

R. L. Smith, that present a significant comparison and contrast with Irvine's study of mafic systems; there is no discussion of high-temperature rheology of the earth's mantle (a planned summary of the subject was prevented by the death of C. Goetze) or of diapir and plume mechanics elucidated by studies by B. D. Marsh, M. Parmentier, and others; and there is no modern assessment of the chemical, mineralogical, and density structure of the source regions for magmas as inferred from both geophysical and geochemical data.

Nonetheless, the breadth and quality of the papers that are included make the book a valuable addition to the bookshelves of geologists, petrologists, geophysicists, and geochemists. The volume should inspire an increase in interdisciplinary emphases in both teaching and research on the origins of magmas and magmatic processes.

THOMAS L. WRIGHT

U.S. Geological Survey,
Reston, Virginia 22092

Tetrapod Origins

The Terrestrial Environment and the Origin of Land Vertebrates. Proceedings of a symposium, Newcastle upon Tyne, England, April 1979. A. L. PANCHEN, Ed. Published for the Systematics Association by Academic Press, New York, 1980. xii, 634 pp., illus. \$87.50. Systematics Association Special Volume No. 15.

The origin of tetrapods has been a subject of debate since the discovery of the first lungfish in 1837. Although the arguments have evolved in response to expanding knowledge of fossil and Recent forms, crossopterygians generally have been considered to be the most likely ancestors to tetrapods. This view has been promulgated thoroughly in textbooks, and there it might have remained as dogma had it not have been for the appearance of Willi Hennig's *Grundzüge einer Theorie der phylogenetischen Systematik* in 1950. The full impact of Hennig's novel approach to the evaluation of homologies (dubbed "Hennig's principle" by Brundin in 1966) did not reach the community of English-speaking systematic biologists until a translation of the book (*Phylogenetic Systematics*, University of Illinois Press) appeared in 1966. A new generation of systematists has since surfaced—the cladists, armed with a new philosophical tool to assess phylogenetic problems. The most significant outcome of this systematic upheaval is the renewed interest in old problems

and the animated disagreements that have arisen. The coup is far from complete, as is evidenced by this volume with the vigorous defense of pre-Hennigian systematics by Westoll and Panchen in contrast to the approaches of Patterson, Gardiner, and others.

Patterson and Gardiner resurrect the pre-Darwinian theory that dipnoans are the closest relatives of tetrapods. In defense of this thesis, Patterson applies Hennigian principles to his evaluation of schemes of tetrapod relationships that have been proposed since 1840; this is a synoptic version of the more extensive discussion by Rosen, Forey, Gardiner, and Patterson (*Bull. Am. Mus. Nat. Hist.* 167, 159–267 [1981]). Patterson recapitulates the weaknesses of the most widely used approach, the search for ancestors, and points to the advantages of cladistic diagrams—that is, "their clarity and the ease with which they may be criticized" (p. 169).

A reader who is inclined to criticize will find ample opportunity in Gardiner's paper, "Tetrapod ancestry: a reappraisal." Gardiner bases his scheme of relationships on only a few characters, and of these some are wrong and others inconclusive. For example, true Westoll lines occur only in lungfishes. They are unknown in osteolepidids, panderichthyids, and tetrapods; yet Gardiner claims the presence of Westoll lines in these groups to be an advanced character shared with lungfishes. Moreover, Gardiner homologizes the paired bone I of lungfishes with postparietals in tetrapods; at the same time he homologizes the median bone B of lungfishes with the unpaired postparietal of *Ichthyostega*, an Upper Devonian tetrapod. Thus of the three parietal bones possessed by lungfishes, one is shared with *Ichthyostega* and the other two with all other tetrapods, according to his reasoning. For a more satisfying and complete discussion of the lungfish-tetrapod relationship, the reader is referred to Rosen *et al.* (1981, cited above).

In a volume of this distinction and diversity, it is disappointing that the "prologue" is not a more expansive philosophical dialogue. In it Westoll condemns Hennigian methodology in favor of a "paleontological approach" to the ancestry of tetrapods (see Patterson, *Syst. Zool.* 29, 216–219 [1980], for related commentary). The two approaches need not be totally exclusive of one another, however. The study of "detailed comparative anatomy" and the "consideration of variation within and between subgroups" of fossils (Westoll, pp. 2–3) are the first steps of a cladistic

approach as well as of a "paleontological" one, because first one must identify the characters—that is, the homologies. The philosophical dichotomy emerges in the methods of evaluating these homologies. Correctly applied, the Hennigian approach seeks to assess the validity of every apparent homology by whatever data possible. In contrast, the "paleontological approach" described by Westoll precludes the application of data from comparative anatomical studies and functional analyses of Recent forms to the study of fossils because "much of the material is skeletally incomplete and where even the best material gives negligible information about any structures or functions not affecting the skeleton directly (as by foramina for nerves or vessels, or muscle insertions), is clearly less precise by orders of magnitude." Instead, Westoll advocates reliance on the time sequence of the appearance of fossils and continued search for new material to solve questions of relationship. In this regard, it is unfortunate that Patterson, in his paper "Origin of tetrapods: Historical introduction to the problem," dismisses the fossils, even though the Upper Devonian lungfish *Griphognathus* is critical to the lungfish-tetrapod relationship argument. On the other hand, Janvier ("Osteolepid remains from the Devonian of the Middle East, with particular reference to the endoskeletal shoulder girdle") uses cladistic methodology to generate a scheme of relationships that is favored by Westoll.

The significant suite of characters shared by osteolepidid crossopterygians and tetrapods is not addressed directly, although Janvier, Rackoff, and Holmes provide additional information on the pectoral girdle and limb that favors such a relationship. The tympanum, often considered to be a common feature among all tetrapods, is shown by Carroll to be derived independently in different groups. Carroll's conclusions are supported by the results of the extensive study by Lombard and Bolt (*Biol. J.* 11, 19–76 [1976]).

Nearly a quarter of the contributed papers are reviews of various tetrapod groups based on cladistic analysis. The classifications that have been extracted from these cladograms provide a focus for the attention of non-Hennigian systematists. The new nomenclature that follows from such reassessments frequently is unfamiliar and therefore uncomfortable for many scientists. For example, the term "Batrachosauria" applied to a group of amphibians by Panchen becomes identical with the Reptilia of Heaton. At the same time, the Sey-

mouriamorpha once again are the closest relatives of all other reptiles by virtue of their inclusion with the cotylosauria, the "stem-reptiles." Moreover, it is patently illogical to define reptiles as "tetrapods that produce amniotic eggs, but which have not developed feathers or mammary glands" (p. 541) and place them as an order within the class Amphibia when the latter is in turn defined as "tetrapod gnathostome vertebrates that have not developed extraembryonic (amniotic) membranes in the egg" (p. 540). Opposition to such changes and the confusion that follows is to be expected. Still, we must be cautious in our reluctance to accept the changes—are we opposed to the analytical methodology that generated them, or merely to the changes themselves?

"Stratigraphical order of the fossils, and consideration of environment and mode of life," in Westoll's phrase (p. 3), are accessory to the formulation of a hypothesis of relationships. They are useful adjuncts only insofar as they "can be deduced from geological record." The latter reservation is especially relevant in the case of papers on Upper Paleozoic continental distribution, Carboniferous geography, early land floras, and invertebrate terrestrial faunas and those that deal with the ecology of the flora and vertebrate fauna. Each of these contributions attempts to formulate a historical picture extrapolated from our understanding of the Recent—understanding that, in some cases, is based on examination of museum collections more than a century old. The exercise demands caution. The coincidence or non-coincidence of fossil forms in the geological record and the sedimentological context in which they occurred are matters of inference. The conclusions become all the more tenuous when dependent on a description of a 200- to 400-million-year-old habitat that necessarily has been derived from our knowledge of the ecological requirements of Recent forms. I heartily agree with the spirit of Scott's statement that "the interpretation of ecology from botanical structures can be very misleading and perhaps even dangerous" (p. 93). Thomson provides a parallel example relating to extrapolation of faunal characteristics on the basis of sedimentology. Although earlier he favored freshwater occurrence of crossopterygians in the Upper Devonian (*Biol. Rev.* 44, 132–133 [1969]), he now tends to accept even a marine (coastal) origin of tetrapods based on the distribution patterns of the first Upper Devonian tetrapods and the co-occurring fishes. Despite these reservations, the compilation

of paleogeography, flora, and fauna is the most valuable part of this volume; it provides a broad picture reflecting the present interpretations of the terrestrial environment of the Upper Paleozoic. A reader who looks at this volume for a definitive discussion of the origin of tetrapods will be misled.

HANS-PETER SCHULTZE
*Museum of Natural History,
University of Kansas, Lawrence 66045*

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