically enriched water, and a chemo-electrically active atmosphere). Thus the transformations produce primitive representations of successful evolutions that continue to represent taxa at higher levels than species. These transformations are 'punctuate' at the level of organisms that evolve new orders, classes, and phyla.

As a very rough number concentration model for taxa, suppose numerical measures are adopted as shown in Tab 1.

In the second column, the assumption is made that currently there may be about 10 million (M) species (perhaps 2–3M known, and 10M estimated – Margulis, Schwartz (11)), and that the major taxa of these species are logarithmically distributed (whereupon the crude approximations show up, e.g. 10 kingdoms instead of say 5, 100 phyla instead of say 90, etc.). The last two columns assume 100M and 1,000M species as feasible numbers for all times (see Simpson (3), Cailleux (12), also Schopf (13)).

With this sort of model in mind, we can now proceed to estimate the 'actual' total number of species through all time from 3,800 My to present.

If we assume that there are now 10 M species alive (11), and that new cohorts emerge punctuately at about a 5 My scale (that is we accept our results from (8), compatible with Vail et al. (2), and not too far removed from the marine sample of units used by Raup (1)), with an effectively linear decay out to 300 My, then we can estimate how many sawtooth cohort units – estimated now as producing a tree of species – lie in the present (or any other) 300 My time frame. Since 60 such 5 M year cohort units start up in the past 300 My, there is only one complete new cohort and 59 partial cohort units left. (It is assumed that the only cohorts that can substantially contribute to the current number of species are those newly created in the past 300 My frame). Imagine a unit evolutionary cohort (a sawtooth) to consist of (that is to produce a tree of) n species. Thus the existing number of cohorts from the past 300 My that will contribute to the count is

$$(1+59/60+58/60+57/60+...+1/60)n=10M.$$

That is, the number of species n in such a punctuately appearing cohort is about 330,000 (per 5 My period); this, by the ergodic hypothesis (the physical notion that in an a priori uniform probability phase space, averages in space and time would agree), represents the average number of species that a new cohort will ultimately produce before it becomes extinct.

Under these circumstances, we can estimate the total number of species to have been about 250 M since their origin, if speciation from these new cohort producing organisms were uniform throughout all times, *or* if perhaps their growth were exponential from the beginning (as Cailleux (12) assumed) the number might to more like 100 M. These numbers represent an average smoothed equivalent appearance for speciation up to about one new species per 10–20 years.

Thus, from the previous table we can surmise that such new cohorts appear almost at the prototypic level representing new phyla, certainly a handful of new classes (see the last two table columns. Since it is dubious that many new phyla have appeared in the past 600 My, the rarer events of producing phyla may very well have been more concentrated among productive events during the earlier 3,200 My history).

While these results, in confronting, accepting, and attempting to tame the ideas of a punctuate (or catastrophic) evolution might seen to be at odds with the ideas expressed by Schopf (13) in his assessment of punctuate evolution, I am neutral. I accept all of his comments about errors in assessing the duration of species (i.e., reducing their duration from say 10 My down to perhaps 0.2 My, in any case more likely down to the range 0.1 to 1 My), and the notion that speciation (as it affects the appearance of species) is gradualistic in the majority of cases, That is, I leave the detailed problem of tree evolution of the cohort to the evolutionist, where it very properly belongs. Nevertheless I believe that the notion of punctuate and near continuous evolution can be reconciled and tamed by physical reasoning, perhaps as I have outlined here. It requires no dialectic mysticism, no creatures from outer space, and no death stars. Perhaps, compatible with Raup's data, there are a few large extinctions due to such processes as large meteor falls, but this does not seem to be the main continuously ongoing process.

For those who might consider this paper purely conjectural, rather than hard science, it is simple enough to propose tests. They are to be conducted on a graph like or similar to the one in Raup. Consider a real or imagined 'mapping' of phylogenetic evolution against a horizontal flow of time, e.g., by 5 My units. For example, as a background mapping, broad strips of phyla may be imagined, from their beginning appearance in the fossil record to their disappearance (see, for example, Simpson (14)). These strips can be numbered. Note that one cannot start as firm a separation with kingdoms, since the number of kingdoms, estimated from 1 to 5, and their membership is still controversial.

At one or more starting points within each phylum strip, horizontal strips can be drawn to indicate the beginning (and ends) of classes. For each phylum, these narrower class strips can be numbered. Then within each class strip, at one or more points, horizontal strips can be drawn to represent order divisions, and continuing so on to the final narrow unit strips for species.

Actually, of course, such a figure can only be drawn conceptually, because such a life tree transforms the world of living organisms by its branching into our estimate of say 250 M species starting from a conceptualization of perhaps a hundred or so phyla. But given that conceptual background, we can now conjure up local tests of our thesis.

Against such a background, a species may be depicted as an elongated rectangle, its numbered height a unit of speciation, and its width the life of that species (perhaps 0.1 to 10 My). A higher taxon level, e.g., genus, will consist of an elongated rectangle containing many species rectangles, whose height may number many species units distributed along its vertical ordinate, and along whose width the temporal location of each species will be found. Such nesting continues for higher taxa up to some level that the reader wishes to test.

Suppose we wish to test for cohort aggregation at the level of families that appear at a particular point in time. One examines a considerable number of higher ordered classes that existed at that time in a chosen habitat. One elects a particular time (e.g., a 5 My vertical strip) and disregards all families that have appeared earlier. Also one blanks out all families that began more than a few 5 My strips later among those classes. By accounting for the evolutionary history of species lying within these time-clustered families over the next few hundred My, one ascertains whether their aggregate appearance and disappearance formed one or more (or none) coherent cohorts possessing the ramp-step form of taxon mortality postulated. Similar tests can be made for other taxon levels, e.g., genera, orders, or classes.

What is to be tested here is how inclusive is the cohort ordering to be found in the detailed fossil record. Clearly, from the beginning of their studies, what geologists know is tied up with correlations between sedimentary strata and fossils. All that is proposed here is a more directed mechanistic relation in the details of that correlation.

In addition, on a more experimental side, I would also infer (e.g., see (10)), 'predict' if you will, that life evolution or creation experiments conducted in reasonable numbers at properly stirred triple state interfaces could produce interesting biochemical yields.

Final Commentary

The author is unable to assess the total force of his arguments, only minimally to defend the following argument: (a) that there is a near periodic record of stratigraphic events on earth; (b) that such a record is in synchrony with its probable physical cause, sedimentation produced by the earth's hydrological cycle; (c) that there is a changing record of fossil remains of biological organisms within those stratigraphic horizons; (d) that following any one such changing record demonstrates a relatively uniform scaling of disappearance of that record, indicating near uniformity of that record of existing species within each such 'horizon' alternating with the change of each horizon; (e) that these changes in horizon are associated and have to be associated with significant upheaval in plates and their continental riders; (f) that the scale of each stratigraphic horizon fits the process of continental erosion by the hydrological cycle; (g) that the near constancy of the fossil record during each such scaled process implies that not very much speciation took place in that epoch, i.e., representing epochs of basically 'gradual' evolution (driven presumably by point mutations); (h) on the other hand rapid changes (losses) in speciation indicates that epochs of significant continental upheaval had to be associated with drastic effects on existing biological species; (i) students of the fossil record (for example, Rensch (15)) have indicated a differing turnover scale for various taxonomic levels; in particular Simpson's studies (14) seem to indicate that the turnover scale at the genetic level of phyla is of the order 100 My; (j) clearly the existing number of species at any time (e.g., 10 M at present) is a very insignificant fraction of the total number of species through all biohistorical times (e.g., 3,800 My), implying the requirement for a near equilibrium – even if considerably fluctuating – over that total time, requiring production and disappearance to be nearly in synchrony; (k) for the process presented by Raup to remain uniform for 600 My means that its near equilibrium, e.g., at 300 My scale (the scale for disappearance of a markable pseudocohort of species into the noise level of all ongoing species) has to consist of two production processes as well as disappearance processes: rapid production and slow production and/or rapid disappearance and slow disappearance, almost certainly 3 out of 4 of these steps (with perhaps 1 involving a null class); (l) if these were not the two pairs of processes, there is no way that the isochronous nesting exhibited by Raup could have produced its accounting scheme. Any more force to the argument will have to be provided by a much more detailed fossil record. This author is not prepared nor competent at this time to offer or derive such a record.

Afterthoughts

The Raup data set is difficult to interpret. Some reviewers have suggested that I have misunderstood that data set. That may be. I have reinterpreted it taking into account their comments. The reader can feel free to interpret that data set as he or she wishes (or to disregard it). However, as a rather recent book (M. Grene *Dimensions of Darwinism,* Cambridge Univ. Press, 1983) that captures the philosophy of the evolutionary problem quite well states (p. 7) "The history of biology, Ernst Mayr writes, is not so much the history of theories (let alone of 'facts') as it is of concepts". In reading that book and the many experts being discussed, one is left with the impression of a greater number of concepts based on rather small, parochial, nearly 'anecdotal' studies upon which to base rather unitary 'one plank' theories of evolution. I cannot claim to have studied (as yet) any exceptionally large fossil record data set, only bits and pieces, but something better is needed than the comment S. J. Gould offers (p. 71) from Kinsey's 1937 view that "in his article, Kinsey strongly advocated the central theme of the developing synthesis: Evolution at all scales, particularly macroevolution, could be explained by the genetic mechanisms observed in laboratories and local populations. '. . . I shall undertake to show that the same genetics [Mendelian genetics as the hereditary mechanism for the evolution of species as well as laboratory races] is all that is involved in the origin and development of the characteristics of higher categories.'

"Yet in his major monograph of 1930 . . . Kinsey defended a position that put him outside the synthesis by modern definitions . . . In his section on 'mutation' in the origin of *Cynips* species, he contrasted two points of view: the first, supported by 'laboratory studies' held that 'changes in genes occur . . . as mutations which are complete as soon as they have occurred'; and the second defined as the 'neo-Darwinian conception of fluctuating variations' which, by being accumulated over many generations and bent in a given direction by the force of natural selection, would gradually give rise to the character of new species.' . . .

"Kinsey then explicitly defended the 'genetic' view for speciation, in *Cynips* . . . and promptly committed a second . . . apostacy from later conceptions of the synthesis: He denied that most of the morphological expressions of species-forming mutations had any adaptive significance . . .

"This brief synopsis of Kinsey's views raises a dilemma: How could a man who seemed so much 'in' the synthesis (as later defined) by his defense of genetic continuity in causation, be so far out of it in his explicitly antiadaptionist views and his defense of discontinuous origin . . . for new species . . ."

I take solace in Gould's resolution: "This dilemma can be resolved (ironically, since professional students of evolution must face it) by recognizing a property of science that monolithic, textbookish interpretations ignore at their peril: Theories evolve too", even if the path taken here differs very significantly from Kinsey's and Gould's concept of that evolutionary problem for species.

Acknowledment

This paper was respectfully submitted to honor the memory of Tom Schopf and the contributions of George Simpson.

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