FORUM

Using fossil leaves as paleoprecipitation indicators: An Eocene example: Comment and Reply

COMMENT

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Wilf et al. (1998) analyzed leaf sizes in modern vegetation and concluded that leaf sizes accurately predict mean annual precipitation (MAP). However, we question the methods employed by these authors to derive leaf size; the modern samples are not comparable to one another or to fossil leaf assemblages, and the influence of temperature on leaf size is ignored.

Data for some samples were derived primarily from sizes cited in floral manuals, which cover the entire range of a species. Can this method produce even approximately valid size data? We compiled data for eight sites on the island of Yakushima in southern Japan. These sites were collected for CLAMP (Climate-Leaf Analysis Multivariate Program; Wolfe, 1993, 1995) samples; the full range of physiognomy, including leaf size, of each species of woody dicot was collected in limited areas analogous to areas represented by fossil leaf assemblages. Leaf sizes were calculated according to the method of Wilf et al.: The smallest and largest leaf sizes for species in the sample were based on two-thirds the length times the width for (1) the shortest and/or narrowest leaves and (2) the longest and/or broadest leaves; the resulting areas were converted to natural logs and then averaged to yield a mean natural log of the leaf area, which was then averaged for each sample. The same procedure was used for data taken from the pertinent floral manual (Ohwi, 1984). Obviously this procedure cannot validly delimit the smallest or the largest leaf sizes in every species, because in many instances, the shortest and narrowest measurements were not necessarily found on the same leaf, and likewise for the longest and widest measurements. In 25%–30% of the species analyzed, the low-end extreme measurements occurred on different leaves, as did the high-end extremes.

Leaf areas derived from actual samples are markedly smaller (Table 1) than those derived from Ohwi (1984). Comparison was also made for sizes of a sample from Ketchikan, Alaska, to data from the pertinent manual (Vierick and Little, 1972). These comparisons indicate that (1) manual-derived data have a different mean leaf size than sample-derived data from a restricted climate zone and (2) size relates poorly to MAP, especially for temperate, high rainfall samples. Using Wilf et al.'s equations and mean leaf sizes, predicted MAP for the Yakushima samples is ~113–133 cm, and for Ketchikan, 64 cm.

Neither the manual-derived plots nor the sample-derived plots for Yakushima fit Wilf et al.'s Figure 2 regression, and for Ketchikan, which has milder winters than the two Pennsylvania samples used by Wilf et al., both manual- and sample-derived plots also deviate markedly from other plots. Regression of leaf size against MAP with the addition of the Yakushima and Ketchikan samples as in Wilf et al.'s Figure 2 reduces the r^2 to 0.35. Leaf sizes from manuals do not yield valid site-specific data; more work may be involved in obtaining actual samples, as in CLAMP, but clearly actual collections are needed for valid calibration of physiognomy to climate.

Leaf-size data employed by Wilf et al. from different samples are not comparable. Sarmiento (1972) measured only canopy leaves and Bongers and Popma (1990) measured only "sun-leaves" (presumably = canopy), and canopy and/or sun leaves are smaller than shade and/or subcanopy leaves (e.g., Richards, 1996). Only part of the flora was included in the size analyses, because subcanopy trees and shrubs were excluded. In contrast, data reported by Dolph and Dilcher (1980) represented all woody plants in a sample plot. The data compiled from Hall and Swaine (1981) were based on averages for each species of "leaves of mature plants not saplings" (p.105), although Hall and Swaine (p. 49) recognized that "the leaves of many species . . . are much larger . . . in the young sapling stage than in the canopy." Dolph and Dilcher's (1980) samples are comparable to what might be found in the fossil record, but the samples based on Hall and Swaine (1981) were derived from thousands of square kilometers.

Leaf size, as in the instances of many other physiognomic character states, cannot be correlated in an isolated, univariate fashion to any one environmental parameter. Large leaves require both high moisture and high heat (Richards, 1996, p. 100). For example, lowland Yakushima samples have a lower score in the mesophyll categories (~16%–24%) than do samples from Fiji (32%–59%), although lowland Yakushima has considerably higher MAP (~430 vs. 200–300 cm) than does Fiji. However, Fiji is warmer, with a MAT of ~25 °C as opposed to ~19 °C, and thus the climate is more conducive to large leaves.

Another example of the influence of temperature on leaf size is subalpine (including subarctic) mesic vegetation relative to non-subalpine mesic vegetation (Table 2). The reduction in leaf size in subalpine vegetation is surely not the result of reduction in MAP, because these subalpine samples have higher MAP, and this reduction cannot be attributed to winter cold, because these subalpine samples have higher CMMT (cold-month mean temperature). Low heat during, and brevity of, the growing season are major features of subalpine climates and reduce average leaf size; fossil assemblages that display physiognomy characteristic of subalpine vegetation are found in the Paleogene of Idaho and Colorado (Wolfe et al., 1998) and in the Miocene of Alaska and Kamchatka (Wolfe, 1994). The complexity of the interactions of various environmental parameters that produces various compromises in physiognomic adaptations demands a more sophisticated approach than presented by Wilf et al.

TABLE 1. COMPARISONS OF LEAF SIZES DERIVED FROM FLORAL MANUALS TO ACTUAL SIZES IN AN ALTITUDINAL TRANSECT ON YAKUSHIMA AND AT KETCHIKAN

Sample	No. spp.	Manual mean natural log	Actual mean natural log	% large leaves	MAP (cm)
Yakushima 10 m	52	7.31	7.18	23	~430
Yakushima 10 m	41	7.23	6.87	16	~430
Yakushima 260 m	40	7.53	7.14	24	~670
Yakushima 420 m	40	7.37	7.00	21	~760
Yakushima 700 m	35	7.46	6.92	14	~860
Yakushima 800 m	32	7.23	7.02	18	~880
Yakushima 1080 m	26	7.34	6.93	11	~920
Yakushima 1350 m	17	7.42	7.11	13	~950
Ketchikan, Alaska	24	6.19	5.60	16	~405

Note: Large leaves are in the mesophyll 1 (or larger) size of Wolfe (1993).

TABLE 2. COMPARISON OF THREE HOKKAIDO NON-SUBARCTIC SAMPLES TO THREE SUBARCTIC/SUBALPINE SAMPLES FROM WESTERN UNITED STATES

Sample	No. spp.	CMMT (°C)	MAP (cm)	% small leaves
Kogawa, Hokkaido	43	-10.1	135	2
Teshio, Hokkaido	26	-10.4	138	2
Nukabira, Hokkaido	29	-10.7	160	3
Ketchikan, Alaska	24	0.5	405	38
Laurel Mtn., Oregon	24	2.5	271	22
Gov't Camp, Oregon	29	-1.5	219	22

Note: Small leaves are in the leptophyll 2 (or smaller) size of Wolfe (1993).

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REPLY

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We feel Wolfe and Uemura's criticisms are inaccurate and do not offer a serious challenge to our paper.

(1) Leaf size was approximated from published length:width minima and maxima for only five of our 50 modern samples (numbers 10, 19, 22, 39, and 43). If these five samples are removed, the effect on the correlation in our Figure 2 is not significant (r^2 increases from 0.760 to 0.783, slope from 1.39 to 1.41, p remains at 10^{-15}). Thus, contrary to Wolfe and Uemura's claim, the few data derived in this way did not compromise the relationship between leaf size and precipitation that we detected. Furthermore, the Eocene paleoprecipitation estimates that we presented were all derived from minimum/maximum areas for each fossil species, measured from actual specimens, and are not subject to any problems potentially introduced by approximation from the literature.

(2) As we noted (p. 205), leaf size appears to decrease, not increase, at extreme mean annual precipitation (MAP). The nine sites listed in Wolfe and Uemura's Table 1 are as wet to more than twice as wet as the rainiest sites in our data set. Contrary to their claim, the small leaf sizes recorded by Wolfe and Uemura do not invalidate our correlation, which is based on less extreme rainfall values. The data they cite from Ohwi corroborate the pattern of leaf size decline with very high precipitation in both warm and cool climates (but see point 5b regarding the CLAMP samples).

(3) Wolfe and Uemura state that the effect of temperature on leaf size was ignored, noting that temperature has a large negative effect on leaf area in subalpine vegetation. However, we avoided subalpine areas in our data set for this very reason (p. 204) and also discussed the role of temperature in our introduction.

(4) The point that the samples in our database "are not comparable" is partially true but not important. Differences in leaf size calculation and data collection should introduce noise into the dataset and reduce the significance of the correlation between leaf size and precipitation shown in our Figure 2, thus biasing against our conclusions. The fact that a highly significant correlation remains is evidence that the variation in methods did not overwhelm the powerful signal.

TABLE 1. PERCENT LARGE LEAVES* IN CLAMP SAMPLES VS. COMPARABLE FIELD-COLLECTED SAMPLES

	CLAMP[1]	This Reply[5]
(1) Barro Colorado Island, Panamá	49	59
(2) Guánica Forest, Puerto Rico	10	17
(3) Smithsonian Environmental Research Center, Maryland	18	51
(4) Southern Pennsylvania	14	49
(5) Northern Pennsylvania	19	40

*%Mesophyll 1 + % Mesophyll 2, as directed by Wolfe (1993).
[1]Data from Wolfe (1993): (4) = Arendtsville; (5) = Tunkhannock.
[5](1) = same leaves as CLAMP sample (see Wilf, 1997); (2) = "subsample" of Wilf (1997); (3) our sample #16; (4 and 5) = York and Allegheny "subsamples" of Wilf (1997)- climates nearly identical to the corresponding CLAMP samples selected (Wolfe, 1993; Wilf, 1997).

(5) Wolfe and Uemura state that many of our size data are not "valid" for comparison with precipitation because they include leaves collected over too large an area. They argue that local samples, such as those in the CLAMP database (Wolfe, 1993), are more appropriate because they are "analogous" to fossil assemblages. We disagree.

(a) Fossil assemblages vary greatly in their diversity, the area they sample, and presumably the fidelity with which they represent the original source vegetation. They also have undergone various types and amounts of taphonomic alteration and have been collected with varying intensities (e.g., Behrensmeyer and Hook, 1992). The strategy of very local sampling of living vegetation mimics some fossil assemblages. However, this procedure also results in a poor representation of the physiognomic range of living vegetation and has an unquantified effect on correlations of leaf size and shape with climate. The goal for baseline studies of living plants should be to sample as completely and carefully as possible so that the correlations between leaf physiognomy and climate can be known with the greatest precision. We should, correspondingly, be sampling fossils more thoroughly and trying to approximate the original leaf size spectrum of ancient source forests, not degrading modern samples in ways that may or may not match the taphonomic alteration and spatial limitation of fossil assemblages.

(b) The CLAMP samples clearly miss the larger leaves that are present in vegetation, as shown in our original Figure 3. It is probably this omission, and not the drawbacks of scoring from manuals as stated by Wolfe and Uemura, that results in manual-derived leaf area being higher than that of the CLAMP samples in their Table 1. The failure of CLAMP samples to include large leaves also can be demonstrated by comparing samples that are in the CLAMP database with our field-collected samples from the same locations or from climatically equivalent areas in the same region (Table 1). Most telling is the sample from Barro Colorado Island, Panama, for which Wolfe (1993) reports 10% fewer large leaves than we found, even though the same leaves were measured.

(6) With regard to the suitability of a univariate approach, we acknowledge that a method that simultaneously considers the effects on leaf size and shape of many variables such as precipitation, temperature, seasonality, soil characteristics, etc. might be more desirable. However, the accuracy of such an approach needs to be tested on a robust database. Unfortunately, CLAMP samples, in general, have too few species, are collected from areas that are too limited, and do not adequately represent the physiognomy of the vegetation that they are intended to sample (see also Wilf, 1997). Therefore, for the time being, we feel that the strong univariate correlation we demonstrated is a useful index of paleoprecipitation when used with the cautions given in our paper. We hope that it will be superceded by improved methodologies based on well-sampled field collections of living vegetation from a wide variety of continents and climates.

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Interplay of static loads and subduction dynamics in foreland basins: Reciprocal stratigraphies and the "missing" peripheral bulge: Comment and Reply

COMMENT

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Catuneanu et al. (1997) highlighted the importance of dynamic topography in contributing to tectonic subsidence and consequently stratal patterns in foreland basins. They suggested that subsidence due to dynamic topography, on a longer wavelength than that generated by flexural loading, can create additional accommodation on and cratonward of the peripheral forebulge, leading to preservation of reciprocal strata. However, their work contained a number of weaknesses and appears to overlook some previous research in this area.

We feel Catuneanu et al. made a number of errors in describing how dynamic topography varies with slab dip and subduction rate. They stated that dynamic topography will increase in amplitude when subduction rate increases. This is not necessarily true, since subduction rate does not directly control convective corner flow; rather, the thermal age and geometry of the subducting lithosphere are the important parameters (e.g., Burgess et al., 1997; Gurnis, 1992). Similarly, a decrease in slab dip will, as Catuneanu et al. stated, increase distal dynamic topography, but may not decrease proximal dynamic topography. For example, Gurnis (1992) demonstrated that both the magnitude and the wavelength of the dynamic topographic depression increase as slab dip decreases.

An important shortcoming in the Catuneanu et al. model is the emphasis on variations in magnitude of the orogenic flexural load, ignoring variations in load position. Indeed, they described the flexural load as "static." However, horizontal translation of orogenic loads, and resulting migration of the peripheral bulge and associated changes in accommodation space, are well documented (e.g., Flemings and Jordan, 1990; Allen et al., 1991; Peper et al., 1992). Thrust-tip advance rates range from relatively low values such as 1.4 mm yr^{-1} in the Cretaceous Sevier orogenic belt (Royse et al., 1975), and 2.5 to 3.5 mm yr^{-1} in the Swiss Alps (Allen et al., 1991), to higher rates such as 6 to 16 mm yr^{-1} in the Argentinian Precordillera thrust belt (Sarewitz, 1988). Forward modeling by Flemings and Jordan (1990) illustrates links between episodic cratonward migration of a thrust sheet and both proximal and distal changes in accommodation. Thus, it is entirely incorrect to consider the forebulge as static in space. What are the implications of varying orogenic load magnitude, combined with cratonward load migration, for reciprocal strata? Cratonward migration of the thrust load may accentuate the effects of increasing load magnitudes, but offset the effects of decreasing load magnitudes, respectively accentuating or subduing development of reciprocal strata.

As Catuneanu et al. stated, reciprocal strata are improbable when dynamic subsidence exceeds static uplift of the peripheral bulge. Relative amplitudes of the peripheral forebulge and dynamic topography around the forebulge, and the rates at which subsidence and uplift occur by flexure and dynamic topography, respectively, are thus important considerations. Flexural modeling of orogenic and sedimentary loading using a broken linear elastic plate with thicknesses ranging from 5 to 75 km shows that the forebulge amplitude does not exceed ~200 m, or less than 2.5% of total basin depth (Sinclair et al., 1991). Modeled forebulge amplitudes can be compared with amplitudes of dynamic topography predicted using a three-dimensional finite element convection model (CITCOM), as described in Burgess et al. (1997). Such comparison shows that, for subducting slabs with dips ranging from near horizontal to ~20°, at distances <1750 km from the subduction zone, the forebulge amplitude would be insignificant compared to amplitudes of dynamic topography. For a slab at 45°, the forebulge amplitude would be insignificant at <800 km. For a slab at 70°, this distance is ~600 km. Clearly, based on these model results, formation of reciprocal stratal patterns is unlikely with shallowly dipping slabs unless the peripheral bulge is situated more than 1700 km from the subduction zone. Conversely, dynamic topography above slabs dipping at 45° or more is unlikely to significantly affect stratal patterns around peripheral bulges >800 km from the subduction zone. Rates and timing of subsidence generated by dynamic topography must also be considered. To generate reciprocal strata, sedimentation rates would need to approximately match subsidence and uplift rates due to orogenic flexural loading. Subsidence from flexural loading would in turn have to match subsidence rates due to dynamic topography generated as a subducting slab penetrates the mantle.

In the Cretaceous Western Interior basin, Campanian and Maastrictian strata were deposited over an anomalously long wavelength, as first identified by Cross and Pilger (1978) and Cross (1986). These authors suggested subcrustal loading due to shallow-angle subduction of the Farallon slab as the mechanism responsible for generating the accommodation space filled by the Campanian–Maastrictian strata. Neither work is referenced by Catuneanu et al., who discussed the use of reciprocal strata to identify influence of dynamic topography in creating long-wavelength accommodation in the basin. If reciprocal strata are present, so must be some significant thickness of strata preserved beyond the wavelength of flexural loading. These strata indicate possible influence of dynamic topography on formation of the foreland basin, as observed by Cross (1986), without the need to identify correlative contrasting stacking patterns around the peripheral bulge. Reciprocal stratal patterns may well exist in this basin, but were not required to identify influence of a long-wavelength subsidence mechanism.

In summary, the situation is considerably more complicated than suggested by Catuneanu et al. A full quantitative analysis of the interplay between changing magnitudes of orogenic loading, horizontal load migration, dynamic topography, deposition, and erosion is required. Forward modeling studies combining these processes are probably the best way to determine if reciprocal strata can form as described.

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REPLY

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Peter Burgess raises some issues that merit a response. Our paper is a short topical article that presents a mechanism for the formation of reciprocal stratigraphic sequences and explains the apparent absence of a stratigraphic signature of the peripheral bulge in some foreland basins.

Our proposed explanation is based on the superposition of two mechanical processes in combination with sedimentation and erosion. The two processes are lithospheric flexure, caused by supra- and sub-lithospheric "static" loads, and lithospheric subsidence and/or warping by mantle flows, particularly the "dynamic" effects of viscous corner flows caused by subducting slabs. Both of these mechanisms have a simple physical basis. Quantitative models exist for both processes, but these lead to model-dependent predictions. We chose to explain our superposition mechanism conceptually because we doubt that models can predict the superimposed effects accurately. This is particularly true because the explanation is based on the difference between the static and dynamic vertical lithospheric displacements considered in an incremental (as opposed to total) manner. The references were chosen accordingly to be representative of the basic principles of the two processes.

Our section "Conceptual Interpretation of Reciprocal Stratigraphies" focused on the effects of incremental changes in the dynamic and static loads on changes in accommodation space. Not all stratigraphic responses are described, but some "other stratigraphic responses" that "can be envisaged" were also mentioned. Of greater interest is whether such signatures have been identified but lack an explanation, or will be identified by further research stimulated by these simple concepts.

DYNAMICAL TOPOGRAPHY

Our statement that downward dynamical deflection is amplified when subduction rate increases (other factors remaining unchanged) is based on kinematically controlled viscous corner flow calculations (e.g., Tovish et al., 1978). This relationship is, in our opinion, likely to be correct to first order. We agree that in dynamical models the subduction rate will itself depend on the thermal and/or density fields. Nevertheless, subduction rate can often be constrained from plate reconstructions and is, therefore, useful in the analysis of foreland basin stratigraphy when thermal and/or density conditions are not known.

We agree that there may be circumstances for which proximal subsidence will have increased after a decrease in slab dip. However, even for the example from Gurnis (1992), cited by Burgess, there was some loss of proximal accommodation space because "the continental surface nearest the trench rebounded; as a result sedimentary sequences were uplifted and tilted."

LOAD POSITION AND "STATIC" TERMINOLOGY

We apply the term "static" to loads that are in equilibrium when velocities are zero. "Static" is used in contrast with "dynamic" forces and/or loads caused by mantle flows. Unfortunately, "static" has more than two meanings, but we did not mean to imply stationary.

Burgess notes that "thrust tips" advance and quotes relevant rates, but these may not be a good measure of the migration rate of the appropriately "weighted" static load that is responsible for the horizontal migration of the flexural peripheral bulge. Although this is a model-dependent conclusion, it can be argued on the basis of Coulomb critical wedge mechanics that in a "retro" setting, the wedge load must grow self-similarly in order to propagate the thrust front. We do, however, agree that static peripheral bulges will evolve by lateral migration, in situ growth, or a combination of these effects. We chose to present the concepts in terms of amplitude changes because it is simple, not because we are unaware that the deformation front advances cratonward.

PROBABILITY OF RECIPROCAL STRATA

Burgess quotes absolute amplitudes of the static peripheral bulge and dynamic topography from model calculations. However, our description of how these vertical deflections combine is based on incremental changes in the two components, not their total magnitudes. We do not expect the entire sedimentary fill of a foreland basin to be characterized by reciprocal stratigraphies of the type we describe. Instead, preferred circumstances for their formation occur when the static uplift velocity of the peripheral bulge is comparable to the subsidence velocity owing to the dynamic effect, and the converse.

CRETACEOUS WESTERN INTERIOR BASIN

According to Burgess et al. (1997), Mitrovica et al. (1989) were the first to propose dynamical topography as the mechanism responsible for the anomalous distribution of Campanian to Maastrichtian deposition in the western United States (see also Beaumont, 1982). There was no intent to deny that Cross and Pilger (1978) recognized the anomalous deposition. Our focus is not, however, the anomalous deposition per se, but the processes that create accommodation space and their consequences for stratigraphy within this region of anomalous deposition.

We agree that dynamical topography has been used as an explanation for the anomalous Cretaceous deposition, e.g., Mitrovica et al. (1989). Their work indicates that a "significant thickness of strata" is "preserved beyond the wavelength of the flexural loading," as Burgess states. We (Catuneanu et al., 1997) also commented in this regard that the dynamical topography may explain this region, which has been termed the "back bulge basin" or "eastern platform basin." Our purpose was not to demonstrate the "possible influence of dynamic topography on the formation of a foreland basin." It was, instead, to suggest the type of observational evidence that may allow the separation of the dynamic and static components. For example, it would be interesting to map the static peripheral bulge within the broader basin. The interplay may even have economic implications.

Forward modeling may be appropriate, bearing in mind the model-dependent results (for example, the tendency for mantle flow models to over predict surface-boundary deformation [Lithgow-Bertelloni and Gurnis, 1997]). Observational evidence is probably more important.

Peter Burgess has misinterpreted aspects of our paper, and we accept responsibility for any lack of clarity. We therefore thank him for raising these issues.

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Fossil gap analysis supports early Tertiary origin of trophically diverse avian orders: Comment and Reply

COMMENT

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Bleiweiss (1998) used gap analysis of the fossil records of three avian orders to argue that they originated (and diversified) after the K-T boundary. This is in contrast to molecular clock data, which suggest the modern orders diverged from each other deep in the Cretaceous, perhaps 100 Ma (Hedges et al., 1996; Cooper and Penny, 1997). Here I argue that while the gap analysis does support the conclusion that the diversification within each of these modern orders occurred after the Cretaceous, it is also consistent with molecular data that suggest the divergence between the orders was deep in the Cretaceous, rather than in the Tertiary.

Bleiweiss (1998) used Strauss and Sadler's (1989) method for adding confidence intervals on the end points of stratigraphic ranges (classic confidence intervals). This method implicitly assumes that the probability of recovering fossils is uniform with time (Fig. 1A) (Strauss and Sadler, 1989; Marshall, 1990, 1998). All else being equal, the probability of recovering fossils of a higher taxon is likely to be proportional to the number of species extant at any given time. Thus, classic confidence intervals will underestimate times of origin if clades had long initial histories of low, or cryptic, diversity. This limitation of classic confidence intervals may be circumvented with generalized confidence intervals (Marshall, 1997), which make use of specified nonuniform fossil recovery potentials. To illustrate how misleading the assumption of uniform fossil recovery potential may be, consider the estimated time of origin (actually the origination time of the first diagnosable synapomorphy) of the Caprimulgiformes (goatsuckers). Suppose they originated deep in the Cretaceous, but that their diversity remained low until after the Cretaceous. A corresponding fossil recovery potential is shown in Figure 1B. Using this fossil recovery curve, the generalized 95% confidence interval now extends deep into the Cretaceous (Fig. 1A), consistent with the molecular data, and in contrast to the classic 95% confidence interval (Bleiweiss, 1998; Fig. 1A).

Of course, the exemplar fossil recovery potential curve shown in Figure 1B is just one of many possible curves, and the length of the confidence interval is sensitive to the exact shape of the chosen curve. For example, if we assume the Caprimulgiformes diversified at the Paleocene-Eocene boundary, then the generalized confidence interval would be even longer. At present, there is no obvious way to construct curves for these taxa, so it is unclear how to reliably use confidence intervals to estimate the uncertainties in their times of origin. But given that many higher taxa had long early histories with relatively low diversities, the generalized confidence intervals suggest the real possibility of a deep origin for the modern avian orders.

Now in Bleiweiss's (1998) analysis, the 95% classic confidence interval for the Apodiformes (swifts and hummingbirds), and the Strigiformes (owls) does not extend to the K-T boundary, but only just extends into the Cretaceous for the Caprimulgiformes. These results suggest these clades were unlikely to have had Tertiary levels of diversity in the Cretaceous: The gap analysis does support Bleiweiss's (1998) claim that the diversification (in distinction to the origin) of these clades was post-Cretaceous.

In summary, gap analysis supports the hypothesis that the modern orders of birds diversified in the Tertiary. However, under simple (but not unrealistic) models of diversification, gap analysis with generalized confidence intervals (Marshall, 1997) indicates the fossil record is consistent with the molecular clock data that suggest deep Cretaceous divergences for the avian orders, although the fossil record does not contradict the hypothesis that these orders may have had Tertiary originations.

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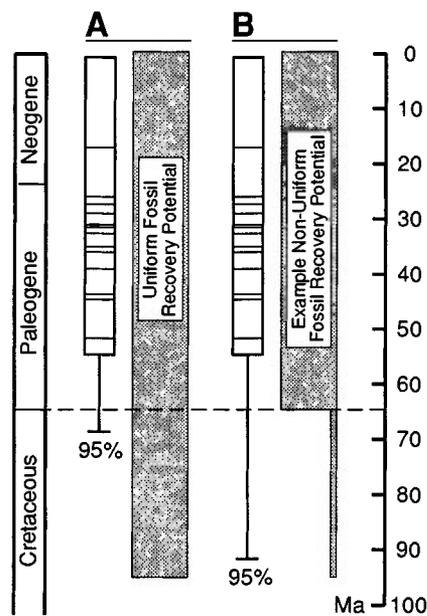
Figure 1. Origins of Caprimulgiformes (goatsuckers). (A) Classic confidence interval analysis conducted by Bleiweiss (1998) assumes uniform fossil recovery potential. Under this assumption, 95% confidence interval on observed stratigraphic range just extends into top of Cretaceous. (B) However, generalized 95% confidence interval is much longer if one assumes group was extant in Cretaceous, but was only represented by a one-tenth standing diversity present in Tertiary. In contrast to Bleiweiss (1998), I have only included fossil occurrences (indicated by horizontal bars; Recent is ignored).

REPLY

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Marshall suggests that a cryptic Cretaceous divergence, characterized by low species diversity and, hence, a low fossil recovery potential, could reconcile the apparent conflict between molecular and fossil evidence for the origin of modern avian orders. Marshall's generalization that many higher taxa had long early histories with relatively low diversities probably applies to the lineage that gave rise to the modern avian orders, the Ornithurines, whose Mesozoic-age fossils are less numerous than those of

the archaic Enantiornithines. But the hypothesis that the modern orders themselves fit this pattern is problematic, for reasons outlined below.

Synapomorphies of Modern Orders. Marshall equates ordinal origination with the appearance of the first diagnosable synapomorphies. If modern orders arose within the mid-Cretaceous, then earliest Tertiary fossils should be easy to assign to modern orders. As noted by Feduccia (1996), however, the earliest remains of Ornithurines with affinities to modern orders (from the Late Cretaceous and earliest Paleogene) are mosaics of characters that define living orders: *Presbyornis* (shorebird-duck) and *Rhynchaeites* (shorebird-ibis), among others (Feduccia, 1996). Notably, many of these mosaic forms lived in lacustrine environments and some were apparently colonial, features that make them abundant as fossils where they have been found; these same mosaic taxa are unknown before the Late Cretaceous.

Rapid or Gradual Divergence. The hypothesis that modern orders of birds arose in the mid-Cretaceous typically has been linked to a gradual pattern for their divergence (Cooper and Penny, 1997). Molecular phylogenies based on whole (single-copy) genome analysis by DNA hybridization (Bleiweiss et al., 1994, 1995) suggest that many modern avian orders diverged rapidly (indicated by short internodes connecting branches at the base of the tree). This arrangement is obtained even with suitable corrections for compression of genetic distances at extreme levels of divergence (Bleiweiss et al., 1995). Thus, a rapid radiation indicated by several molecular phylogenies is consistent with the pattern observed in the fossil record.

Biases in Molecular Clocks. The inconsistency between the avian fossil record and molecular clock data parallels a more general tendency for molecular clock-based estimates of divergence dates to greatly exceed those indicated by the fossil record (see Ayala et al., 1998, for discussion of possible analytical problems associated with application of the molecular clock). The discrepancies extend to different levels of the taxonomic hierarchy, including phyla (Wray et al., 1996), orders of tetrapods (Hedges et al., 1996; Cooper and Penny, 1997; Kuhmar and Hedges, 1998), and species of birds (Klicka and Zink, 1997). This pattern may reflect the same bias in the fossil record for all these groups. Alternatively, the molecular clock (rate of genetic substitution) may speed up in a clade undergoing evolutionary radiation, resulting in an overestimate of the divergence date (Vermeij, 1996). One possible mechanism for such a speed up is speciation; this process and its attendant phenomena are associated with both radiation and increased rates of molecular evolution (Barraclough et al., 1996).

In summary, Marshall's assumption of an early interval of low diversity is plausible and could reconcile the molecular and fossil data. Various other lines of evidence suggest alternative evolutionary patterns, however. Until these alternatives can be tested more thoroughly, an assumption of uniform probability of fossil recovery is the appropriate working null hypothesis, and one that is consistent with the fossil record (Bleiweiss, 1998).

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