

Warmer paleotemperatures for terrestrial ecosystems

Elizabeth A. Kowalski and David L. Dilcher*

Florida Museum of Natural History, University of Florida, P.O. Box 117800, Gainesville, FL 32611

Contributed by David L. Dilcher, November 14, 2002

Floras of predominantly wet-soil environments show a greater than expected proportion of toothed leaves, affecting the outcome of leaf physiognomically based temperature estimates. New analyses of foliar physiognomy of plants growing in predominantly wet soils in modern forests suggest that current methods of inferring paleotemperatures from fossil floras yield underestimates of 2.5–10°C. The changes we propose bring terrestrial paleotemperature estimates into agreement with temperatures inferred from other biological and geological proxies and strengthen the use of leaf physiognomy as a method for climate reconstruction.

Accurate estimates of paleoclimates are essential for reconstructing both past and future climate scenarios. Relationships between extant leaf morphological characters and climate have been used to determine terrestrial paleoclimates using leaf fossils (1–7). This has been one of the most widely applied and precise methods of determining terrestrial paleoclimates. As such, paleotemperature estimates based on leaf physiognomy are often used to calibrate, refute, or validate climate predictions based on other biological and geological proxies and world climate models (8–10). Therefore, it is necessary for leaf-physiognomically derived paleotemperature estimates to be as accurate as possible.

Throughout the past century, the technique of estimating paleotemperature from leaf physiognomy has progressed from using a general observation of leaf morphologic trends (1) to estimate paleoclimates to using a number of statistically significant mathematical relationships between leaf morphologic characters and corresponding climate parameters (2–7). The technique is being further refined by the collection of hundreds of well-documented modern samples from which the predictive equations are calculated and by increasing the geographic area from which the data have been collected to represent all six vegetated continents (e.g., refs. 4, 5, and 11). These techniques have been used numerous times to calculate paleotemperatures of fossil sites, thus presenting a record of terrestrial climate change throughout the Cretaceous and Cenozoic periods (e.g., refs. 3 and 12–14).

Predictive equations used to determine paleotemperature from fossil floras are based on established relationships observed between dicotyledonous leaf morphological characters and climate parameters in modern plant communities (3–7). The relationship between leaf morphological characters and climate is thought to reflect the constrained physiological adaptations of leaf physiognomy to climate regimes (2, 15, 16). Similar combinations of leaf characters tend to be common in floras living in similar climates (11, 17), even those that are widely separated geographically and compositionally (2, 18). By quantifying the leaf morphological characters of numerous plant communities living in different climate regimes, statistical relationships have been calculated that predict mean annual temperature (MAT) from dicotyledonous leaf morphological characters. These predictive equations are one of the more robust methods of estimating terrestrial MAT, and the process of refining these equations toward greater accuracy over a wider range of conditions is ongoing.

The data used to create these equations are derived for the most part from nonwetland environments (4, 5). Low-lying

habitats with wet soils comprise only 11% of the 106 sites collected for the first CLAMP database (5). Other data sets contain even fewer wet sites (19, 20). However, the vast majority of macrofossil floras were deposited in low-lying wet environments, e.g., floodplains, swamps, lakes, and deltas (21). Most leaves fall directly below the tree canopy from which they are derived, with little subsequent transport (22, 23). Those that survive some transport also come from lakeside or streamside environments. Thus, fossil leaf assemblages preserved in wet environments usually represent local wetland, riparian, or lakeshore vegetation (24–27). Because modern data sets used to create predictive equations for paleotemperature are not primarily compiled from floras analogous to those found in the fossil record, they are not the best proxy for application to fossil leaf assemblages to determine the paleotemperature of the fossil sites.

While testing the applicability of several published MAT predictive equations to many modern floras in Eastern North America (Fig. 1, Table 1), we noticed that the temperature estimates of two sites in the southeastern U.S. were consistently low, regardless of the method used to calculate MAT (Table 2, Fig. 1A). These sites, Panther Refuge and Big Hammock, have wet soils throughout the year and experience long periods of annual inundation. An additional site, Archbold, has sandy soil but is located adjacent to a lake. At Archbold, nine of the sampled species were within one tree canopy width of the lake, whereas the other 11 species were growing beyond the lake on drier soil. Temperature estimates of Archbold are mixed, with two equations underestimating MAT and two correctly estimating MAT (Table 2, Fig. 1A). Each of these three sites is considered to be analogous to a fossil deposition site due to its proximity to standing water, and thus the consistent underestimation of temperature using leaf morphologic characters is troubling. We sampled a fourth site, Dilcher's Woods (Table 1), to determine whether samples from different habitats within the same environmental regime yield different MAT estimates. Although <20 m in elevation, Dilcher's Woods has both swamp habitat and upland ridge habitat within a 25-ha area. Although leaf morphologic characters of both habitats yield underestimates of MAT, the estimates from the swamp habitat are consistently lower (Table 2, Fig. 1B). Our data indicate that MAT calculated from leaves derived from wet habitats with annual standing water are consistently underestimated compared with drier sites.

The high percentage of species with toothed leaves in riparian and wetland habitats results in the colder temperature estimates mentioned above, compared with estimates calculated from the regional vegetation surrounding these habitats. This trend has been documented in the Amazon Basin of Ecuador (28, 29) and in New Caledonia (12), where temperature estimates calculated from riparian and inundated habitats are consistently colder than estimates calculated from leaves from terra firma or upland habitat leaf data. Based on an analysis of leaves in a small lake in Indiana, Roth and Dilcher (25) suggested that fossil plants from lacustrine deposits would also underestimate paleo-

Abbreviations: MAT, mean annual temperature; WMA, Wildlife Management Area; MLR, multiple linear regression.

*To whom correspondence should be addressed. E-mail: dilcher@flmnh.ufl.edu.

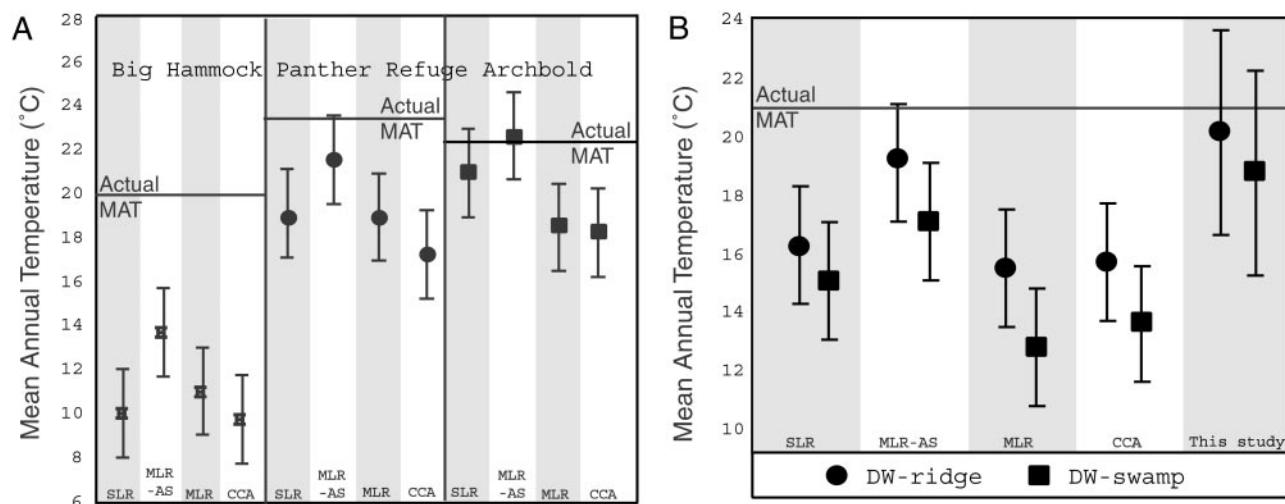


Fig. 1. Predicted MAT results. The equation used to predict MAT at each site is shown at the base of each column. Equation source and abbreviations are shown in Table 2. The error depicted for all published equations is $\pm 2^\circ\text{C}$, the suggested minimum error for MAT prediction (19). (A) Results for three southeastern U.S. sites. The solid lines depict the observed MAT for each site, whereas data points depict the predicted MAT for each site for each of the four equations tested. (B) Results for Dilcher's Woods. Plot of observed (solid line) and predicted (circles and squares) MAT for each of the two sampled localities within Dilcher's Woods. Error for the new provisional equation is $\pm 3.6^\circ\text{C}$. Leaf samples were collected for this study at four sites in the Eastern U.S. (Table 1), with two collections made at Dilcher's Woods to contrast soil moisture amounts, one from a well-drained upland ridge and the other from annually inundated swampland. At each site, we collected 15–50 leaves from each of 20–30 native species of dicotyledonous tree, shrub, and liana. Leaves were collected with a pole pruner (with extensions) from large trees and lianas, and with a hand pruner for smaller trees and shrubs, then placed in a herbarium press and dried. Leaf samples are stored in the Florida Museum of Natural History Paleobotany Collection. Leaves were examined for the presence of 31 leaf physiognomic characters as defined by Wolfe (5). For each of the sites, the percent presence of each character was calculated (Table 4). These values were used to estimate MAT for each site by using four published predictive methods (refs. 3–7; Table 2). The methods were selected to span the range (simple linear regression, multiple linear regression, canonical correspondence analysis) used to predict climate parameters from leaf physiognomic characters. A preliminary least-squares linear regression equation was calculated from MAT and leaf margin data from 10 modern sites with wet or swampy soils (Table 5) by using *SPSS* Version 10. Five of the sites are from this study; Little Pee Dee data were collected later than the original four sites, and the remainders are included in the *CLAMP* database (5). The resultant equation [$\text{MAT} = 0.363 \times (\% \text{ species with entire margins}) + 2.223$ ($R^2 = 0.80$, $P \ll 0.001$, $SE = 3.6^\circ\text{C}$)] was used to reestimate MAT for 16 sites from the Cretaceous, Cenozoic, and Recent periods (13, 14, 28–31) (Table 3). Temperature at the five modern sites was reestimated by removing that site from the regression equation, recalculating the regression, and using the resultant regression to estimate the MAT of the site.

temperature due to taphonomic biases. Low paleotemperature estimates have been noted from the fossil record of Germany, where *CLAMP* and leaf margin analysis estimates for Mio-Pliocene fossil deposits in lacustrine and fluvial sediments are at least 2.5°C lower than estimates calculated by using a coexistence

approach (30). The trend toward more toothed species in wet environments has also been recorded in the Cretaceous Patut Flora of Greenland, where high numbers of toothed species in back-swamp habitats also resulted in low temperature estimates for this environment (31).

Table 1. Data, including environmental description, for each site

Site	MAT (C)	Latitude (N)	Longitude (W)	No. of species	Environment
Big Hammock WMA, Georgia	20.0	31.86	82.11	26	Floodplain–swamp
Dilcher's Woods–swamp, Florida	21.0	29.60	82.20	25	Swamp, standing water
Dilcher's Woods–upland, Florida	21.0	29.60	82.20	24	Southern ridge–sandhill
Archbold, Florida	22.3	27.18	81.35	20	Southern ridge–sandhill
Florida Panther Refuge, Florida	23.4	26.17	81.34	25	Swamp, standing water

WMA, Wildlife Management Area.

Table 2. Observed and predicted MAT for five sites

Site	Actual MAT (C)	Predicted SLR* (3, 4)	MLR (6)	MLR-AS (3)	CCA (5, 7)	SLR†
Big Hammock WMA	20	10.0	11.0	13.7	9.7	11.8
Dilcher's Woods–swamp	21	15.2	13.0	17.3	13.8	18.6
Dilcher's Woods–upland	21	16.4	15.7	19.3	15.9	20.2
Archbold	22.3	21.0	18.5	22.7	18.3	27.8
Florida Panther Refuge	23.4	18.9	18.9	21.5	17.2	23.2

*Method types are as follows: SLR, simple linear regression; MLR, multiple linear regression; AS, arcsine transformed; CCA, canonical correspondence analysis.

†This study. Reference for each equation indicated. Equations are listed in Table 6.

Table 3. Published and reestimated MAT for Cretaceous, Tertiary, and Recent sites

Country/state	Site	Time period	MAT1* (C)	MAT2† (C)	MAT3‡ (C)
Greenland (31)	PRP	Late Cretaceous	10	12.7	14–15
	BS	Late Cretaceous	7	9.8	14–15
	4TV	Late Cretaceous	6	8.0	14–15
	3CMP	Late Cretaceous	5	6.9	14–15
Wyoming (13)	Big Multi Quarry	Late Paleocene	19.5	24.0	20–26 (35)
Oregon (14)	King's Gap	Late Eocene	15.5 (4)	19.3	19–23 (36)
	Sumner Spring	Late Eocene	6.6 (4)	8.8	19–23 (36)
	Nichols Spring	Early Oligocene	6.6 (4)	8.8	16–20 (36)
	Canal	Early Oligocene	6.0 (4)	8.0	16–20 (36)
Germany (30)	Enspel	Late Oligocene	12.4 (19)	15.1	15.9–16.6
	Rott	Late Oligocene	11.8 (19)	14.3	16.5–20.8
	Frenchen Mine	Late Miocene	8.8 (19)	10.6	14.0–14.4
	Hambach Mine/7F	Late Miocene	9.1 (19)	10.9	14.0–15.8
	Hambach Mine/9A	Early Pliocene	6.2 (19)	7.3	13.3–13.8
Ecuador (28)	Yasuni-lacustrine	Recent	23.7 (4)	29.0	26.5
	Yasuni combined river	Recent	21.5 (4)	26.3	26.5

*Estimated MAT from the original publication. Regression equation reference indicated.

†Estimated MAT calculated with the provisional linear regression introduced in this report.

‡Estimated MAT using deep-sea or surface oxygen isotopes (Greenland, Wyoming, and Oregon samples), a coexistence approach (German samples), or actual data (Recent Ecuadorian samples). Value reference indicated.

The presence of many different species of liana may explain the increased numbers of toothed species living in tropical riparian habitats (28), but this is not the case for the wetland

habitats sampled in the Southeastern U.S. Only one sample, Big Hammock, has more than one sampled species of liana, and both Archbold and Dilcher's Woods have no sampled liana representatives. This suggests that the numbers of tree and shrub species with toothed leaves are inherently higher in wetlands than in better-drained habitats. Toothed leaves appear to be advantageous to woody plants in wetlands regardless of plant form. The exact physiology explaining the advantage to toothed leaves in wet or cool environments is unknown, and explanations for the presence of teeth range from promotion of water conductance and reduction of leaf temperature (32) to rapid expansion of the leaf as it unfurls (33). Most studies agree that teeth draw water through a leaf more quickly than do leaves with entire margins (e.g., refs. 32 and 34). This may be of benefit in extremely wet environments, where the leaf's compromise of higher water loss for more rapid early growth is ameliorated by abundant water supplies.

We calculated a new linear regression equation (Fig. 1) by using leaf-margin data from 10 modern sites derived from this study and the CLAMP database (5) to determine whether a predictive equation derived solely from wet-soil sites would increase the estimate of MAT at modern sites analogous to fossil deposition sites. We used this equation to recalculate the MAT of 14 fossil and two modern sites (13, 14, 28–31) whose tem-

Table 4. Proportions of leaf morphological characters for the five tested sites

Leaf character	Big Hammock WMA	Dilcher's Woods-swamp	Dilcher's Woods-upland	Archbold	Florida Panther Refuge
Lobed	0.23	0.08	0.08	0.05	0.08
No teeth	0.29	0.46	0.50	0.65	0.58
Teeth regular	0.60	0.42	0.35	0.28	0.34
Teeth close	0.60	0.40	0.31	0.18	0.30
Teeth round	0.25	0.16	0.31	0.10	0.22
Teeth acute	0.42	0.38	0.19	0.25	0.20
Teeth compound	0.23	0.06	0.04	0.0	0.04
Nanophyll	0.0	0.0	0.0	0.03	0.0
Leptophyll 1	0.0	0.0	0.04	0.03	0.0
Leptophyll 2	0.05	0.04	0.08	0.06	0.02
Microphyll 1	0.21	0.09	0.21	0.25	0.09
Microphyll 2	0.40	0.35	0.33	0.40	0.42
Microphyll 3	0.19	0.25	0.23	0.19	0.24
Mesophyll 1	0.09	0.21	0.05	0.05	0.14
Mesophyll 2	0.05	0.04	0.03	0.0	0.05
Mesophyll 3	0.03	0.02	0.02	0.0	0.04
Apex emarginate	0.06	0.0	0.06	0.13	0.20
Apex round	0.12	0.12	0.33	0.25	0.26
Apex acute	0.88	0.86	0.60	0.70	0.70
Apex attenuate	0.0	0.02	0.06	0.03	0.04
Base cordate	0.17	0.18	0.13	0.03	0.14
Base round	0.17	0.08	0.08	0.03	0.06
Base acute	0.65	0.74	0.79	0.95	0.80
L:W <1:1	0.06	0.08	0.02	0.03	0.0
L:W 1–2:1	0.49	0.22	0.31	0.31	0.18
L:W 2–3:1	0.28	0.49	0.44	0.44	0.41
L:W 3–4:1	0.09	0.11	0.15	0.09	0.21
L:W >4:1	0.04	0.09	0.08	0.14	0.17
Shape obovate	0.19	0.18	0.23	0.20	0.16
Shape elliptic	0.63	0.70	0.69	0.65	0.62
Shape ovate	0.17	0.12	0.08	0.15	0.24

Table 5. Data used to calculate preliminary linear regression equation

Site	State	MAT (C)	% entire-margined species
Lake Placid (5)	New York	4.0	10
Wanakena (5)	New York	5.0	23
Dannemora (5)	New York	7.0	13
Battle Creek (5)	Maryland	13.0	29
Little Pee Dee WMA	South Carolina	18.0	41
Big Hammock WMA	Georgia	20.0	29
Dilcher's Woods lowland	Florida	21.0	46
Dilcher's Woods upland	Florida	21.0	50
Archbold	Florida	22.3	65
Panther Refuge	Florida	23.4	58

Table 6. Published equations for predicting MAT

Simple linear regression (SLR) (4):
 $\text{MAT} = 1.14 + 0.306(\% \text{no teeth})^*$

MLR (6):
 $\text{MAT} = 9.865 + 0.207(\% \text{no teeth}) - 0.058(\% \text{Base round})^\dagger - 0.202(\% < 1:1)^\ddagger$

MLR-arc sine transformed (MLR-AS) (3):
 $2.536 + 17.372(\% \text{no teeth}) + 2.896(\% \text{emarginate})^\ddagger - 8.592(\% < 1:1)$

Canonical correspondence analysis (CCA) (1, 7):
 Uses the computer program CANOCO[§]

*Leaf morphology characters are defined by Wolfe (5). The term %no teeth indicates the proportion of species in the flora with entire-margined leaves.

†The term %base round indicates the proportion of species with a round (not acute or cordate) base; %<1:1 indicates the proportion of species with a length to width ratio of less than 1:1.

‡%emarginate refers to the proportion of species with an emarginate apex. The alternative character state is lack of emarginate apex.

§CANOCO (37), a computer program, is used to ordinate all 31 characters defined by Wolfe (5) coincidentally with climatic characters. The resulting axis scores are converted to absolute temperatures by using multiple regression equations available on the web from Jack A. Wolfe (<http://tabitha.open.ac.uk/spicer/CLAMP/Clampset1.html>) (University of Arizona).

peratures had been previously calculated by using leaf margin data (Table 3). For the majority of the sites, the previously estimated MAT was presumed to be too low. The revised estimates using our new wet-site regression equation are warmer and more closely approximate MAT estimates made from isotope analysis or coexistence approaches (Table 3). Clearly, soil type is relevant and should be taken into account during the

collection of modern foliar physiognomic data. The new equation should ideally be calculated from a greater number of sites and thus is considered provisional.

Our results indicate that MAT will be underestimated from the data based on fossil leaves collected from wet sites of deposition when existing predictive equations are used. Therefore, MAT based on current foliar physiognomy studies of most fossil sites has been underestimated. We suggest that predictive equations based on the modern correlation between leaf morphology and climate be recalculated using a new database of leaf characters and climate variables derived primarily from modern sites that are more analogous to fossil deposition sites. This database should include a high percentage of wet environments, typical of environments in which the plants that produced the fossil leaves grew before the leaves were deposited. The reestimation of 16 wet-soil sites using our new linear regression equation calculated using only data from sites with wet soils clearly demonstrates that this approach is preferable when estimating the paleo-MAT of terrestrial ecosystems. World climate models need to recalibrate paleotemperature values derived from foliar physiognomy to reflect this new equation.

We thank Michael Wiemann, Bonnie Jacobs, and Scott Wing for helpful comments and review and Terry Lott, Mihai Popa, Yondong Wang, Banian Sun, and Kate Skroski for help with sampling. We also thank Archbold Biological Station, the Georgia State Department of Natural Resources, and the Florida Panther Refuge for collection permission and access. Funding was provided by National Science Foundation Grant EAR-9905668, "Temperature Prediction from Wood and Leaf Physiognomy," to D.L.D. This paper is University of Florida contribution to paleobiology publication no. 551.

- Bailey, I. W. & Sinnott, E. W. (1915) *Science* **41**, 831–834.
- Wolfe, J. A. (1978) *Am. Sci.* **66**, 694–703.
- Wing, S. & Greenwood, D. R. (1993) *Philos. Trans. R. Soc. London B* **341**, 243–252.
- Wolfe, J. A. (1979) *U.S. Geol. Surv. Prof. Pap.* **1106**, 1–37.
- Wolfe, J. A. (1993) *U.S. Geol. Surv. Bull.* **2040**, 1–71.
- Wiemann, M. C., Manchester, S. R., Dilcher, D. L., Hinojosa, L. F. & Wheeler, E. (1998) *Am. J. Bot.* **85**, 1796–1802.
- Wolfe, J. A. (1995) *Annu. Rev. Earth Planet. Sci.* **23**, 119–142.
- Sloan, L. C. & Morrill, C. (1998) *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **144**, 21–35.
- Spicer, R. A. & Herman, A. B. (1998) *Paleontol. J.* **32**, 105–118.
- Wing, S., Wolfe, J. A., Seal, I., Robert R. & Rye, R. O. (1993) *Geology* **21**, 1051–1052.
- Dolph, G. E. & Dilcher, D. L. (1980) *Biotropica* **12**, 91–99.
- Wolfe, J. A. (1990) *Nature* **343**, 153–156.
- Wilf, P., Beard, K. C., Davies-Vollum, K. S. & Norejko, J. W. (1998) *Palaaios* **13**, 514–532.
- Smith, G. A., Manchester, S. R., Ashwill, M., McIntosh, W. C. & Conrey, R. M. (1998) *Geol. Soc. Am. Bull.* **110**, 759–778.
- Parkhurst, D. F. & Loucks, O. L. (1972) *J. Ecol.* **60**, 505–537.
- Uhl, D. & Mosbrugger, V. (1999) *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **149**, 15–26.
- Givnish, T. J. (1987) *New Phytol.* **106**, 131–160.
- Halloy, S. R. P. & Mark, A. F. (1996) *J. Royal Soc. New Zealand* **26**, 41–78.
- Wilf, P. (1997) *Paleobiology* **23**, 373–390.
- Gregory-Wodzicki, K. M. (2000) *Paleobiology* **26**, 668–688.
- Gastaldo, R. A. (1992) *Palaeobotanist* **41**, 211–223.
- Burnham, R. J., Wing, S. & Parker, G. (1992) *Paleobiology* **18**, 30–49.
- Gastaldo, R. A., Ferguson, D. K., Walther, H. & Rabold, J. M. (1996) *Rev. Palaeobot. Palynol.* **91**, 1–21.
- MacGinitie, H. D. (1953) *Carnegie Inst. Wash. Publ.* **599**, 1–188.
- Roth, J. L. & Dilcher, D. L. (1978) *Cour. Forsch. Inst. Senckenberg* **30**, 165–171.
- Potter, F. W., Jr., & Dilcher, D. L. (1980) in *Biostratigraphy of Fossil Plants*, eds. Dilcher, D. L. & Taylor, T. N. (Dowden, Hutchinson and Ross, Stroudsburg, PA), pp. 211–225.
- Ferguson, D. K. (1985) *Rev. Palaeobot. Palynol.* **46**, 117–188.
- Burnham, R. J., Pitman, N. C., Johnson, K. R. & Wilf, P. (2001) *Am. J. Bot.* **88**, 1096–1102.
- Kowalski, E. A. (2002) *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **188**, 141–165.
- Utescher, T., Mosbrugger, V. & Ashraf, A. R. (2000) *Palaaios* **15**, 430–449.
- Boyd, A. (1994) *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **112**, 261–278.
- Gutschick, V. P. (1999) *New Phytol.* **143**, 3–18.
- Baker-Brosh, K. F. & Peet, R. (1997) *Ecology* **78**, 1250–1255.
- Mosbrugger, V. & Roth, A. (1996) *Rev. Palaeobot. Palynol.* **90**, 195–207.
- Berggren, W. A., Lucas, S. G. & Aubry, M.-P. (1998) in *Late Paleocene–Early Eocene Climatic and Biotic Events in the Marine and Terrestrial Records*, eds. Aubry, M.-P., Lucas, S. G. & Berggren, W. A. (Columbia Univ. Press, New York), pp. 1–17.
- Savin, S. M., Douglas, R. G. & Stehli, F. G. (1975) *Geol. Soc. Am. Bull.* **86**, 1499–1510.
- ter Braak, C. (1991) CANOCO—A FORTRAN Program for Canonical Correspondence Ordination (Microcomputer Power, Ithaca, NY).