

REVIEWS AND COMMENTS

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THE BIOLOGY AND PHYSIOLOGY OF THE LIVING COELACANTH. Edited by J. E. McCosker and M. D. Lagios. 1979. Occasional Papers of the California Academy of Sciences 134, 1-175, \$10.00.—When T. S. Westoll noted in 1960 that the main outlines of vertebrate evolution have been relatively well established, he could not have foreseen the current controversies over the relationships of most major primitive chordate lineages which call into question some of our cherished beliefs about the pattern of vertebrate evolution. The Cyclostomes, once believed to be a monophyletic lineage, now appear to be diphyletic (Hardisty, 1979) with lampreys more closely related to gnathostomes than to hagfishes. The acanthodians, hypothesized to be teleostomes by Miles (1973, 1977), Romer (1966) and Wiley (1979), have been related to elasmobranchs by Jarvik (1977). Rhipidistians appear to be polyphyletic (Andrews, 1973) and lungfishes, generally considered now to be the closest living relatives of tetrapods, have been relegated to the position of primitive sister group to coelacanths plus actinopterygians plus choanates by von Wahlert (1968).

The coelacanths, long considered to be crossopterygians (Romer, 1966) have not been immune from the upheaval in primitive vertebrate relationships, as this volume edited by McCosker and Lagios demonstrates. At least three different views on the relationships of coelacanths are presented: Lagios considers coelacanths to be related to chondrichthyans; Wiley hypothesizes that coelacanths form the primitive sister group of actinopterygians, dipnoans and choanates; and Compagno links the coelacanths with the rhipidistians.

These views on coelacanth relationships are presented with other papers on biochemistry and protein evolution in primitive fishes all of which formed the basis for the AAAS symposium in 1977 on "Relationships of primitive fishes, with particular reference to the coelacanth." This volume includes two introductory papers of historical interest, one by M. Cour-

tenay-Latimer describing her discovery of the first coelacanth, and a paper by Margaret Smith recounting the influence of the coelacanth on the course of African ichthyology. McCosker then summarizes the limited information on the natural history of the coelacanth (most have been caught at depths between 50 and 400 m), discusses the results of stomach contents analyses, and discusses the interesting hypothesis that *Latimeria* may be found in association with submarine freshwater aquifers. A useful update of the coelacanth capture list providing data for C70 through C88 is also included. Other work on coelacanth biology includes that of Griffith and Pang on osmoregulation, Rasmussen on the composition of ventricular and notochordal fluids, Miller on mineralized tissues, and Lombardini et al. on intracellular osmoregulation. Summaries of cytogenetic data, growth hormones and creatine kinase isozyme evolution encompass a broader comparative range including most primitive vertebrate lineages.

Lagios' paper on the coelacanths and Chondrichthyes as sister groups (a view also championed by Løvtrup, 1977) is perhaps the sharpest contrast to traditional views of coelacanth relationships. Lagios bases his hypothesis on four sets of characters: the pituitary complex, the rectal gland, the physiology of urea retention and pancreatic morphology. The Chondrichthyes and coelacanths apparently share an anterior extension of the ventral lobe of the pars distalis of the pituitary complex which receives its blood supply from the internal carotid arteries. The rectal glands of coelacanths and elasmobranchs are also very similar in gross morphology, relationships to the rectum and histology. The retention of urea in the blood and tissues to attain equal osmolality with seawater is another feature common to chondrichthyans and coelacanths as is a specialized tubular structure of the islets of Langerhans in the pancreas. Lagios concludes that "... recent paleontologic reappraisal has demonstrated that features once considered synapomorphic, thereby uniting the coelacanth with the extinct Rhipidistia, are in fact plesiomorphic characters" and that "... the coelacanth ... probably

represents an archaic sister group to the Chondrichthyes—or briefly, a paleozoic shark-like fish.” If such a reappraisal exists, I am unaware of it.

Wiley, Griffith and Pang, and Compagno all take issue with the hypothesis of Lagios and attempt to refute it both by listing numerous characters which contradict it and by showing that the supposed shared features between coelacanths and chondrichthyans are not homologous. Griffith and Pang note the presence of urea retention in many other vertebrates (lungfishes, anurans, some primitive actinopterygians) and point out that although urea is retained in both coelacanths and chondrichthyans, the mechanism of retention and blood ionic composition relative to sea water is very different in the two groups. They further argue that the ovoviparous reproductive mode is tied to the phenomenon of urea retention because of problems faced by embryos in retaining urea. Relatively high surface area in embryos promotes urea loss and may necessitate retention of the embryos within the body of the adult until a larger size is reached. Thus, if internal fertilization is tied to urea retention, and internal fertilization is not primitive for vertebrates, then urea retention like internal fertilization must have evolved independently in sharks and coelacanths.

The rectal gland similarity is disputed by Wiley who notes that rectal glands are absent in holocephalans and this character thus indicates that elasmobranchs and *Latimeria* are more closely related to each other than either is to holocephalans. The pituitary structure similarities are hypothesized to be primitive as *Polypterus* shares several attributes of the elasmobranch and coelacanth structure, and other synapomorphies (such as those postulated by Løvtrup, 1977) are either primitive for gnathostomes (gray matter patterns, presence of Mauthner cells) or have yet to be investigated comparatively.

Wiley and Compagno both present alternative hypotheses of coelacanth relationships which they feel are better corroborated than that of Lagios. Compagno supports what I will consider to be the “traditional hypothesis” (Romer, 1966) in which the coelacanths and rhipidistians (Crossopterygii) are the sister group of the lungfishes, while the actinopterygians are the sister group of the lungfishes and crossopterygians together (=Sarcopterygii). Wiley (based on five characters) supports an alterna-

tive in which the actinopterygians form the sister group of the dipnoans and tetrapods with the coelacanths comprising the sister group of that assemblage. Elsewhere, I have supported yet another hypothesis (Lauder, 1980; Liem and Lauder, 1980), that of Miles (1977), (also see the cladogram of Dingerkus, p. 125 this volume) in which the coelacanths are the sister group of the dipnoans plus tetrapods. This hypothesis, the views of Wiley, Compagno, Griffith, and the traditional hypothesis are all in agreement in including the coelacanths within the Osteichthyes, thus excluding the possibility of chondrichthyian relationships. The evidence for this includes the presence of ventral and lateral cranial fissures, medial insertion of the adductor mandibulae muscle on the lower jaw (Lauder, 1980), structure of the hyoid and gill arches, dermal bones of the palate, braincase, opercular series, lower jaw, shoulder girdle, upper jaw and skull, presence of a swimbladder, lepidotrichia, dorsal ribs, imbricating scale rows, presence of both endochondral and perichondral bony ossifications [see summaries by Compagno, Wiley, Miles (1977), and Liem and Lauder (1980)]. Thus over 30 characters place the coelacanths within the Osteichthyes and refute the hypothesis of chondrichthyian relationships.

There are a number of other characters, some only recently discovered, that contradict the hypothesis of Wiley (1979, and this volume). Coelacanths, dipnoans and tetrapods share the presence of a posterior vena cava (Lauder, 1979; Millot and Anthony, 1978) which is a modification of the primitive pattern of venous return to the heart. This vessel is a dominant feature of the venous system in coelacanths, lungfishes and tetrapods and to my knowledge no other group possesses a comparable modification. Other characters uniting coelacanths, dipnoans and tetrapods into a monophyletic group include the presence of true enamel in the teeth (Smith, 1978; Miller, this volume) and a double articulation of the hyomandibula with the neurocranium. Liem and Lauder (1980) and Compagno list other characters supporting a monophyletic Sarcopterygii. Characters uniting the Dipnoi and Tetrapoda into a monophyletic assemblage include the presence of cosmine, the presence of a supraotic cavity in the cranium (Miles, 1977), multiple pharyngoclaviculari muscles (Wiley, 1979), and numerous features of the circulatory system (Gardiner, 1973).

The hypothesis supported above is in conflict with the traditional hypothesis only in so far as the relative positions of the coelacanth and lungfishes are concerned. The traditional hypothesis is based on the intracranial joint as a synapomorphy excluding dipnoans from choanate relationship, and the homology of the intracranial joint between rhipidistians and coelacanth has been extensively questioned recently (Bjerring, 1973, 1978; Miles, 1977; Wiley, 1979). The ventral otic fissure, the ventral part of the intracranial joint (Gardiner and Bartram, 1977), appears to be primitive for teleostomes while the anatomical relationships of the dorsal aspect of the intracranial joint appear to be different in coelacanth and rhipidistians (Wiley's article, p. 64 in this volume, for a summary of evidence). The other alternative, Wiley's hypothesis, requires independent derivation of several characters including a posterior vena cava and tetrapod-like enamel. In summary, the evidence strongly supports inclusion of the coelacanth in the Osteichthyes and indicates that *Latimeria* is most closely related to dipnoans and tetrapods.

This volume on the biology and physiology of coelacanth provides an important stimulus to future work on the relationships of the actinists. While I find the hypothesis of Lagios unconvincing, it is clear that coelacanth share several interesting features with elasmobranchs that bear further investigation. The existence of several competing hypotheses of coelacanth relationship within the Osteichthyes will ensure a stimulating and lively debate over the next decade which will undoubtedly see major advances in our understanding of the pattern of gnathostome diversification.

LITERATURE CITED

- ANDREWS, S. M. 1973. Interrelationships of crossopterygians, p. 137-177. *In: Interrelationships of fishes.* P. H. Greenwood, R. S. Miles and C. Patterson (eds.). Academic Press, London.
- BJERRING, H. C. 1973. Relationships of coelacanthiforms, p. 179-205. *Ibid.*
- BJERRING, H. C. 1978. The "intracranial joint" versus the "ventral otic fissure." *Acta. Zool.* 59:203-214.
- GARDINER, B. G. 1973. Interrelationships of teleostomes, p. 105-135. *In: Interrelationships of fishes.* P. H. Greenwood, R. S. Miles and C. Patterson (eds.). Academic Press, London.
- GARDINER, B. G., AND A. W. H. BARTRAM. 1977. The homologies of the ventral cranial fissures in osteichthyans, p. 227-245. *In: Problems in vertebrate evolution.* S. M. Andrews, R. S. Miles and A. D. Walker (eds.). Academic Press, London.
- HARDISTY, M. W. 1979. *Biology of the cyclostomes.* Chapman and Hall, London.
- JARVIK, E. 1977. The systematic position of the acanthodian fishes. *In: Problems in vertebrate evolution.* S. M. Andrews, R. S. Miles and A. D. Walker (eds.). Academic Press, London.
- LAUDER, G. V. 1979. Review of *Anatomie de Latimeria chalumnae*, Tome III. *Copeia* 1979:560-562.
- . 1980. On the evolution of the jaw adductor musculature in primitive gnathostome fishes. *Breviora* (in press).
- LIEM, K. F., AND G. V. LAUDER. 1980. The evolution and interrelationships of the actinopterygian fishes. *In: Fish neurobiology and behavior.* R. Davis and R. Glenn Northcutt (eds.). University of Michigan Press.
- LOVTRUP, S. 1977. *The phylogeny of the vertebrata.* John Wiley and Sons, New York.
- MILES, R. S. 1973. Relationships of acanthodians, p. 63-103. *In: Interrelationships of fishes.* P. H. Greenwood, R. S. Miles and C. Patterson (eds.). Academic Press, London.
- . 1977. Dipnoan (lungfish) skulls and the relationships of the group: a study based on new species from the Devonian of Australia. *Zool. J. Linn. Soc.* 61:1-328.
- MILLOT, J., J. ANTHONY AND D. ROBINEAU. 1978. *Anatomie de Latimeria chalumnae*, Tome III. Editions C.N.R.S., Paris.
- ROMER, A. S. 1966. *Vertebrate paleontology.* University of Chicago Press, Chicago.
- SMITH, M. M. 1978. Enamel in the oral teeth of *Latimeria chalumnae*: a scanning electronmicroscope study. *J. Zool., Lond.* 185:355-369.
- VON WAHLERT, G. 1968. *Latimeria und die Geschichte der Wirbeltiere. Eine evolutions biologische Untersuchung.* Gustav Fischer Verlag, Stuttgart.
- WESTOLL, T. S. 1960. Recent advances in the paleontology of fishes. *Liverpool Manch. Geol. J.* 2:568-596.
- WILEY, E. O. 1979. Ventral gill arch muscles and gnathostome phylogeny, with a new classification of the Vertebrata. *Zool. J. Linn. Soc.* 67:149-179.
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INLAND FISHES OF WASHINGTON. By Richard S. Wydoski and Richard R. Whitney. 1980. University of Washington Press, Seattle and London, xxxii, 220 pp. illus. \$8.95 paper, \$17.50 hardbound.—This book contains most of the elements one expects in a state fish book: