

days were those that lasted for long after they were supposed to recede, and which reached heights of a metre or more above that of AD 741/742. Only at that height would the flood reach the ground upon which most, if not all, the towns and villages of Egypt were built. Such dangerous floods were common during the fourteenth century and have been singled out by the historians, who dwelt at length on their devastating effects. The readings of the Roda nilometer have been widely scrutinized by scientists and I know of no one who classified the flood of AD 741/742 as exceptionally high or devastating. This conclusion is confirmed by a review of the earlier<sup>5,6</sup> and more recent literature<sup>7,8</sup>. I believe, therefore, that Stanley *et al.* need to re-examine their data in the light of this evidence.

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Palaeobotany

## Atmospheric CO<sub>2</sub> from fossil plant cuticles

Plants respond to changes in atmospheric carbon dioxide levels by regulating the number of stomata in their leaves. In his reconstruction of a continuous, 300-million-year record of atmospheric CO<sub>2</sub>, Retallack bases his curve on stomatal counts of fossil plant cuticles taken from published micrographs<sup>1</sup>. However, the preservation of cuticles from Permian times is generally too fragmentary for the stomatal index to be reliably determined, the micrographs used could have biased the results, and there are important errors in the supplementary data<sup>1</sup> — all of which cast doubt on the Permian part of Retallack's record.

Not only do the fragmentary preservation of Permian plant cuticles and the small number of specimens counted call into question the statistical validity of Retallack's stomatal index, but the record may also be biased by reliance on cuticle micrographs that are not representative. In many species, stomata are not evenly distributed — for example, *Autunia conferta* and *Peltaspermum retensorium* have very different abaxial (lower) and adaxial (upper) leaf cuticles, particularly with regard to stomata distribution<sup>2–5</sup>. The

thinner abaxial cuticles have many more stomata, but their cell patterns can be indistinct (the positions of stomata are indicated by papillae on the subsidiary cells).

Most of the micrographs used by Retallack show adaxial cuticles with stomata concentrated between the veins, notably in the central part of the pinnules (leaflets); stomata are rare or absent on the rest of the adaxial side. In *P. retensorium*, stomata are present only in the basal part of the pinnules<sup>5</sup>; over 90% of the adaxial surface lacks stomata. The photographs used by Retallack mostly show stomata-bearing pieces of cuticle because stomata are of primary importance for taxonomy; stomata-poor or stomata-free cuticles are rarely shown in such images. Counting only these cuticles may lead to unreliable estimates of stomatal indices. Substantial variations in stomatal index have been reported in extant plants and such data should be interpreted with caution<sup>6,7</sup>.

Retallack's data<sup>1</sup> for the Permian contain several errors: stomatal counts are given for locations that have yielded no cuticle (for example, Sobernheim and Saxony '*Autunia conferta*'), and for material not illustrated in this context (Lebach: *A. conferta*). Ages given for some Permian localities are doubtful (Sobernheim is given as 280 ± 3 Myr (basal part of the Nahe Group (N 4); ref. 8), which is too young: the Grenzlager volcanism that immediately underlies the Nahe Group has been dated (by Rb–Sr dating) at 290.7 ± 0.9 Myr; ref. 9); Frankenberg (253 ± 2 Myr) and Geismar (256 ± 2 Myr) are different designations<sup>1</sup> for the same locality, which is of the same age as the British Zechstein localities (Middridge, Kimberly, Cinderhill: 258 ± 2 Myr). Also, Lebach (Sakmarian: 285 ± 3 Myr) and Rümmlbach (Sakmarian–Artinskian: 283 ± 3 Myr) are outcrops in the same horizon (top Lauterecken–Oderenheim Formation (L–O 10); ref. 8), underlying the Grenzlager volcanics<sup>9</sup>, so Retallack's age for Lebach/Rümmlbach is too young). The actual record is thus much more punctuated than proposed<sup>1</sup>.

Expansion of the atmospheric-CO<sub>2</sub> curve into the Palaeozoic era is important, but this should be based on critical evaluation of more reliable data.

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*Retallack replies* — My data on the stomatal density of fossil plants through time<sup>1</sup> was made available to encourage refinements such as that now offered by Kerp. His corrections make no significant difference to my published curves, but future refinement should improve this palaeobotanical archive of atmospheric CO<sub>2</sub> levels.

Kerp's characterization of stomatal distribution on Permian seed-fern leaves is similar to the situation in *Lepidopteris stormbergensis*, which has a highly variable stomatal index<sup>2,3</sup>. My rarefaction analysis of several fossil species, including those described by Kerp, shows *L. stormbergensis* to be the most variable taxon of my compilation; I therefore used this species to set the lower boundary for reliable analyses at 500 epidermal cells<sup>1</sup>. The stomatal index of living *Ginkgo biloba* can be determined reliably by counting as few as 50 cells; other species represented by the thousands of cells needed for rarefaction analysis fell between these extremes.

Differences between Kerp's taxonomic names and mine reflect a different view of palaeobotanical nomenclature. He gives fossil leaves the same name as reproductive structures that are considered on evidence of varying quality to have belonged to the same plant. This is risky, because few, if any, of the taxa studied have reproductive structures attached to leaves. In my compilation of fossil leaves<sup>1</sup>, I listed names as he cited them for ease of reference, but in quotes to indicate deviation from traditional palaeobotanical form genera, such as the leaf genus *Rhachiphyllum*. Such taxonomic considerations do not affect the inferred CO<sub>2</sub> curve, because each determination is made using a collection of leaves at a single locality that are thought to belong to the same species of the same geological age.

I welcome Kerp's comments on local stratigraphic relationships. He has indicated that there are problems with fossil plant cuticles that he previously labelled as being from Sobernheim<sup>4</sup>, Lebach<sup>4</sup> and Saxony<sup>5</sup> (pointing out that the cuticle from Saxony is not '*Autunia conferta*', and '*Autunia conferta*' from 'Lebach' and 'Sobernheim' is really all from Langenthal, for which amended stomatal data are: stomatal index = 8.6 ± 1.1; Ne = 797, Ns = 80, Nf = 3). The best way forward is to count more cells from more fossils, at more localities tied to better-dated successions.

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