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A CRITIQUE OF THE THEORETICAL BASIS OF LEAF MARGIN ANALYSIS

Gary E. Dolph
Indiana University at Kokomo
Kokomo, Indiana 46904-9003

ABSTRACT: One aspect of paleobotanical research involves estimating the paleoclimates under which fossil floras lived. Angiosperm paleobotanists use foliar physiognomy, primarily leaf margin analysis, to estimate paleoclimate. Several crucial questions must be answered before leaf margin analysis can be used to precisely estimate paleoclimate. The most basic question is whether or not the foliar physiognomy of eastern Asia should be used as a standard against which all other foliar physiognomic analyses must be judged. A careful analysis of Wolfe's data on the foliar physiognomy of eastern Asia shows that this area is unacceptable as a standard for foliar physiognomic studies.

THE VEGETATION OF EASTERN NORTH AMERICA

The most prolific writer on the topic of foliar physiognomy over the last decade has been Jack Wolfe. However, Wolfe has chosen to disregard the vegetation of eastern North America in his study of foliar physiognomy. He has offered two main reasons why eastern North America cannot be used to study the relationship between climate and leaf margin type.

First, the vegetation of eastern North America is "depauperate." The climatic deterioration that occurred at the end of the Middle-Late Oligocene (now the end of the Eocene) resulted in a tremendous decrease in the number of species present in the flora of eastern North America (Wolfe, 1969a). This loss of diversity has not been compensated for. The disappearance of tropical forest from the southeastern United States resulted in the elimination of a potential source of new species for the temperate forest (Wolfe, 1969a). In addition, eastern North America became floristically isolated from other temperate areas both in Europe and western North America at the end of the Eocene (Wolfe, 1969a, 1987b). As a result, other temperate areas could not contribute species to increase floral diversity in the eastern United States. Finally, eastern North America is a region of low topographic diversity (Wolfe, 1969a) and, as a result, of low endemism. Wolfe concludes that these three factors cause eastern North America to have a depauperate flora.

Second, the effect of Arctic cold fronts since the Miocene and the effect of the Ice Ages in recent times have prevented the already depauperate vegetation from evolving the folar physiognomy of the normal climax vegetation for eastern North America. Although leaf form may not be closely associated with climate immediately after a major climatic shift, given enough time a close correlation will develop (Wolfe and Upchurch, 1987a). Wolfe believes that more than one million years (or in the case of the Paleocene rain forest, millions of years) must pass before the vegetation takes on its "climax" characteristics. The change will occur only if geographic and/or evolutionary factors are favorable (Wolfe and Upchurch, 1987a). Wolfe (1979) believes that insufficient time has elapsed since the last glaciation in eastern North America for the balance between climate and foliar physiognomy to be achieved. The cold waves that sweep across eastern North America (Wolfe, 1971, 1979, 1980, 1985) as a result of the increasing altitude of the mountains along the Pacific Coast (Wolfe, 1985, 1987a) may prevent this balance from ever being reached.

Initially, Wolfe considered the depauperate flora of eastern North America to be equivalent to the arrested secondary successional vegetation of the Notophyllous Broad-Leaved Evergreen Forest of eastern Asia (Wolfe, 1979, 1985). Later, when analyzing the evolutionary history of deciduous vegetation, Wolfe (1987a) postulated that five vegetational zones should exist in eastern North America: the Notophyllous Broad-Leaved Evergreen Forest, the Mixed Broad-Leaved Evergreen and Coniferous Forest, the Mixed Broad-Leaved Evergreen and Deciduous Forest, the Mixed Mesophytic Forest, and the Mixed Northern Hardwood Forest.

The Mixed Broad-Leaved Evergreen and Coniferous Forest and the Notophyllous Broad-Leaved Evergreen Forest are missing in eastern North America. Thus, the full range of "climax" vegetation in eastern North America does not exist. The actual vegetation is in "quasisuccession." Wolfe defines quasisuccession as the long-term mimicry on an evolutionary time scale of short-term ecological succession (Wolfe, 1987a, 1987b; Wolfe and Upchurch, 1986, 1987b). Quasisuccessional or non-climax vegetation cannot be used to generate the leaf margin percentages necessary to estimate mean annual temperature (Wolfe, 1979; Wolfe and Upchurch, 1987a).

Wolfe (1979, 1980, 1985) believes that the most important limiting factor active in eastern North America is the continuing presence of Arctic cold fronts. Other researchers do not agree. Greller (1989) has shown that the limits of the Boreal Conifer Forest, the Conifer/Deciduous Dicot Forest, and the Deciduous Forest of eastern North America are controlled by summer warmth (*sensu* Bailey, 1960, 1964) as measured by the highest average monthly summer temperature. This conclusion agrees with that of Dolph (1987), who showed that the foliar physiognomy of the vegetation of southern Indiana is controlled most strongly by summer and not year-around climatic conditions.

Greller did find (1989) that the northern limits of the Deciduous Dicot/Evergreen Dicot/Conifer Forest, the Temperate Broadleaved Evergreen Forest, and the Tropical Forest are controlled in part by winter cold. However, other factors including annual warmth, temperateness (*sensu* Bailey, 1960, 1964), and frost frequency also play a role. Greller (1989) believes that the most crucial parameter is probably frost frequency. These results show that the actual role of climate in determining foliar physiognomy in eastern North America is much more complex than Wolfe realized, although distribution of the tropical taxa and the evergreen dicots is controlled in part by winter cold.

THE VEGETATION OF EASTERN ASIA

Wolfe (1979) offers two reasons why the vegetation of eastern Asia is much more attuned to climate than the vegetation of eastern North America. First, the vegetation of eastern Asia is more diverse than the vegetation of North America. A greater number of species increases the likelihood that evolutionary modifications tying leaf form to climate will exist. Second, except for alpine glaciation, eastern Asia was unglaciated during the Quaternary. The Arctic cold fronts that sweep across eastern North America did not and do not occur in eastern Asia. Therefore, sufficient time has elapsed for the vegetation to become ecologically attuned to climate in eastern Asia.

The forest types identified by Wolfe (1979) in eastern Asia are the standard against which he compares all other vegetation (e.g., Wolfe, 1987a). The forests of Australasia and western North America can be defined using his system. The forests of eastern North America and Europe cannot. If data do not fit the system, they are ignored or discarded. For this reason, the effect of fog on the distribution of redwoods in the western United States is dismissed as a gross coincidence (Wolfe, 1979). Wolfe believes that the actual limiting factor in redwood distribution is temperature. Greller (1989) noted that Wolfe's system is "inappropriate" for eastern North America. This does not mean that the vegetation of eastern North America is "anomalous" and unworthy of study, as Wolfe would have us believe.

Wolfe's (1979) basic assumption, that the foliar physiognomy of eastern Asia is more closely attuned to climate than the foliar physiognomy of eastern North America, cannot be true, if climatic fluctuations and floral migrations occurred in eastern Asia during the Tertiary and, in particular, during the Quaternary. Paleoclimatic and paleobotanical studies in China and Japan show that climatic fluctuations as well as floral migrations and extinctions did occur. Wolfe's (1985) views on the distribution of major vegetational types through the Cenozoic in eastern Asia are incorrect.

THE PALEOGENE VEGETATION AND CLIMATE OF EASTERN ASIA

During the Paleogene, four distinct climatic belts existed in China (Wang Pinxian, 1984). From north to south, these belts were the warm temperate belt (humid, as evidenced by the formation of coal and oil shale), the warm temperate/subtropical belt (alternating dry and humid conditions), the arid subtropical belt (hot and dry, as evidenced by evaporite deposits and xerophytic plant remains), and the subtropical/tropical belt (hot and humid, as evidenced by the formation of coal and oil shale).

These paleoenvironmental differences were associated with a number of paleofloristic regions. Between three (Guo, 1984) to possibly six (Wang Xianzeng, 1984) types of vegetation were found in China during the Eocene. In northern China, broadleaved deciduous forests containing a few conifers and evergreen trees existed under a humid, subtropical climate. In central China, an arid subtropical environment supported xeromorphic vegetation. In southern China, a humid, tropical environment supported broad-leaved evergreen and deciduous forests (Guo, 1984).

Wolfe (1985) presents a much simpler picture of climate and vegetation in the Chinese Paleogene. During the latest Paleocene-Early Eocene, Wolfe recognizes only Tropical Rain Forest in China and other parts of eastern Asia (Wolfe, 1985, Fig. 5). However, no data points were given in Wolfe's publication for eastern Asia and his physiognomic mapping apparently represents a continuation of trends he believes existed in Europe and North America.

During the Eocene, Wolfe (1985) maps four types of forest in China — Notophyllous Broad-Leaved Evergreen Forest, Paratropical Rain Forest, Tropical/Paratropical Semideciduous Forest, and Tropical Rain Forest. Wolfe noted that the boundary between these forests would migrate depending on whether the vegetation existed during a warm or cool interval. In general, the boundary between the Tropical and Paratropical Rain Forest had been displaced 5° to 10° toward the Equator during the Eocene. In contrast to Guo (1984), who found few evergreen dicots in northern China, Wolfe (1985) characterized the region as being dominated by evergreen forest. Once more, Wolfe (1985, Fig. 8) presents no data points to support his mapping.

THE NEOGENE VEGETATION AND CLIMATE OF EASTERN ASIA

The closure of the Tethys at the Eocene-Oligocene boundary and the start of uplift of the Qinghai/Xizang Plateau at the beginning of the Neogene caused the four climatic belts of the Paleogene to be replaced by three new belts: the Qinghai/Xizang humid temperate belt, the northwest arid belt, and the east China monsoon belt (Wang Pinxian, 1984).

During the Paleogene, the climatic zones ran from east to west across all of eastern Asia. Geologic events in eastern Asia associated with the closure of the Tethys and uplift of the Qinghai/Xizang Plateau caused a total change in circulation patterns and moisture availability during the Neogene. During the Paleogene, humidity had decreased from west to east, but during the Neogene, humidity decreased from east to west.

The change in circulation patterns and moisture availability occurred gradually. During much of the Neogene, the mountains of the Qinghai/Xizang Plateau had insufficient elevation to impede atmospheric circulation. As late as the Pliocene, the Qinghai/Xizang Plateau was relatively warm and moist as evidenced by the occurrence of a *Hipparion* fauna, the deposition of coal, and the development of paleokarst (Wang Pinxian, 1984).

The most obvious climatic change during the Neogene was the development of the east China monsoon belt. The east China monsoon belt had several climatic subzones ranging from warm-temperate to tropical from north to south (Wang Pinxian, 1984). Climatic fluctuation associated with marine transgression also occurred in eastern China. The late Oligocene-Miocene Leizhou Peninsula had a humid temperate-subtropical climate. Following marine transgression in the Miocene, the climate became warm, humid, and tropical (Wang Pinxian, 1984).

In summary, Chinese researchers (Guo, 1984; Wang Xianzeng, 1984) believe that during the Oligocene and into the Miocene, the climate gradually became cooler and drier. The change in climate caused the tropical and subtropical floral elements to move further south (Guo, 1984; Wang Xianzeng, 1984). The cooler, drier climate was due to the retreat of the Tethys from western Asia, the start of the Qinghai/Xizang orogeny, and the development of monsoonal circulation in eastern China. Except for the retreat of the Tethys, the changes occurred gradually from the Paleogene-Neogene boundary up to the Quaternary (Wang Pinxian, 1984).

In the Miocene, Song, *et al.* (1984) recorded three floristic regions in China: the Qinghai/Xizang *Quercus/Betula* Thicket Floristic Region (with two provinces), the Inland Forest-Meadow and Steppe Floristic Region (with three provinces), and the Eastern Monsoon Broad-leaved Forest Floristic Region (with three provinces). The Qinghai/Xizang *Quercus/Betula* Thicket Floristic Region was covered by temperate forest rich in Betulaceae, Ulmaceae, *Quercus*, and Juglandaceae in the Early Miocene, but as uplift occurred in the Late Miocene, a forest dominated by alpine *Quercus*, Ulmaceae, and Salicaceae developed as a result of a cooler, less moist climate.

The Inland Forest-Meadow and Steppe Floristic Region had an arid to semi-arid, cool to warm temperate climate. This floristic region was dominated by herbs and shrubs of the Compositae, Chenopodiaceae, and *Nitraria* with interspersed woodlands of temperate trees (Betulaceae, Ulmaceae, Fagaceae, and Juglandaceae). Conifer forests covered the mountains.

The Eastern Monsoon Broad-leaved Forest Floristic Region had a warm, moist climate that varied from temperate in the north to tropical in the south. The common temperate families were the Betulaceae, Ulmaceae, Fagaceae, Salicaceae, Aceraceae, Leguminosae, Rosaceae, Myricaceae, and Juglandaceae. These families decreased in importance southward in favor of a more tropical element. A number of subtropical families including the Lauraceae, Nyssaceae, and Magnoliaceae were present in the southern part of the Eastern Monsoon Broad-leaved Forest Floristic Region as well as the tropical families Annonaceae, Rutaceae, Santalaceae, and Sonneratiaceae.

In contrast to the Chinese researchers, Wolfe (1985, Fig. 11) recognized four forest types during the Miocene in eastern Asia — the Paratropical Rain Forest, the Notophyllous Broad-Leaved Evergreen Forest, the Mixed Northern Hardwood Forest, and the Mixed Coniferous Forest. Data to support Wolfe's view came from northern Vietnam, Taiwan, Japan, and Korea but not from China.

The vegetation zones identified by Wolfe (1985) in the Miocene do not agree with those of Chinese researchers (Song, *et al.*, 1984). Wolfe notes that Mixed Coniferous Forest is found in southwestern China. Song, *et al.* (1984) map this region as the Plateau Floristic Subregion of the Qinghai/Xizang *Quercus/Betula* Thicket Floristic Region. During the Miocene, this region supported temperate dicot-dominated forest. Pine pollen is common only in the Inland Forest-Meadow and Steppe Floristic Region, where the conifers were restricted to the mountains. Wolfe maps (1985) the Inland Forest-Meadow and Steppe Floristic Region as Mixed Northern Hardwood Forest.

Southeastern China supported a subtropical-tropical forest in the Miocene (Song, *et al.*, 1984). However, Wolfe (1985) classified the vegetation as Notophyllous Broad-Leaved Evergreen Forest. Wolfe's regions which have mean annual temperatures equivalent to the subtropics and tropics, the Paratropical and Tropical Rain Forest, occur only in southern Asia and the adjacent islands at this time. By Wolfe's classification, the presence of Notophyllous Broad-Leaved Evergreen Forest in southeastern China indicates a mean annual temperature between 13°C and 20°C. Song, *et al.* (1984) classified the area as tropical to subtropical. The mean annual temperature of southeastern China should be greater than 18°C in the subtropics and 24°C in the tropics (Holdridge, 1967). Thus, in southeastern China clear disagreements exist between Wolfe and Chinese researchers on both the types of vegetation found in the region and the prevailing mean annual temperature.

THE QUATERNARY VEGETATION AND CLIMATE OF EASTERN ASIA

Major uplift of the Qinghai/Xizang Plateau during the Middle Pleistocene intensified the monsoonal climate of eastern China (Wang Pinxian, 1984) while causing western China (the Qinghai/Xizang Plateau itself) to become colder and drier (Liu and Ding, 1984). Four cyclic alpine glaciations occurred on the Qinghai/Xizang Plateau and throughout the mountains of western China (Wang Pinxian, 1984): the Early Pleistocene Xixabangma glaciation, the Middle Pleistocene Nienniexungla glaciation, the Late Pleistocene Qomolangma glaciation, and the Holocene Rongbude glaciation. Sandy (Shamo) and stony (Gobi) deserts, although present since the Late Cretaceous/Early Tertiary, commenced major expansions in China during the Pleistocene (Wang Pinxian, 1984; Zhao and Xing, 1984). The large amounts of loess covering much of central and northern China had their source in these deserts (Wang Pinxian, 1984).

Glaciation, if not present in eastern China, caused considerable latitudinal movement of the climatic belts in this region. The unglaciated portions of western China did not suffer as much as eastern China because the mountains of western China prevented the southern flow of Siberian air. In eastern China, a district "cold trough" developed (Wang Pinxian, 1984). Nineteen major climatic shifts between warm, humid and cold, dry climates are documented in northern China (Liu and Ding, 1984). At least three cycles of humid and dry climates have been found in the coastal areas of the Gulf of Tonkin. Alteration of climate extended to the tropical/subtropical zones of China (Wang Pinxian, 1984).

At times during the Quaternary, sea level was lowered sufficiently for Hainan, Taiwan, and Japan to be connected to the mainland (Liu and Ding, 1984; Xu Ren, 1984). The movement of the continental margin to the east caused the overall climate of China to become more arid than it is at present. The overall trend during the Pleistocene led to the retreat of the warm, moist environments of the Pliocene southward from approximately 42°N latitude to about 25°N to 30°N latitude today.

During the Late Pleistocene in China, the boreal forest was displaced from 9° to 10° southward in latitude as mean annual temperature dropped from between 9°C to 11°C. Temperature decreases in south China were approximately 5°C, enough to prevent a subtropical climate from existing (Zhang Lansheng, 1984). During the Late Pleistocene, wooly rhinoceros (*Coelodonta antiquitatis*) and wooly mammoth (*Mammuthus primigenius*) ranged as far south as the Yangtze River Valley (Wang Pinxian, 1984). At the same time, vast deserts appeared in northwest China as the climate became drier, and xerophyllous plant families such as the Ephedraceae and Chenopodiaceae underwent considerable diversification. Elements of the northern and southern floras became intermingled as a result of repeated migrations (Wang Pinxian, 1984). Similar patterns of plant migration are encountered in the Neogene and Quaternary of Japan (Tanai, 1961; Tanai and Huzioka, 1967; Tsuda, *et al.*, 1984; Yasuda, 1984).

Three major Holocene climatic stages are known in China (Wang Pinxian, 1984): in the Early Holocene (10000 BP to 8000 BP), the mean annual temperature was 5°C to 6°C lower than at present; in the Middle Holocene (8000 BP to 3000 BP), it was 2°C to 4°C higher than at present; and in the Late Holocene (3000 BP to the present), a cooling trend with frequent 2°C to 4°C fluctuations was recorded.

The number of environmental belts in China increased from either three (Wang Pinxian, 1984) or four (Liu and Ding, 1984) in the Pliocene/Early Pleistocene up to thirteen at the present time (Liu and Ding, 1984). In contrast, Wolfe recognizes from five (Wolfe, 1971) to eleven (Wolfe, 1979) climatic zones in modern China. Although Wolfe's total (11) is quite close to the total (13) of Liu and Ding, a comparison of their climatic maps (Liu and Ding, 1984, Fig. 13; Wolfe, 1979, Plate 1) indicates there is no correlation between their climatic zones and those of Wolfe. Wolfe has not discussed the climatic and floral changes found in China during the Quaternary in any of his publications.

STABILITY OF THE VEGETATION AND CLIMATE OF EASTERN ASIA

A careful analysis of the vegetational history of China indicates that a stable vegetation has not existed in eastern Asia for the millions of years required by Wolfe (1979, 1987a) to allow the development of a close correlation between foliar physiognomy and climate. The Arctic cold fronts that are so crucial to Wolfe's criticism of the vegetation of eastern North America played and are continuing to play an active role in eastern Asia.

During the Pleistocene, the average January temperature in all of eastern China with the exception of the extreme southeastern portion was -5°C or less (Zhang Lansheng, 1984). A mean cold month temperature of less than -2°C would be sufficient to eliminate the Mixed Mesophytic Forest, the Mixed Broad-Leaved Evergreen and Coniferous

Forest, the Mixed Broad-Leaved Evergreen and Deciduous Forest, the Notophyllous Broad-Leaved Evergreen Forest, the Microphyllous Broad-Leaved Evergreen Forest, the Paratropical Rain Forest, and the Tropical Rain Forest from China. Using Wolfe's (1987a) own criteria, the vast majority of the landscape of China was covered by tundra, taiga, Mixed Coniferous Forest, and Mixed Northern Hardwood Forest.

No correlation exists between the vegetation types outlined by Chinese workers and the physiognomic types of vegetation recognized by Wolfe (1985) through the Cenozoic. Events in China during the Pleistocene indicate that the vegetation of eastern Asia underwent changes as severe as those encountered in eastern North America. All the failings listed for the vegetation of eastern North America are exhibited by the vegetation of eastern Asia — namely, extinction of major portions of the existing floras, introduction of a major new floral element (the boreal forest) to the region, extensive migration and intermingling of the vegetation, and evolution and diversification of formerly minor plant groups (Li, *et al.*, 1984; Wang Xianzeng, 1984).

Thus, the current vegetation of eastern Asia is not uniquely suited for studying the relationship between leaf form and climate. The current vegetation pattern and, therefore, the variation in leaf form are simply points on a continuum of environmental and vegetational change. Wolfe once realized that vegetation is continuously changing. His arguments against the existence of the Arcto-Tertiary Geoflora (Wolfe, 1969a, 1969b) indicate this quite clearly. His views on the study of foliar physiognomy in modern vegetation should be changed to reflect this fact.

CONCLUSIONS

A careful analysis of Wolfe's data sources has indicated that the vegetation of eastern Asia is not uniquely suited to the study of foliar physiognomy. If Wolfe truly believes that the most important limiting factor active in eastern North America is the continuing presence of Arctic cold fronts (Wolfe, 1979, 1980, 1985), then he cannot dismiss the role of this factor in eastern Asia. In addition to this theoretical issue, Wolfe's research also shows a number of methodological flaws.

Wolfe (1981) has complained about "the gross nature of a county-by-county compilation" of species presence such as Dolph and Dilcher (1979) used in their study of the foliar physiognomy of North and South Carolina. An analysis of Wolfe's data indicates that his sample areas are much larger (i.e., much grosser) than those used by Dolph and Dilcher.

Wolfe (1981) claims that his study of the climate and vegetation of eastern Asia (Wolfe, 1979) is based on quadrat studies and local floras. As proof, he cites the study of Sato (1946) in Japan and the flora of Hong Kong. Sato did use quadrat studies. However, he was the only author cited by Wolfe who did so. In addition, Wolfe never used Sato's data to establish his initial correlation between leaf margin variation and mean annual temperature (Wolfe, 1971).

Of the eighteen sample areas listed by Wolfe (1971), only Hong Kong has a smaller area (1,061 km^2) than the average sample area (1,486 km^2) used by Dolph and Dilcher (1979) in North and South Carolina. Wolfe's sample areas (Wolfe, 1971) ranged from a low of 1,061 km^2 (Hong Kong) to a high of 483,840 km^2 (Manchuria). The average size of Wolfe's sample areas was 62,793 km^2. Some of Wolfe's sample areas are larger than those used by Dolph and Dilcher by a factor of 325. None of Wolfe's sample areas are smaller than the average sample area (1,019 km^2) used by Dolph (1984) in Indiana.

Wolfe (1981) states in relation to the study of leaf margin variation in North and South Carolina (Dolph and Dilcher, 1979) that "if leaf margin data are averaged for a county, then so should temperature data." This suggestion is meaningless, because accurate weather data are not available from every county in any state. The optimum solution is to use the highest possible density of reliable weather stations.

The area of the Carolinas is 216,995 km². One hundred twelve weather stations were found in the Carolinas which provided adequate weather information for analysis. The weather station density in the Carolinas is one weather station for every 1,937 km².

In a more recent study, Dolph (1984, 1987) analyzed the vegetation of Indiana. The area of Indiana is 93,720 km². Sixty-five weather stations provided usable data in Indiana. One weather station occurs approximately every 1,442 km² in Indiana.

In his study of the forests and climate of eastern Asia, Wolfe (1979) analyzed an area of approximately 8,652,800 km² in which 427 weather stations were found. The weather station density was one weather station for every 20,264 km². The actual density of weather stations providing reliable data in the Carolinas was at least 10 times greater than Wolfe's density in China. In Indiana, the density was 14 times as great.

A careful look at Wolfe's criticisms (1981) of the foliar physiognomic study of the Carolinas (Dolph and Dilcher, 1979) raises the question of how carefully this study was read. Wolfe (1981) criticized Dolph and Dilcher's (1979) study, because the variation in leaf margin type with respect to mean annual biotemperature and not mean annual temperature was mapped. Wolfe (1979) dismisses any use of mean annual biotemperature, because he believes that leaf margin variation is much more closely correlated with mean annual temperature than with mean annual biotemperature.

The mean annual biotemperature is the sum of the mean temperatures greater than 0° C and less than 30° C for a specific time period divided by the total number of time units for which data were available in that time period (Holdridge, 1967; Holdridge, *et al.*, 1971). The method of calculation reflects the belief that temperature only affects the plants over the range where they are physiologically active; that is, between 0° C and 30° C. When calculating mean annual biotemperature, if no values are below 0° C or above 30° C, the mean annual biotemperature will equal the mean annual temperature. This was the case in the Carolinas (Dolph and Dilcher, 1979), where "... the biotemperature at each station was equal to the mean annual temperature at that station." Therefore, Wolfe's criticism has no factual basis.

The fatal flaws in his theoretical choice of eastern Asia as a standard as well as his methodological errors show why Wolfe's (1981) application of foliar physiognomy is not internally consistant. Although he presents data showing that a perfect correlation (the Pearson product-moment correlation coefficient is 0.98) exists between the variation in leaf margin type and mean annual temperature in the modern vegetation of eastern Asia, Wolfe (1981) is satisfied if the same method can position paleoisotherms within 100 km to 200 km of their actual position. Given the flawed nature of the theory, it is amazing that the paleoisotherms are even that accurate. Paleoclimate maps and floral classifications based on the foliar physiognomy method should be carefully scrutinized before they are accepted as accurate.

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