Typical Triassic Gondwanan floral elements in the Upper Permian of the paleotropics

Hans Kerp
Abdalla Abu Hamad*
Birgit Vörding
— Forschungsstelle für Paläobotanik, Universität Münster, Hindenburgplatz 57, 48143 Münster, Germany
Klaus Bandel — Geologisch-Paläontologisches Institut, Universität Hamburg, Bundesstrasse 55, 20146 Hamburg, Germany

ABSTRACT

Permian floras of the Middle East often show a mixture of Euramerican, Cathaysian, and Gondwanan elements. We report several species of *Dicroidium*, a seed fern typical for the Triassic of Gondwana, from the Upper Permian of the Dead Sea region. This is the earliest unequivocal record and the most northerly occurrence of this genus, suggesting that it may have evolved during the Permian in the paleotropics. With the decline and eventual extinction of the typical Permian Glossopteris flora, *Dicroidium* may have migrated southward. As the climate ameliorated in the Triassic, *Dicroidium* could have spread farther, eventually colonizing all of Gondwana, where it became one of the dominant floral elements.

Keywords: floral provinces, Permian-Triassic transition, migration, pteridosperms.

INTRODUCTION

Paleozoic floral provincialization began in the Early Carboniferous and culminated in the Permian (Wnuk, 1996). At the end of the Permian, locally, 95% of the peat-forming plant species became extinct (Michaelsen, 2002), although it also has been argued that the scale and timing of effects of the end-Permian biotic crisis varied markedly between different regions (Rees, 2002). Several groups became extinct, whereas others suffered a strong decline. Therefore, the discovery of a Late Permian flora from the Middle East with foliage assignable to the Gondwanan seed fern genus *Dicroidium*, which is generally considered to be restricted to the Triassic (Anderson et al., 1999), is most remarkable. This is not only the earliest record of *Dicroidium*, but also the most northerly occurrence of a genus that became highly successful in Gondwana in the Triassic.

GEOLOGICAL SETTING AND AGE

Plant remains were collected from the Um Irna Formation in Wadi Himara, Dead Sea region, Jordan (Fig. 1). This 67 m thick clastic sequence unconformably overlies the Cambrian Um Ishrin Formation (Bandel and Khoury, 1981) and consists of a series of predominantly sandy fining-upward sequences with paleosols with ferruginous pisoliths. In the lower part of the formation, grayish-brownish siltstone and claystone lenses, with abundant plant material, are interpreted as abandoned channel fills of a distal braided river system (Makhlouf et al., 1991).

The rich and well-preserved microflora is dominated by *Falcisporites*, occurring in large clusters and as individual pollen grains. *Falcisporites* is known from the Upper Permian, but percentages of up to 50% are normally only found in Triassic rocks. This pollen type has been attributed to *Dicroidium* (Balme, 1995), the dominant constituent of the Wadi Himara macroflora. In addition, nearly sixty other palynomorph taxa have been identified that clearly indicate a Late Permian age, including *Lueckisporites virkkiae*, *Klausipollenites schaubergeri*, *Nuskoisporites dulhuntyi*, and *Jugasporites delasaucei*. Another flora from a nearby locality in the upper part of the Um Irna Formation contains several typical Late Permian Cathaysian taxa, including *Lobatannularia* and *Gigantonoclea* (Mustafa, 2003). The Ma'in Formation, which overlies the Um Irna Formation with an erosional contact, yielded a low-diversity microflora, dominated by lycopsid spores (*Endosporites papillatus*, *Densoisporites nejburgii*) and acritarchs (*Veryhachium* sp.), an assemblage typical for the Lower Triassic (Eshet, 1990; Looy et al., 1999).

THE UM IRNA FLORA

Mummified leaves with excellently preserved cuticles are abundant in the lower part of the Um Irna Formation, including up to 30 cm long, almost complete, bifurcated fronds. Based on gross morphology and cuticle structure, two species of *Dicroidium* can readily be distinguished; bulk macerations have yielded at least three other possible *Dicroidium* species. Although the generic assignment of the plant remains is clear, they cannot be attributed to previously described species of *Dicroidium*. Apart from *Dicroidium*, the plant-bearing beds contain a few unidentifiable fern fragments and relatively large amounts of charcoal.

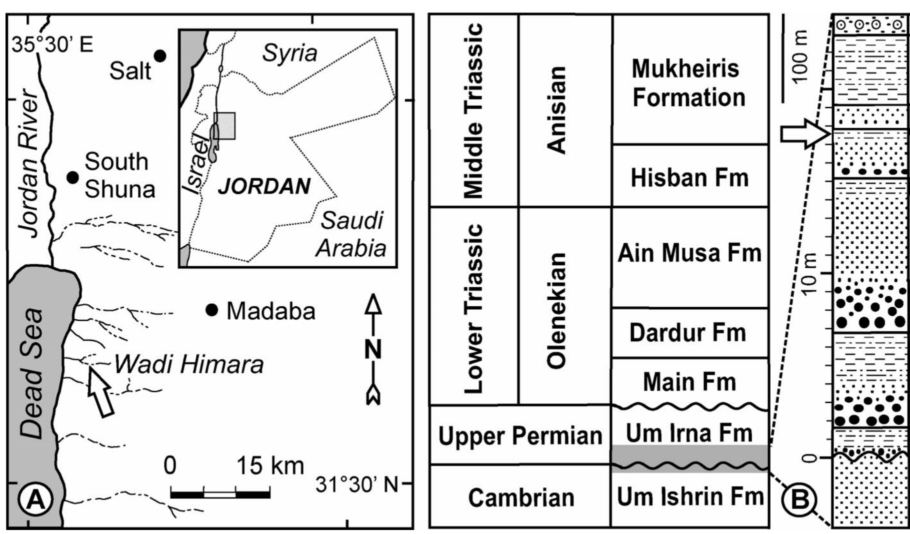

Figure 1. A: Geographical position of Wadi Himara locality (arrow). B: Stratigraphic subdivision of the Upper Permian–Lower Triassic in Dead Sea region with a schematic section of lower part of the Um Irna Formation and position of the plant-bearing horizon (arrow).

*Current address: The University of Jordan, Department of Environmental and Applied Geology, Amman 11942, Jordan; E-mail: Abdalla80@hotmail.com.

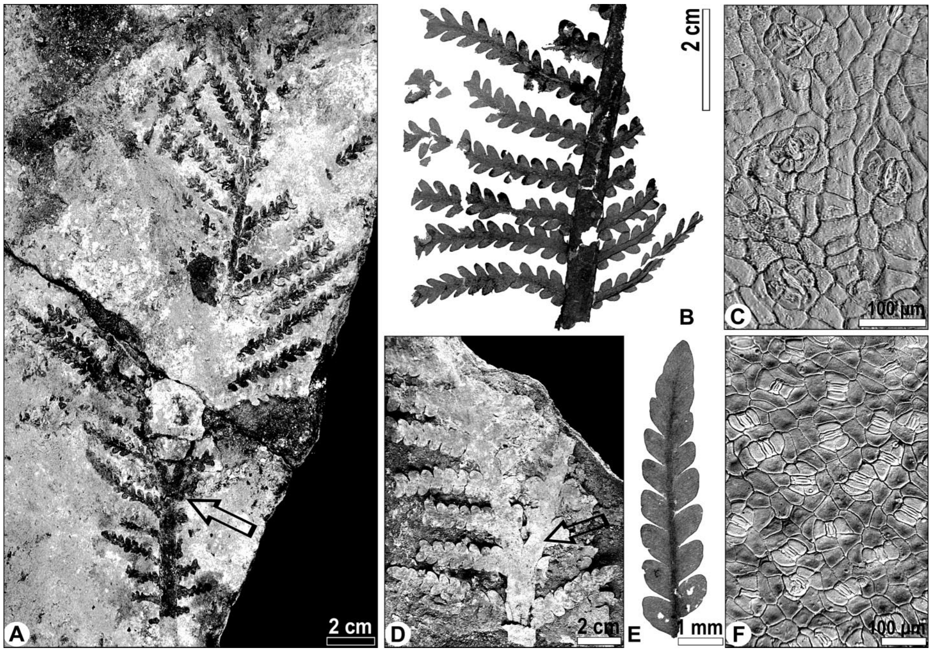

Figure 2. A–C: *Dicroidium* sp. A. A: Frond showing typical bifurcation (arrow). B: Cuticle of a pinna. C: Cuticle of lower pinnule surface stomata with ring of equally strongly cutinized subsidiary cells. D–F: *Dicroidium* sp. B. D: Frond showing typical bifurcation (arrow). E: Pinna apex. F: Cuticle of lower pinnule surface showing stomata with weakly cutinized lateral subsidiary cells.

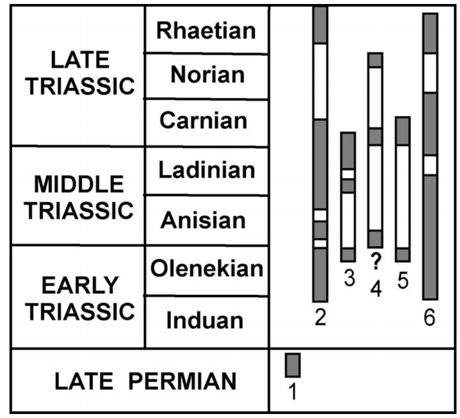

Figure 3. Stratigraphic ranges of the genus *Dicroidium* in the Middle East and various parts of Gondwana. 1—Jordan; 2—Australia and New Zealand; 3—Antarctica; 4—India; 5—South America; 6—southern Africa.

The two species represented by larger specimens, here informally named *Dicroidium* sp. A and *Dicroidium* sp. B, have bifurcated, bipinnate fronds. *Dicroidium* sp. A (Figs. 2A–2C) has densely spaced, tongue-shaped pinnules with broadly tongue-shaped terminal pinnules, whereas *Dicroidium* sp. B (Figs. 2D–2F) has narrower, triangular pinnules and narrow, acute terminal pinnae. The two species are easily distinguishable by their stomata. *Dicroidium* sp. A has stomata with a ring of four to seven equally strongly cutinized subsidiary cells, whereas *Dicroidium* sp. B. usually has stomata with four subsidiary cells, of which the lateral ones are weakly cutinized (Figs. 2C and 2F). In both species, cuticles are of medium thickness and stomata are not sunken.

The absence of typical wetland plants and the low percentage of spores (<20% of the total assemblage) are indicative of extrabasinal vegetation sensu Pfefferkorn (1980). The lithology points to a tropical summer wet climate; soils with ferruginous pisoliths are typically formed in hot and humid climates with a high annual rainfall and a short dry season (Driessen et al., 2001).

STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION OF *DICROIDIUM*

Dicroidium, a corystosperm, is found in the Lower Triassic but is more common in the Middle and Upper Triassic (Anderson and Anderson, 1983). To date, the earliest unequivocal representatives of the genus (*D. narrabeenense*, *D. zuberi*) are known from the Narrabeen Group and the Newport Formation (lower Olenekian) of eastern Australia (Retallack, 1977), whereas the last occurrences are in the Rhaetian (Fig. 3). *Dicroidium* is a typical Gondwanan taxon, occurring at paleolatitudes above 35° S in southern Africa, Australia, New Zealand, India, Argentina, Chile, southern Brazil, and the Antarctic (Fig. 4). The material reported here thus represents both the earliest and the most northern occurrence of a genus that is traditionally regarded as a typical Triassic Gondwanan element.

MIDDLE AND LATE PERMIAN FLORAS OF THE MIDDLE EAST

In the Late Permian, the Arabian plate was connected to the African plate, and the Dead Sea region was a lowland area located in the equatorial belt at ~15° S (Scotese and Langford, 1995; Ziegler et al., 1997). Comparisons with other Permian floras from the Middle East (Fig. 5) are of special interest with regard to paleophytogeography.

In the Middle Permian (Wordian) Gharif Formation of central Oman, Euramerican taxa (e.g., the conifer *Otovicia hypnoides*) are associated with Cathaysian elements such as *Gigantopteris* and *Tingia*, and with Gondwanan elements such as various glossopterids (Berthelin et al., 2003). Cathaysian elements also have been recorded from Iraq, Saudi Arabia, and Oman. A small flora, exclusively consisting of Cathaysian taxa, is known from the Upper Permian of western Iraq (Čtyroký, 1973). The flora of the Unayzah Member (Khuff Formation, early Late Permian) of Qasim Province, Saudi Arabia, is dominated by pecopterids and sphenopsids, suggesting a warm and humid climate. Several taxa, e.g., *Lobatannularia* and a gigantopterid, are typically Cathaysian. The overlying Khuff Member yielded taeniopterid leaves and Euramerican-type conifers (El-Khayal and Wagner, 1985). Another mixed flora from the Upper Permian of Hazro, southeast Turkey (Wagner, 1962; Archangelsky and Wagner, 1983), predominantly consisting of sphenopsids and ferns, includes a number of typical Cathaysian taxa, e.g., *Lobatannularia* and *Gigantopteris*, but also Gondwanan elements such as *Glossopteris* and *Botrychiopsis*. Middle and Late Permian floras from the Middle East thus often show a mixture of elements from several floral provinces. Not only Cathaysian elements reached the limits of their geographical distribution, but also Gondwanan elements such as glossopterids.

In contrast, Late Permian floras from the southern Alps (Italy), which are ~25° north of the paleoequator (Scotese, 2002; Ziegler et al., 1997), are dominated by conifers, with peltasperms and ginkgophytes as additional elements (Visscher et al., 2001). Plants display xeromorphic features, i.e., thick cuticles, often with prominent papillae, sunken stomata, and strongly cutinized subsidiary cells; leaves are often thick and fleshy. Typical conifer prepollen known from the Upper Permian of the southern Alps also has been found in the Um Irna Formation, e.g., *Lueckisporites virkkiae*, *Jugasporites delasaucei*, and *Nuskoisporites dulhuntyi*.

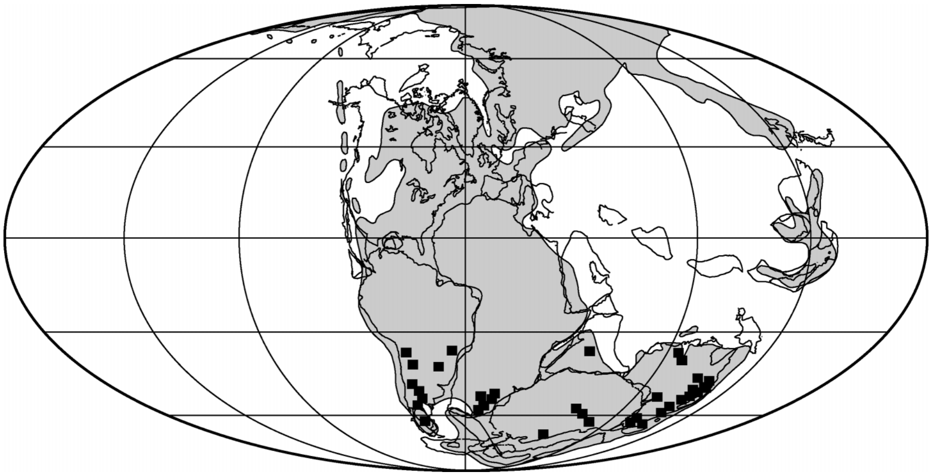

Figure 4. Distribution of *Dicroidium* in the Triassic. Map modified after Scotese (2002).

SURVIVORS OF THE END-PERMIAN BIOTIC CRISIS

Many plant taxa, such as gigantopterids, *Tingia*, and *Lobatannularia*, became extinct at the end of the Permian, while others diminished dramatically and eventually also perished, such as the glossopterids. However, a few Triassic floras with *Dicroidium* and glossopterids are known from South Africa, India, and Australia (e.g., Bharadwaj and Srivastava, 1969; Anderson and Anderson, 1985; Holmes, 1992). On the other hand, plants with Mesozoic affinities, primarily Northern Hemisphere conifers and cycads (e.g., *Swedenborgia*, *Dioonitocarpidium*), have been described from the Lower Permian of Texas (DiMichele et al., 2001). During the Permian, Texas was a lowland area positioned at a similar latitude as Jordan, but north of the equator, and separated from the Southern Hemisphere by a mountain chain (Fig. 6), the altitude of which is still a matter of debate (Fluteau et al., 2001).

In Gondwana, the Permian-Triassic transition is characterized by a shift from cold temperate to cool temperate conditions (Retallack and Krull, 1999; Kidder and Worsley, 2004). Based on sedimentological, paleopedological, and paleobotanical evidence, the earliest Triassic is considered to have been significantly warmer and more seasonally dry than the latest Permian (McLoughlin et al., 1997; Ward et al., 2000; Michaelsen, 2002). The Early Triassic vegetation of Gondwana was dominated by lycopsids and conifers. More diverse *Dicroidium*-dominated floras did not appear prior to the Middle Triassic (Retallack, 1995).

Two seed fern groups were obviously not adversely affected by the end-Permian biotic crisis, i.e., corystosperms and peltasperms. With the present discovery, the corystosperm *Dicroidium* is one of the very few genera known, to date, that survived the end-Permian biotic crisis. *Dicroidium* is not currently known from the lowermost Triassic; however, the floral record of the Lower Triassic is generally poor. During the Early Triassic, the climate became increasingly favorable and Gondwana moved farther northward. Corystosperms fully expanded during the Middle Triassic, when they reached their maximum diversity and distribution, inhabiting large parts of Gondwana. Peltasperms, a group of shrubby, mesic to xeric plants, which first appeared during the latest Carboniferous (Kerp, 1996), are known from the Permian of Euramerica, Angara, and Cathaysia. This group also migrated southward, and appeared in Gondwana in the earliest Triassic (Retallack, 2002).

CONCLUSIONS

Although the picture is still incomplete, it is clear that Middle and Late Permian floras from the Middle East contain elements from several floral provinces. This region occurs at the intersection of several floral provinces, and seems to be crucial for understanding late Paleozoic phytogeography. The presence of *Dicroidium* in the Upper Permian of Jordan shows that corystosperms have evolved during the Permian, apparently in extrabasinal tropical lowland areas.

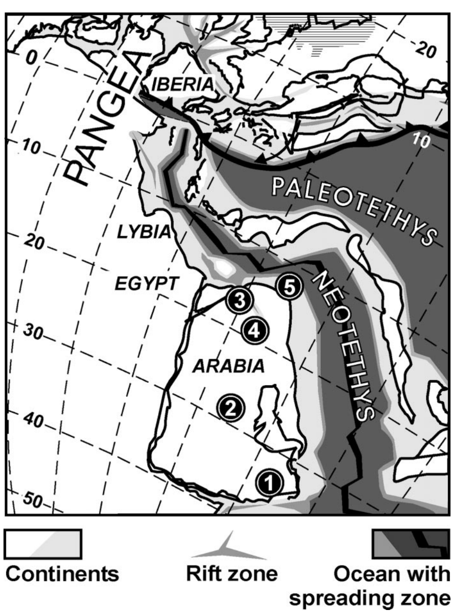

Figure 5. Paleogeographical map of the Permian of the Paleo- and Neotethys region with floras discussed in the text. Map modified from Stampfli and Borel (2001). 1—central Oman; 2—Saudi Arabia; 3—Dead Sea, Jordan; 4—Ga'ara, Iraq; 5—Hazro, Turkey.

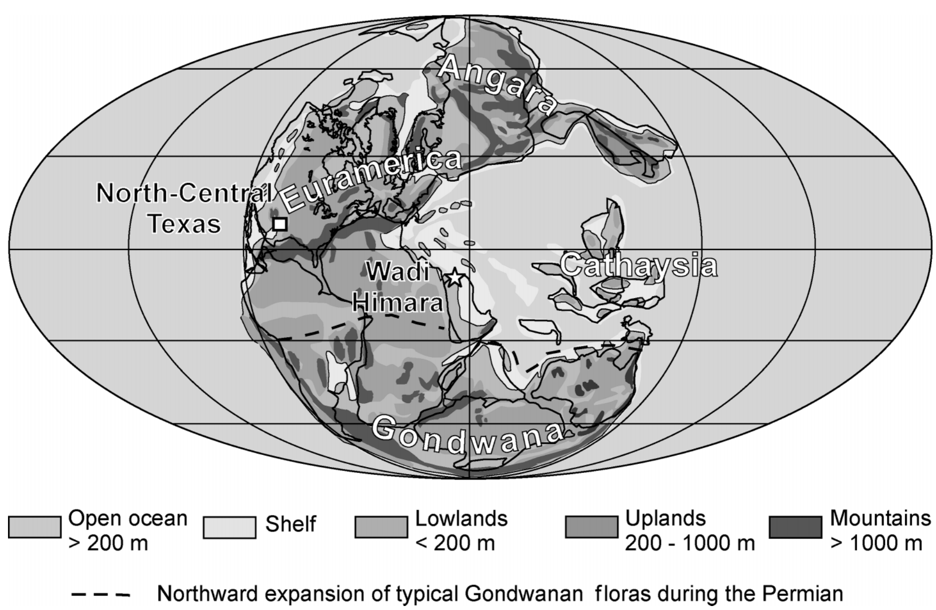

Figure 6. Paleogeographic map of Late Permian with positions of Wadi Himara flora, north-central Texas flora, and northward expansion of typical Gondwanan floras. Map modified from Ziegler et al. (1997).

Possible causes for the end-Permian biotic crisis still remain a matter of debate. However, it becomes increasingly clear that the Permian-Triassic transition is marked by a climatic change. Global warming resulted in an expansion of the tropical belt, a poleward shift of adjacent climate zones, and a contraction of the more temperate and cool zones at higher latitudes. A further complication for the Permo-Triassic is that, in time, continents moved northward through climatic belts. Future studies should focus on the paleotropics, where effects of climatic changes were probably less severe than elsewhere. Unfortunately, very little is known about Late Permian and Early Triassic tropical floras. However, recent finds of typical Mesozoic conifers and cycads in Texas and *Dicroidium* in Jordan suggest that, during the Permian, the tropics, and particularly extrabasinal settings, might have been a radiation center for ''Mesozoic'' gymnosperms. With the climatic amelioration in Gondwana in the Early Triassic, the genus *Dicroidium* may have migrated southward and become a dominant constituent of many Gondwanan floras, whereas on the northern side of the mountain belt, conifers and cycads expanded northward to colonize large parts of the Northern Hemisphere.

ACKNOWLEDGMENTS

We thank M. Berthelin, B. Bomfleur, H. Hass (Münster), and M. Krings (München) for constructive discussions. This project was funded by the Deutsche Forschungsgemeinschaft (grants BA 675/26-1-3 to KB and KE 584/11-1 to HK). A. Abu Hamad thanks the Natural Resources Authority (Amman, Jordan) for the opportunity to carry out this work.

REFERENCES CITED

Anderson, J.M., and Anderson, H.M., 1983, Palaeoflora of southern Africa—Molteno Formation, Volume 1, Part 1—Introduction/Part 2—*Dicroidium*: Rotterdam, Balkema, 227 p.

Anderson, J.M., and Anderson, H., 1985, Palaeoflora of South Africa, Prodromus of South African megafloras: Devonian to lower Cretaceous: Rotterdam, Balkema, 423 p.

Anderson, J.M., Anderson, H.M., Archangelsky, S., Bamford, M., Chandra, S., Dettmann, M., Hill, R., McLoughlin, S., and Rösler, O., 1999, Patterns of Gondwana plant colonisation and diversification: Journal of African Earth Sciences, v. 28, p. 145–157, doi: 10.1016/S0899-5362(98)00083-9.

Archangelsky, S., and Wagner, R.H., 1983, *Glossopteris anatolica* sp. nov. from uppermost Permian strata in southeast Turkey: Bulletin of the British Museum of Natural History: v. 37, p. 81–91.

Balme, B.E., 1995, Fossil in situ spores and pollen grains: An annotated catalogue: Review of Palaeobotany and Palynology, v. 87, p. 81–323, doi: 10.1016/0034-6667(95)93235-X.

Bandel, K., and Khoury, H., 1981, Lithostratigraphy of the Triassic in Jordan: Facies, v. 4, p. 1–26.

Berthelin, M., Broutin, J., Kerp, H., Crasquin-Soleau, S., Platel, J.-P., and Roger, J., 2003, The Oman Gharif mixed paleoflora: A useful tool for testing Permian Pangea reconstructions: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 196, p. 85–98, doi: 10.1016/S0031-0182(03)00314-6.

Bharadwaj, D.C., and Srivastava, S.C., 1969, A Triassic microflora from India: Palaeontographica B, v. 125, p. 119–149.

Čtyroký, P., 1973, Permian flora from the Ga'ara region (western Iraq): Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, v. 1973, p. 383–388.

DiMichele, W.A., Mamay, S.H., Chaney, D.S., Hook, R.W., and Nelson, W.J., 2001, An Early Permian flora with Late Permian and Mesozoic affinities from north-central Texas: Journal of Paleontology, v. 75, p. 449–460.

Driessen, P., Deckers, J., Spaargaren, O., and Nachtergaele, F., 2001, Lecture notes on the major soils of the world: Rome, FAO, http://www.fao.org/documents/show_cdr.asp?url_file=/DOCREP/003/Y1899E/y1899e00.htm (August 2005).

El-Khayal, A.A., and Wagner, R.H., 1985, Upper Permian stratigraphy and megafloras of Saudi Arabia: Palaeogeographic and climatic implications, *in* Compte Rendu Dixième Congrès International de Stratigraphie et de Géologie du Carbonifère, Madrid, 1983, Volume 3: Madrid, Instituto Geológico y Minero de España, p. 17–26.

Eshet, Y., 1990, Paleozoic-Mesozoic palynology of Israel, I: Palynological aspects of the Permo-Triassic succession in the subsurface of Israel: Geological Survey of Israel Bulletin, v. 81, p. 1–57.

Fluteau, F., Besse, J., Broutin, J., and Ramstein, G., 2001, The Late Permian climate: What can be inferred from modelling concerning Pangea scenarios and Hercynian range altitude?: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 167, p. 39–71, doi: 10.1016/S0031-0182(00)00230-3.

Holmes, W.B.K., 1992, *Glossopteris*-like leaves from the Triassic of western Australia: Geophytology, v. 22, p. 119–125.

Kerp, H., 1996, Post-Variscan late Palaeozoic Northern Hemisphere gymnosperms: The onset to the Mesozoic: Review of Palaeobotany and Palynology, v. 90, p. 263–285, doi: 10.1016/0034-6667(95)00087-9.

Kidder, D.L., and Worsley, T.R., 2004, Causes and consequences of extreme Permo-Triassic warming to globally equable climate and relation to the Permo-Triassic extinction and recovery: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 203, p. 207–237, doi: 10.1016/S0031-0182(03)00667-9.

Looy, C.V., Brugman, W.A., Dilcher, D.L., and Visscher, H., 1999, The delayed resurgence of equatorial forests after the Permian-Triassic ecological crisis: Proceedings of the National Academy of Sciences of the United States of America, v. 96, p. 13,857–13,862, doi: 10.1073/pnas.96.24.13857.

Makhlouf, I.M., Turner, B.R., and Abed, A.M., 1991, Depositional facies and environments in the Permian Umm Irna Formation, Dead Sea area, Jordan: Sedimentary Geology, v. 73, p. 117–139, doi: 10.1016/0037-0738(91)90026-A.

McLoughlin, S., Lindström, S., and Drinnan, A.N., 1997, Gondwanan floristics and sedimentological trends during the Permian-Triassic transition: New evidence from the Amery Group, northern Prince Charles Mountains, East Antarctica: Antarctic Science, v. 9, p. 281–298.

Michaelsen, P., 2002, Mass extinction of peat-forming plants and the effect on fluvial styles across the Permian-Triassic boundary, northern Bowen Basin, Australia: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 179, p. 173–188.

Mustafa, H., 2003, A Late Permian Cathaysia flora from the Dead Sea area, Jordan: Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, v. 2003, p. 35–49.

Pfefferkorn, H.W., 1980, A note on the term ''upland flora'': Review of Palaeobotany and Palynology, v. 30, p. 157–158, doi: 10.1016/0034-6667(80)90011-1.

Rees, P.M., 2002, Land-plant diversity and the end-Permian mass extinction: Geology, v. 30, p. 827–830, doi: 10.1130/0091-7613(2002)030<0827:LPDATE>2.0.CO;2.

Retallack, G.J., 1977, Reconstructing Triassic vegetation of eastern Australasia: A new approach for the biostratigraphy of Gondwanaland: Alcheringa, v. 1, p. 247–277.

Retallack, G.J., 1995, Permian-Triassic life crisis on land: Science, v. 267, p. 77–80.

Retallack, G.J., 2002, *Lepidopteris callipteroides*, an earliest Triassic seed fern of the Sydney Basin, southeastern Australia: Alcheringa, v. 26, p. 475–500.

Retallack, G.J., and Krull, E.S., 1999, Landscape ecological shift at the Permian-Triassic boundary in Antarctica: Australian Journal of Earth Sciences, v. 46, p. 785–812, doi: 10.1046/j.1440-0952.1999.00745.x.

Scotese, C.R., 2002, Paleomap: http://www.scotese.com (November 2005).

Scotese, C.R., and Langford, R.P., 1995, Pangea and the paleogeography of the Permian, *in* Scholle, P.A., et al., eds., The Permian of northern Pangea: New York, Springer-Verlag, p. 3–19.

Stampfli, G., and Borel, G., 2001, Late Permian, *in* Stampfli, G., et al., eds., The paleotectonic atlas of the Peritethyan Domains: Katlenburg-Lindau, European Geophysical Union, CD-ROM.

Visscher, H., Kerp, H., Clement-Westerhof, J.A., and Looy, C.V., 2001, Permian floras of the southern Alps: Naturae Bresciana, v. 25, p. 117–123.

Wagner, R.H., 1962, On a mixed Cathaysia and Gondwana flora from SE Anatolia (Turkey), *in* Compte Rendu du IVe Congrès pour l'Avancement des Études de Stratigraphie et de Géologie du Carbonifère, Volume 3: Maastricht, Ernest van Aelst, p. 745–752.

Ward, P.D., Montgomery, D.R., and Smith, R., 2000, Altered river morphology in South Africa related to the Permian-Triassic extinction: Science, v. 289, p. 1740–1743, doi: 10.1126/science.289.5485.1740.

Wnuk, C., 1996, The development of floristic provinciality during the middle and late Paleozoic: Review of Palaeobotany and Palynology, v. 90, p. 5–40, doi: 10.1016/0034-6667(95)00022-4.

Ziegler, A.M., Hulver, M.L., and Rowley, D.B., 1997, Permian world topography and climate, *in* Martini, I.P., ed., Late glacial and post-glacial environmental changes—Quaternary, Carboniferous-Permian and Proterozoic: New York, Oxford University Press, p. 111–146.

Manuscript received 20 August 2005
Revised manuscript received 25 November 2005
Manuscript accepted 5 December 2005

Printed in USA