

- liaris, *H. melanotis*, *Euphonia xanthogaster* (Andean foothill races), *Tangara arthus*, *Diglossa lafresnayii*, *Basileuterus tristriatus*, *B. coronatus*, *Conirostrum sitticolor*, and *Cyanolyca viridicyana*. R. A. Paynter, Jr. [*Bull. Mus. Comp. Zool.* 148, 323 (1978)], pointed out the leapfrog pattern in *Atlapetes*. One of the leapfrog patterns rests on an undescribed new subspecies in *Pseudotriccus ruficeps* (T. S. Schulenberg, in preparation).
9. *Metallura aeneocauda* supersp., *Schizoeaca fuliginosa* supersp., and *Diglossa carbonaria* supersp.
 10. *Chamaepetes goudotii*, *Atlapetes rufinucha*, *Chlorospingus ophthalmicus*; *Schizoeaca fuliginosa* supersp. For discussion of variation in *Schizoeaca*, see J. V. Remsen [*Proc. Biol. Soc. Wash.* 94, 1068 (1981)].
 11. It is assumed that the virtual absence of reports of such patterns in other areas reflects a low incidence rather than lack of thorough study. The likelihood of the latter seems remote because geographic variation in birds has been much more thoroughly studied in North America, Eurasia, Africa, and Australasia than in South America; scrutiny of syntheses of geographic variation in these regions reveals no clear cases of the leapfrog pattern within a given biotic region, although instances of presumed convergence, mostly interpretable as examples of Gloger's rule, can be identified where regions similar in climate or habitat are separated by a climate differing in these respects [A. Keast, *Bull. Mus. Comp. Zool.* 123, 305 (1961); B. P. Hall and R. E. Moreau, *An Atlas of Speciation in African Passerine Birds* (Trustees of the British Museum of Natural History, London, 1970); D. W. Snow, Ed., *An Atlas of Speciation in African Non-Passerine Birds* (Trustees of the British Museum of Natural History, London, 1978); C. Harrison, *An Atlas of the Birds of the Western Palearctic* (Princeton Univ. Press, Princeton, N.J., 1982)].
 12. J. M. Diamond, *Science* 179, 759 (1973).
 13. *Haplospiza rustica* (T. A. Parker III and J. V. Remsen, in preparation).
 14. The term "polytypic subspecies" has been applied to such cases by E. O. Wilson and W. L. Brown, Jr. [*Syst. Zool.* 2, 97 (1953)]. Although climatological data are generally unavailable for forested regions of the humid eastern Andes, it seems highly unlikely that any subtle geographic differences that may exist would be sufficient to promote the radical and abrupt phenotypic changes that characterize geographic variation in Andean birds. Mayr's [*Ibis* 101, 293 (1959)] broader definition of polytypic subspecies would encompass the leapfrog pattern.
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 16. F. M. Chapman, *Bull. Am. Mus. Nat. Hist.* 48, 243 (1923).
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 19. The Andean bird collections at the Museum of Zoology of Louisiana State University have been generously supported by J. S. McIlhenny, B. M. Odom, H. Irving, and L. Schweppe. G. Barrowclough, G. Bejarano, R. Bleiweiss, B. S. Bowen, G. R. Graves, M. S. Hafner, N. K. Johnson, R. R. Koford, S. M. Lanyon, J. P. O'Neill, and F. Vuilleumier provided many constructive criticisms of the manuscript.

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Arctic Biostratigraphic Heterochrony

Hickey *et al.* (1) described the magnetic stratigraphy (not magnetic anomaly profile) and biostratigraphy of Upper Cretaceous and Lower Cenozoic sediments of the Eureka Sound Formation (2, 3) of arctic Canada and claimed that there is substantial heterochrony of biostratigraphic units. Their conclusions, if correct, have great ramifications with respect to the correlation and evolution of the North American biota and to the underlying bases for biostratigraphy in general. Although the conclusions rest almost entirely on the magnetostratigraphy of the sediments in question, the data as presented cannot be assessed; indeed, the paleomagnetic work (4) is essentially unpublished except in abstract (5). Nevertheless, the summary of numeric data (1, reference 14) leads us to believe that the magnetic stratigraphy is suspect and that the correlation of supposed magnetozones to the geomagnetic polarity time scale is very insecure.

A necessary criterion for assigning normal or reversed polarity to a sample direction is whether the calculated virtual geomagnetic pole (VGP) for the north-seeking magnetization falls, respectively, at high northern or high southern paleolatitudes with respect to the mean paleomagnetic pole; the polarity should be regarded as indeterminate if the VGP falls at intermediate latitudes—for example, within 45° of the paleoequator. Such intermediate positions can be records of

excursions or polarity transitions of the geomagnetic field but more frequently are indicative of poor data, the result of sample misorientation or mismeasurements, unresolved complex magnetizations, or other experimental errors and inadequacies in the magnetic record.

The poor internal consistency of the paleomagnetic data used by Hickey *et al.* compromises any precise interpretation of the stratigraphic polarity sequence. The parameter *K* (estimate of Fisher's precision parameter) is a measure of dispersion in the directional data; when *K* approaches zero the directions are uniformly distributed on a sphere and are random, whereas for large values of *K* the directions are confined to a small portion of the sphere near to the mean direction (6). The cited value for *K* is 2.4 for the 158 sample VGP's used to construct the magnetic polarity stratigraphy. It is useful to calculate from *K* the radii of the circles whose centers are the mean and which contain specified percentages of the sample VGP's (7). For the given value of *K* and a Fisherian distribution, 50 percent of the sample VGP's are expected to lie within about 44°, and 63 percent (the circular standard deviation, analogous to the standard deviation of the normal distribution) lie within about 52° of the estimated overall mean paleomagnetic pole position. In other words, the sense of polarity of more than a third to almost half the samples should be

considered indeterminate because their VGP positions are expected to fall in low paleolatitudes and farther than 45° from the paleomagnetic pole. This leaves no more than 100 and as few as 80 samples to determine the polarity sequence of about 3500 m of section.

The large dispersion in the paleomagnetic data strongly suggests the presence of pervasive spurious or secondary magnetizations and a low fidelity record of the geomagnetic field. Relevant evidence from laboratory or field tests was not presented to suggest otherwise. Although we cannot ascertain the stratigraphic distribution of the 80 to 100 samples that might provide interpretable polarity information, if they were uniformly distributed through the composite section spanning about 40 million years (Campanian to Early Eocene), then an average temporal resolution of no better than 0.4 million years is possible. Considering that polarity chrons and subchrons in the Late Cretaceous and Early Tertiary have durations of similar order (8–11) and that about 30 percent of the sections are unexposed, we believe that the polarity sequence of the Eureka Sound Formation sections must be considered poorly constrained. Since correlation to the geomagnetic polarity time scale depends critically on recognizing a characteristic pattern of normal and reverse polarity intervals, the inclusion of magnetozones on the basis of ambiguous or missing data will change the magnetic stratigraphy in significant ways.

The poor paleomagnetic data, the ambiguities in independent lithostratigraphic correlation between sections, and the lack of evidence concerning possible unconformities and time gaps within the Eureka Sound Formation (notably between informal members III and IV which contain the terrestrial vertebrates) are impediments to a meaningful discussion of alternative magnetochronologic correlations. It should suffice to mention that in general the correlation of a normal polarity magnetozones with chron C24N because it is "stuttered" (1) is not diagnostic on its own, since for example the younger chron C23N is also "stuttered" (8–12). Chron C33N was identified supposedly on the basis of the stratigraphic thickness of the normal polarity magnetozones, "corroborated" by fossils, but in fact the basis was mainly biostratigraphic, bringing the argument full circle.

Paleobotanical and other evidence indicates that polar climate in the Late Cretaceous and Early Tertiary, although seasonal, was more moderate than that of today. Therefore one might expect

that when global temperature gradients increased in the late Cenozoic, heterochroneity would be strongly evident. For mammals, at the generic level comparable to the taxonomic levels used in the biostratigraphic correlation of the vertebrates of informal member IV of the Eureka Sound Formation (1, 2), such is not the case (13–16).

Heterochroneity exists at least to some degree in all biostratigraphy, depending particularly on the ecological requirements and abilities of organisms to adopt rapidly to new environments. Floral heterochroneity may be indicated in the data of Hickey *et al.* (1) on the basis of biostratigraphy alone (coexistence of Campanian marine organisms with plants of “Maestrichtian-Paleocene” aspect). However, Hickey *et al.* (1) failed to draw convincing support from magnetostratigraphy for major heterochroneity of arctic Cretaceous and, particularly, Paleogene biostratigraphic assemblages relative to those of lower latitudes. The magnetostratigraphic data for the Eureka Sound Formation and chronostratigraphic interpretations based on those data are at best inconclusive or overinterpreted. The broad implications of the report of Hickey *et al.* for biostratigraphy demand considerably strengthened data from the Eureka Sound Formation to make a credible case for the severity of heterochroneity for various fossil groups.

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Hickey *et al.* (1) rely on magnetic stratigraphy (2) to show purported biostratigraphic age disparities in the Canadian Arctic, but the magnetostratigraphic correlations are unconvincing. Their composite sequence is based on a group of six partial sections that are correlated with each other entirely on the basis of lithostratigraphy. No marker beds are available, and the authors relied on correlations of lithofacies assemblages. In a deltaic sequence such as the Eureka Sound Formation, this procedure is unreliable because of the high probability of marked diachroneity of lithofacies assemblages.

The four members recognized by West *et al.* (3) and Hickey *et al.* (1) appear to be markedly diachronous (4). They are confined to a relatively small area of central Ellesmere Island [(locations 3 and 4 in (1))] and pass laterally northward and westward into quite different depositional systems. Hickey *et al.* do not provide enough relevant data to assess the lithostratigraphic correlations.

The paleomagnetic age determinations were used to date other sections and outcrops in the eastern Arctic by a process of lithostratigraphic and biostratigraphic correlation—that is “stratigraphic elevation of each of the localities with fossils was determined from measured or reconnaissance sections or from trigonometric extrapolation on aerial photographs” (1). This is not enough. Comparison of field sections with thickness estimates made trigonometrically from aerial photographs can reveal errors of 50 percent or more in results derived by the trigonometric method.

Since information on Cretaceous and Tertiary floras is available from many areas of the world, the palynostratigraphic data of Hickey *et al.* can be compared with those from elsewhere in the Arctic and in lower latitudes. But the data provided by Hickey *et al.* (1) are not

complete. Their zone A contains species of *Wodehouseia*, *Azonia*, *Expressipollis*, *Aquilapollenites*, and other triprojectates characteristic collectively of Maastrichtian in western Canada, Siberia, eastern Asia, Greenland, and the United States (5, 7). Some of these genera range lower into the Campanian, but *Wodehouseia* appears in the Maastrichtian with some species ranging into the basal Paleocene. Similar floras from the Eureka Sound Formation on Ellef Ringnes Island (6) have been compared with Maastrichtian and Danian assemblages from eastern Siberia.

Hickey *et al.*'s zone A floras occur in the upper part of the Kanguk Formation in west central Ellesmere Island. This is consistent with sedimentological evidence indicating a diachronous Kanguk–Eureka Sound contact (4). The foraminiferal biostratigraphy of the Kanguk Formation in this area (8) indicates that the top of the formation is probably late Campanian. However, some elements of the *Verneuilinoides bearpawensis* assemblage characterizing the upper Kanguk Formation range into early Maastrichtian in the western interior, opening the possibility of a somewhat younger age. The Santonian age for the top Kanguk Formation suggested by Hickey *et al.* is not consistent with the foraminiferal evidence; in addition, there are reliably dated diatoms in the *V. bearpawensis* assemblage that occur in a restricted Campanian interval in Alberta and western Siberia (8), and earliest Campanian bivalves and ammonites occur near the bottom of the upper member of the Kanguk Formation in Ellef Ringnes Island (8). The Santonian mollusk locality of Hickey *et al.* may represent an error of location or stratigraphic correlation.

The entry of *Polyvestibulopollenites verus* (Potonie) Thomson and Pflug in the northern Great Plains (9) and Yukon (10) although the genus is known in the latest Maastrichtian of Wyoming and Montana (7). *Triporopollenites mullensis* (Simpson) Rouse and Srivastava and *Paraalnipollenites alterniporus* (Simpson) Srivastava also first appear in zone B; elsewhere they are confined to latest Maastrichtian and Paleogene sediments (10, 11). *Caryapollenites* occurs (1) with the species already mentioned; in Wyoming it becomes frequent in the early Paleocene (12). Stratigraphy of miospore floras and reptilian faunas in the Late Cretaceous and early Tertiary of Alberta (5, 13) show that the floral changes reported by Hickey *et al.* between zones A and B are similar to widespread floral changes associated

with extinction of dinosaurs and are transcontinental in extent (14). Thus, we suggest that the Cretaceous-Tertiary boundary is located close to the zone A-zone B boundary of Hickey *et al.* It would follow that their magnetic anomaly 34 probably is a mislabeled anomaly 30.

Pistillipollenites mcgregorii Rouse, which occurs first in zone C, occurs from the upper Paleocene to the middle Eocene (15), but not down to Campanian as indicated by Hickey *et al.* The upper portion of zone C is characterized by the earliest records of Tiliaceae and Bombacaceae. Pollen closely comparable to extant *Tilia* first appears in western and arctic Canada and elsewhere in North America in the Eocene (12, 16, 17), an age at variance with Hickey *et al.*'s estimated age of upper zone C as late Paleocene. The occurrence of *Pistillipollenites mcgregorii* through to basal zone E would be consistent with a middle Eocene Lutetian age indicated by Hickey *et al.* for this zone.

Thus, the magnetostratigraphy of Hickey *et al.* appears to be seriously in error at the base of their Eureka Sound sections but more in accord with palynostratigraphic data toward the top of the examined interval. The occurrence of Campanian dinoflagellates near the middle of zone B (Paleocene according to pollen data) requires comment. The assemblages include species of *Chatangiella*, *Isabelidium*, *Laciniadinium*, *Trithyrodinium*, *Ginginodinium*, and *Saepodinium*, all of which have been reported in boreal Campanian and in the subjacent Kanguk Shale and correlatives in the Mackenzie Delta and the Anderson Plains (5, 6). Some species of these genera, however, do range into the Maastrichtian (18). Arctic Tertiary basins in Ellesmere and Axel Heiberg islands are characterized by rejuvenation and uplift of marginal areas leading to recycling of older palynomorphs, including Cretaceous, into Tertiary (4). The presence of abundant recycled material may mark the onset of the Eureka Orogeny. In the western Arctic, Paleocene strata deposited in the tectonically active Beaufort-Mackenzie (Richards Island) Basin are characterized by abundant late Cretaceous dinoflagellates with only minor amounts of indigenous Tertiary elements (19). In the southern arctic archipelago on Somerset Island, well-preserved and abundant dinoflagellates, including many reported by Hickey *et al.*, occur in the Eureka Sound Formation (20). These are derived from the Campanian Kanguk Formation and recycled into Paleocene strata (20) with indig-

enous *Momipites*, *Paraalnipollenites*, *Saxonipollis*, *Liquidambar*, *Caryapollenites*, and *Alnus*. We suggest that the dinoflagellates in zone B of Hickey *et al.* are recycled Campanian specimens derived from the uplifted basin margins during the Paleogene.

Finally, with regard to the putative high-latitude origin of certain land plants (1), minor disparities between first occurrences of miospores in the western Arctic and northern mid-latitudes have been reported (16). However, these different ranges are of the order of magnitude of fractions of stages, not of series representing up to 18 million years reported by Hickey *et al.*

We conclude that Hickey *et al.* did not provide rigorous evidence to support their theory of highly diachronic mid-latitude Tertiary floras originating many millions of years earlier in the arctic Late Cretaceous.

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The comments of Kent *et al.* and Norris and Miall about our assertion of arctic heterochroneity (1) fall into three groups: adequacy of the paleomagnetic data and its interpretation, accuracy of our stratigraphic correlations, and the validity of our biostratigraphy. We shall address each category, combining issues raised by both comments.

Our acceptance of the magnetic polarity sequence for the Eureka Sound Formation formulated by Vinson (2) was based on the agreement of his correlations with apparently anomalous aspects of the biostratigraphy that we encountered. Some shortcomings in the paleomagnetic results that Kent *et al.* note were already raised by Vinson (2) and Vinson and Kean (3). Vinson specifically noted that reversed poles were at shallower latitudes than normal poles and that precision parameter *K* increased from 2.4 to 3.6 when the statistical calculations were made on the normal polarity samples separately from the reversed polarity samples. These observations certainly suggest a pervasive secondary normal polarity overprint. They also imply that sections with low-latitude normal polarities may be suspect but that low-latitude reversed polarities most probably represent true reversals. Low-latitude normal polarities are most prominent in member IV [top of section 2 (1, figure 2)], which Vinson (2) admitted to be relatively poor-quality data.

The most reliable magnetic results come from the lower part of the Eureka Sound sequence [sections 3, 4, and 5 (1, figure 2)] in members I and II, which clearly show a well-defined long normal and reversed section based on 40 hand samples (120 measured samples) over a thickness of 1000 m. This probably represents C33N and the associated reversed polarity interval below it. These data alone would push the age of the Eureka Sound Formation back beyond the magnetically relatively noisy Maastrichtian to the relatively quiet early Campanian. The criticism by Kent *et al.* that the placement of C33N was circular ignores our use of parameters such as relative stratigraphic thickness and con-

text as well as apparently anomalous biostratigraphic elements in designating this interval. We would also cite the occurrence of the normal polarity interval designated as C26N just below the well-defined contact between members III and IV in three sections [sections 1, 2, and 3 (1, figure 2)] as an example of internal consistency of the magnetic data (4).

The objections that Norris and Miall raise about the basis for the stratigraphic correlation of the sections used to assemble the magnetic composite at Bay and Strathcona fiords [area 4 (1, figure 1)] is surprising. Vinson's section was based on a composite section measured by Miall (5) and lay as close to his lines of section as possible. Although correlation of the individual sections was mainly by lithologic means, the aerial distance was small (32 km from south to north), and marker beds of limited extent were available. (A pebble conglomerate bed discovered by Miall was used to carry the section across Fossil Bay.) In addition, both the strata and synclinal structure in this area are well exposed, as is the striking contrast between the light-colored marly beds of member III and the somber, terrestrial lithology of members II and IV. Despite extensive foot and helicopter traverses across the Bay Fiord region, we saw no cases where the contacts between members migrated across strike, as would be the case if the members were significantly diachronous there.

In all areas studied, the relevant sections were examined on the ground, and dip and strike measurements were used to control thickness calculations. Our direct observation produced no evidence of angular unconformities in our sections, but the level of our examination does not preclude the possibility of disconformities within the sequence. However, these would extend rather than reduce the interval of time involved. Finally, correlations between our study areas were not based on lithologic correlations but on the palynofloral zonation.

Turning to the biostratigraphic record, we would not dispute most of the assertions as to the ages and ranges of our

palynomorphs that Norris and Miall make based on lower latitude correlations. It was precisely the disparity between the accepted dates for these forms and the apparent magnetostratigraphic correlation that first caused us to examine the possibility of age disparity. More critical to our arguments would be the late Campanian foraminiferal date for the Kanguk Formation of west central Ellesmere Island that Norris and Miall report (see their reference 8), but these data are as yet unavailable to us. The earliest Campanian date for the upper Kanguk of Ellef Ringnes from the same reference lies over 200 km to the southwest of our nearest locality and should be regarded with the same caution for diachronism that Norris and Miall suggest for localities within our area.

As to the late Santonian-early Campanian mollusks that we reported, this locality was precisely located on an aerial photograph, lay in a lithologic sequence agreeing in all particulars with member I of the Eureka Sound Formation (5), and had previously been mapped as Eureka Sound Formation (6). It is not possible for us to exclude the possibility of reworking for the Campanian dinoflagellate assemblage that we noted in member II of the Eureka Sound Formation, especially since the Bay Fiord area in which it occurs lies near the margin of a tectonic basin that was in the early phases of uplift during the deposition of member II. This possibility was considered by Choi and his adviser Traverse (7) but was eventually rejected for the following reasons: (i) lack of any signs of obvious recycling such as damage to or darkening of the grains, especially when compared to grains known to be reworked in the Eureka Sound Formation; (ii) high percentage of the flora composed of dinoflagellates of Campanian affinities [> 25 percent of total palynomorphs (8)]; (iii) lack of features suggesting terrestrial deposition of the rocks containing them (and thus reworking of any marine component); and (iv) apparent concurrence with the magnetic evidence.

Placement of the palynological boundary of the Paleocene-Eocene at the top of zone C was based on the first undoubted

occurrence of *Platycaryapollenites* and the first abundant occurrence of tiliaceous-bombacaceous pollen. Choi (8) notes that both of these forms are found in low numbers in the Paleocene of mid-latitudes. In evaluating the vertebrate fauna that first occurs in the upper part of pollen zone C, we note that the forms include genera that are diagnostic of both the early and middle Eocene and that we know of no other place where there is such a mixture of forms.

In summary, we acknowledge that the magnetic evidence that we cited is not as strong as we thought. However, we would argue that we made a testable assertion based on the apparent concurrence of several independent lines of evidence. The Arctic is and was a region of climatic extremes, and we chose to explain the very real biostratigraphic disparities at polar latitudes (9-11) in terms of heterochroneity. At the very least our study, together with those of Marincovitch *et al.* (10) and Zinsmeister and Feldmann (11), suggests that multiple independent sources of dating must be used at high latitudes. It is also obvious that our hypothesis of heterochroneity needs further corroboration.

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