

## REVIEWS AND COMMENTS

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LUNGFISHES, TETRAPODS, PALEONTOLOGY, AND PLESIOMORPHY. By D. E. Rosen, P. L. Forey, B. G. Gardiner and C. Patterson. 1981. Bulletin of the American Museum of Natural History 167:159-276, \$6.80.—Donn Rosen and his co-authors have produced a monograph of major significance for ichthyologists and students of vertebrate evolution. In this paper they challenge both the current belief that the rhipidistian fishes are ancestral to land vertebrates, and the practice of turning to *Eusthenopteron* and its supposed close relatives for information on selective forces and adaptive morphological changes associated with the origin of tetrapods. The text of the paper is divided into two parts. The first part is a historical analysis and introduction to the problem of lungfish relationships. The authors ask: How is it that pre-Darwinian morphologists had a clear understanding of the problem posed by the lungfishes, but with the acceptance of a theory of evolution in the late nineteenth century, the lungfishes were neglected and the rhipidistians ascended to the position of presumed tetrapod ancestry? What role did fossils and the paleontological predilection for searching for (and finding) ancestral morphotypes play in the analysis of lungfish relationships? These questions are considered in detail and I will return to them below.

The second section of the monograph is a review of many features of lower vertebrate anatomy with the aim of establishing the phylogenetic position of the lungfishes (Dipnoi) vis à vis *Eusthenopteron*, porolepiforms, tetrapods, coelacanths and other primitive gnathostomes. The author's conclusions are at considerable variance with the traditional view taught in courses on chordate biology and vertebrate paleontology. The lungfishes are hypothesized to be the primitive sister group to the tetrapods, the coelacanths the sister group of this lineage, while *Eusthenopteron* is relegated to the position of primitive sister group to this entire assemblage, the Sarcopterygii. Along the way, Rosen et al. argue that lungfishes have a true choana (thus Dipnoi plus Tetrapoda = Choanata), that

*Eusthenopteron* does not, that the rhipidistians are not monophyletic, and that the numerous traditional features (such as limb structure) used to link rhipidistians with tetrapods are either 1) primitive, 2) spurious or 3) convergences. These are claims of some significance. Either the textbooks will have to be rewritten, or Rosen et al. are wrong.

Fortunately, there is a way to decide: examine the characters they used to produce the new phylogenetic arrangement, look for new characters, and test their hypothesis. And this is exactly what future discussion of this monograph should focus on—what are the characters and which groups do they define? There doubtless will be many who will find fault with aspects of the phylogenetic analysis, but unless a more parsimonious phylogeny than that of Rosen et al. is produced, it will be difficult to conclude that *Eusthenopteron* has, indeed, much to do with tetrapod ancestry.

My own reservations about the phylogenetic analysis fall into three categories, but in no case is the final hypothesis changed with respect to the lungfishes and rhipidistians: 1) using the available characters at inappropriate hierarchical levels, 2) using characters in the cladogram that are unsupported in the text and 3) not clearly distinguishing on the cladogram characters observable only in living forms and thus uninformative with respect to the phylogenetic position of fossils. The position of fossil taxa thus looks more corroborated than it really is.

1) Consider the position of the Acanthodii which Rosen et al. place as the primitive sister group of chondrichthyans plus osteichthyans. As evidence they present one character: the "complex endoskeletal support of the paired appendages consisting of a metapterygial axis and radials articulating with the metapterygium and girdle." This excludes the Acanthodii from the Chondrichthyes plus Osteichthyes lineage. But earlier (p. 203) they admit that "... all that is known about endoskeletal fin supports is that in *Acanthodes bronni* the pectoral fin has a few small nodules arranged irregularly at the fin base (Miles, 1973)." Whether the character is appropriate to the Chondrichthyes plus Osteichthyes or to a more inclusive gnathostome clade including the Acanthodii cannot be de-

cided on present evidence. Actually, there are other characters which place *Acanthodes* as the sister group to the Osteichthyes: the presence of dermal sclerotic bones (Moy-Thomas and Miles, 1971), an interhyal bone (Gardiner, 1973:129), branchiostegal rays present and ossified dermal plates covering the gills laterally. Acanthodians thus share two or possibly three (the pneumatic organ) characters used by Rosen et al. as synapomorphies of the Osteichthyes.

2) As an example of a character used in the cladogram that is unsupported in the text, consider the operculum. It appears that a homology is postulated between the endochondral "operculum" of amphibians (embryologically derived from the otic capsule) and the gill cover in lungfishes (p. 258), but no discussion is ever provided of this point. A second case concerns gill arch structure. Character 37, "last gill arch articulates with base of preceding arch rather than with basibranchial," is used to unite coelacanths, lungfishes and tetrapods (=Sarcopterygii) into a monophyletic assemblage excluding *Eusthenopteron*. But the figure of *Eusthenopteron* gill arches (Fig. 48A) reveals that the proximal articulation of ceratobranchial four is unknown. Other workers may wish to question the hypothesized limb rotation of lungfishes, coelacanths and tetrapods and the conclusion that the forelimb and hindlimb are "180° out of phase."

Finally, 3), characters 35, 40 and 41, used (among others) to exclude *Eusthenopteron* from the Sarcopterygii, are features that can only be observed in living forms: a rostral organ, an inferior vena cava and a pulmonary vein. "Tetrapodous locomotion" (character 47) is used to relate dipnoans to primitive tetrapods. While I accept these characters as being indicative of relationship among living groups, it is somewhat misleading to imply that they exclude *Eusthenopteron* from the Sarcopterygii since we are not able to determine if the characters were indeed present. All in all, I would have preferred the character coding method used by Patterson (1977) for indicating which characters above a particular branch point are known from living forms, and which from fossils.

As a final point, a case of character omission occurs in the lower jaw. On page 177, the structure of the mandible is listed as being a feature cited by Westoll (1943) relating rhinidistians to tetrapods and we are promised that the "...

main task in this paper is to review the characters listed above . . . ." But no further mention is made of the mandible.

Despite these reservations, the final cladogram seems robust and some very important conclusions emerge. *Polypterus* is corroborated as a member of the Actinopterygii, and perhaps this paper and that of Patterson (1982) will lay to rest the speculation about *Polypterus* as a sarcopterygian or "brachiopterygian." The porolepiforms are corroborated as a monophyletic assemblage (Gardiner, 1980). Most importantly, the features of the *Eusthenopteron* limb previously believed to indicate relationship with tetrapods are shown to be more primitive (i.e., shared also with coelacanths and lungfishes) and thus indicative of relationship at a more general hierarchical level. Rosen et al. succeed in demonstrating the tetrapod-like nature of the paired appendages in lungfishes and in precisely defining the pattern *Eusthenopteron* shares with the Sarcopterygii: "An exclusively metapterygial pectoral and pelvic fin (loss of all radials anterior to base of metapterygium) supported by a single basal element . . ." (character 24, p. 256).

Now that a corroborated phylogenetic hypothesis has been obtained, what do we do with it, and why has it taken so long for morphologists to recognize the similarities between lungfishes and tetrapods as homologies? Rosen et al. provide an answer to the latter question. Acceptance of a theory of descent with modification obviated the need to characterize the relationships of lungfishes by derived features. The lungfishes were intermediate between "fishes" and amphibians. As Patterson (1980) noted, "With the acceptance of evolution and of a taxonomy of ancestry and descent, the problem that Owen and Bichoff had argued about—how tetrapods are characterized, and whether lungfishes belong with them—simply disappeared." This monograph will have the enormously beneficial effect of returning the arguments about tetrapod ancestry and lower gnathostome relationships to a discussion of characters. How are the major clades defined, are they monophyletic, and at what levels are many of the traditional characters actually indicative of relationship?

As for the usefulness of this hypothesis of gnathostome relationships in resolving other issues, consider the scenario of tetrapod limb origin suggested by Andrews and Westoll

(1970). They proposed (p. 310) that "the tetrapod limb may have been caused to evolve by the combination of a specialized habit of life in water, because of population pressure or as an escape from predators, or perhaps for several reasons." It is difficult to see how any observed pattern of structure in the fossil record could be used to test this hypothesis, but Andrews and Westoll do hypothesize a sequence of structural changes in the limb. By "reconstructing" the ecology of *Eusthenopteron*, they derive from a process-level theory a series of predictions about the sequence of morphological change. "Whereas the need for maneuverability between weeds and in confined spaces in water may have caused the loss of the lepidotrichia (as suggested by Eaton) and also the changes in the shape of the glenoid and (more doubtfully) the elbow, it is most unlikely that it would have caused the development of the carpal joint. It is felt that this would only have developed in response to walking on land and bearing weight near the ends of the appendages." Finally they note, "... most probably, the changes in the proportions of the bones of the shoulder girdle took place last of all, at about the stage shown by *Ichthyostega*."

By providing us with a phylogenetic hypothesis on which the structural features of the forelimb are superimposed, Rosen et al. enable us to test this hypothesis of Andrews and Westoll. It appears from the cladogram that the changes in the shoulder girdle elements took place first; and the Andrews and Westoll "weed ecology hypothesis," proposed to account for the evolution of those structures in the limb used by *Eusthenopteron* for locomotion in confined spaces, fails to explain their presence also in lungfishes and coelacanths. In short, this cladogram of lower gnathostome relationships (a hypothesis of pattern), refutes the current process/scenario explanation of how, and why, the tetrapod limb developed. In fact, because of the distribution of the morphological features described by Rosen et al., the Andrews and Westoll hypothesis is refuted even if lungfishes are not the sister group to tetrapods.

The value of this monograph lies not only in its novel hypothesis of lungfish relationships (about which there will no doubt be considerable argument), but also in providing a test of current adaptive morphological explanations of tetrapod limb origins, a test these explanations fail. In this paper we have a case study of how

a priori process theories can obfuscate the search for patterns of structure, patterns that are needed to reconstruct the history of life as well as to test alternative causal explanations.

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