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Grass/grazer radiations: an interpretation of silica-body diversity

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In this note I postulate that interspecific differences in the morphology and arrangement of silica bodies, the elemental units of the grasses' silica defense method (SDM), should presumably result in some qualitative and/or quantitative differences in their abrasive effects on dental enamel surfaces of grazers. On this basis, it is hypothesized that the defensive diversification presumably afforded to grasses by the SDM through modification in the abrasive properties (qualitative and quantitative) of silica bodies has been influential in the diversification of vertebrate grazers. Unfortunately, no studies have previously examined the relation between silica body morphology and effects, thus both positive and negative empirical evidence bearing on the hypothesis is unavailable. My aim is only to suggest a testable, apparently plausible hypothesis, rather than presenting any empirical validation. Some indirect evidence, however, is consistent with it.

Silica is found in the epidermis of mature grass leaves in the form of discrete particles (silica bodies) produced in the interior of specialized cells (silica cells; Esau 1977). Surface sculpture, shape, size, and distribution pattern of silica bodies on grass epidermis are enormously variable from one species to another, and this variation has always been considered of great taxonomic value (Prat 1932, Metcalfe 1960, Clifford and Watson 1977, Dahlgren and Clifford 1982). A congruence between grass phylogeny and morphological patterns in silica bodies has been customarily implied for a long time by grass taxonomists (e.g., Prat 1932, Dahlgren and Clifford 1982). The main evolutionary trend displayed by silica bodies has been one of steadily increasing morphological complexity, resulting in an increase in the number of sharp ridges and total edge length per volume unit. Although silica bodies are present in other monocot groups (e.g., Zingiberales, Bromeliales, Arecales, Cyperales), it is in grasses (Poales) where they display, by and large, the greatest

morphological variety and complexity. Within Poaceae, the greatest complexity and diversity of silica bodies are found in the most advanced Panicoideae (including Paniceae, Andropogoneae and Chloridoideae), while in the less advanced Pooideae they are much less elaborate (Prat 1932, Clayton 1981). These observations suggest that the broad radiation of silica body morphology initiated with the diversification of Poales, and has since run parallel to the radiation of grasses.

Mechanical abrasion of enamel surfaces is the most peculiar effect of SDM on grazers, since the hardness of silica bodies exceeds that of the enamel, the hardest of the teeth tissues (Baker et al. 1959). Mechanical abrasion by silica has played an important role in the radiation of vertebrate grazers' dental patterns (Guthrie 1971, Stebbins 1981). No study has explored the relation between silica body morphology and arrangement and their effects on enamel abrasion. Some indirect evidence, however, indicates that differences in the morphology and arrangement of silica bodies may result in some qualitative and/or quantitative differences in their abrasive effects on dental enamel surfaces (Walker et al. 1978). If this is proved by future studies, it would be unnecessary to propose a process for the concomitant radiation of grasses and grazers essentially different from that underlying insect-dicot evolutionary interactions (McNaughton and Tarrant 1983), as outlined below.

In chemically active defensive compounds, function is of a chemical (molecule-to-molecule) nature, and these defenses have most often been circumvented by herbivores by molecular procedures (tolerance, detoxification). The radiation in chemical defense by dicot plants has been accompanied by a radiation in invertebrate herbivores on the basis of the evolution of tolerance or detoxification mechanisms (Ehrlich and Raven 1965, Berenbaum 1983). In the case of SDM, function is mostly of a mechanical nature, and this defense is to be circumvented by coarse, mechanical procedures related

to the ways of mechanically handling food. This is precisely what we know about the evolution of grazing vertebrates, in which the evolution of dental patterns is an important aspect to understand the radiation of this group. Within each major defensive "system" (e.g., "glucosinolates", "alkaloids", SDM), gross (chemical) composition is relatively constant, it is fine structure, and accordingly important details of function, that changes between plant species. While within "families" of chemical defensive compounds structure results from the arrangement of atoms and radicals, in SDM structure results from a combination of arrangement, density, shape and sculpture of elemental components (silica bodies). In closing the analogy drawn so far, I hypothesize that radiation of grazing vertebrates has been largely concomitant with adaptive radiation of the SDM of grasses, in a way analogous as to how insect herbivores and chemically defended dicots have concomitantly radiated. I do not intend to mean, however, that diversification in the fine structure of the SDM alone is responsible for the radiation of grazers, but rather that the defensive diversification presumably afforded to grasses by the SDM through modification in the abrasive properties of silica bodies has been influential in the diversification of vertebrate grazers. Two lines of evidence are consistent with this: (1) diversity of silica bodies within the group of monocot plant orders which possess them is strongly related to habitat- or habit-related susceptibility to vertebrate grazing; and (2) within grasses, complexity of silica bodies is precisely greatest in those groups (Panicoideae) which presumably have had a longer history of vertebrate grazing and live in regions where the incidence of grazers is highest.

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Correction

Unfortunately, the equation in "Population growth rate as a measure of individual fitness," by Bertram G. Murray, Jr., in *Oikos* 44: 509–511, was printed incorrectly. It should read, $1 = \sum \lambda_x \mu_x e^{-\alpha x}$.

Ed.