

REVIEW:

THE STRUCTURE, DEVELOPMENT AND EVOLUTION OF REPTILES

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PROFESSOR ANGUS D'ALBINI BELLAIRS Festschrift Volume.

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This thick volume, hardbound under an elegant blue cover with gold lettering, is offered under the usual good publishing standards expected from Academic Press. Even though my own copy had no cover jacket and perhaps suffered from some very minor over inking, making some drawings and photographic plates a little bit too dark, the overall publishing and printing quality is, by and large, excellent.

After the usual general introductory materials, the Introduction chapter itself, by the Editor, Professor M. Ferguson (Manchester) is a lively and informative sketch of Professor d'A. Bellair's career, with many humorous and thought-provoking hints on academic life, past and present. The main content of the book is formed by no less than 27 specialised papers, most of them single-authored. They are arranged under five general themes, forming large chapters or sections, which are successively: Morphology (six papers), Development (six), Physiological Ecology (seven) and Evolution (seven). This provides a sensible framework within which the diversity of the papers could be arrayed, although several papers could easily have been shifted, on logical grounds and content, from one section to another. Such a situation is, to this reviewer, very diagnostic of the current state of the art and trends in Vertebrates Evolutionary Biology, and more will be said on that later.

Because it would not be realistic to try to review uniformly all and every paper in the book, no apologies are due for a more in-depth analysis of some papers than of others, depending on the reviewer's interests and expertise. This admittedly subjective analytical treatment will be balanced, to some extent, by overall synthetic comments on the book as a whole at the end of the review.

Study of the 'Slide-pushing' locomotion, recognised by Carl Gans (Ann Arbor, USA) as a new locomotory process among elongate Squamates, opens the section on morphology. This paper is a clear, concise addition to our knowledge of limbless locomotion.

The study of anterior limb skeleton and musculature in *Varanus* in relation to sprawling gait, by J. M. F. Landsmeer (Leiden, The Netherlands) is an excellent example of the usefulness and relevance of good "classical" anatomy for functional and evolutionary morphology, a fact perhaps too often forgotten in more "fashionable" (i.e. electromicrographic) approaches.

The next paper, by E. N. Arnold (London, England) deals with characters of cloacal and hemipenial musculature among lizards. This paper shows beautifully how the careful comparative study of a complex system can produce important data for the study of relationships. This paper also offers an admirable example of a soft, diplomatic, "cryptoclaicism". While the methodology of inferring relationships is definitely pervaded by a cladistic approach, the paper is "careful" not to offer even one cladogram and rather forcefully concentrates on good empirical data gathering and descriptions.

Next comes a paper by P. C. H. Pritchard (Maitland, Florida, USA) on piscivory of turtles and evolution of long-necked Chelidae. This work offers an interesting methodological contrast with the preceding one.

The Squamate epidermis, as explained in the next paper by P. F. A. Maderson (New York, USA) appears to be an excellent model system for the study of epithelial tissue homeostasis. This most stimulating paper, in fact, brings together many cytological, developmental, physiological and natural history data into mutual interaction, to propose a new synthetic view of squamate skin biology.

The next paper, by R. Presley (Cardiff, Wales) on the problems of tympanic membrane homology closes the section on morphology. Here, Presley offers us, from the point of view of descriptive embryology, a truly admirable piece of work where careful divisions between "Epistemological", historical, descriptive and interpretative sections allows the reader to find its way between Charybde's *anlagen* and Scylla's controversies.

More generally, thanks to works such as this one, it is perfectly clear how and why the good tradition of descriptive, detailed, developmental embryology should be kept alive and healthy within modern evolutionary Biology. Indeed, how could we do without it? Wouldn't it be a good thing for the Universities to keep this beautiful field of knowledge and research alive, even if it is contemptuously labelled a "traditional" one by some potent ignorants?

Section Two, on development, opens with a paper by B. K. Hall (Halifax, Canada) on developmental processes underlying the evolution of cartilage and bone.

The richness of his contribution precludes detailed analysis and comments; it deals especially with the

problems of secondary cartilages, metaplastic bone and (secondary) epiphyseal centres among reptiles. If I fully agree on the all-important issue of timing shifts of developmental processes as a key mechanism in skeletal evolution, I am not fully convinced by the author's contention that reptiles lack secondary cartilages (they appear to be "already" developed among some osseous fishes) and that "reptilian periosteum have limited osteogenic ability".

The next two contributions, one by K. Murreoka and S. Bryant (Irvine, USA) on regeneration and development of vertebrate appendages on the one hand, and the one on pattern formation during development of amniote limbs by L. S. Honig (Los Angeles, USA), on the other, can be treated together. Both papers deal with experimental embryology of vertebrate limbs, the first paper focussing mainly on amphibians, the second one on amniotes, including some reptiles. Elegant experimental approaches, combined with new conceptual frameworks, have both contributed significantly to the recent advances in this fascinating field. But how do cells appear to "know" what they "have to do" at the "right" time and places? This all-important issue of developmental biology is far from settled, as evidenced by these lucid and up to date papers. How relevant and useful the limb development regeneration models are to address the issue meaningfully is also made quite obvious here.

Professor M. Fergusson's paper on craniofacial development in Alligators is the next contribution. This big paper summarises nearly 10 years of work and the author's PhD Thesis. Starting with problems of cleft palate malformations among mammals (a problem with obvious medical and social importance), he went on to realise that the crocodylian secondary palate could be used as a most satisfactory model to understand normal and pathological palate morphogenesis. This, in turn, led to an intensive research project on crocodile development and growth, in order to fully master the model's characteristics. These efforts have been successful enough to push the crocodylians from a position of poorly-known reptiles, as far as development was concerned, to the status of a well standardised, operational model for modern development biology, a not inconsiderable achievement. Fergusson's paper gives much new information on normal and pathological developments of palatal regions and related structures. Although photographic illustrations are numerous and adequate, I would have liked to find some line drawings, for an easier follow up of the descriptions.

The next paper, on amelogenesis in Reptilia and evolutionary aspects of enamel gene products, is co-authored by six scientists, including H. C. Slavkin (Los Angeles, USA) and M. Fergusson. It is perhaps one of the most fascinating papers of the Volume, as it so beautifully blends together the most recent advances of molecular biology and the insights of phylogeny conveyed by the comparative morphologists' tradition. It seems that enamel synthesis is the end result of a single multi-gene family consisting of multiple structural genes coding for enamelin and amelogenin (enamel proteins) throughout the vertebrate phylum, with a high degree of conservation of sequences.

Obviously, much further work of considerable interest is likely to follow.

The last paper in the section on development is a rather short review by K. W. Jones (Edinburgh, Scotland) of the problem of evolution of sex chromosomes in reptiles and mammals, with emphasis on snakes. The paper mainly introduces a model which would account, in evolutionary terms, for the diversity of mechanisms of sex determination within groups, and from one group to another. I have the feeling that the literature coverage, especially regarding the problems of environmental sex determinism among reptiles, is rather on the light side.

The next section, dealing with physiological ecology, starts with an interesting work of G. J. Webb (Kensington, Australia) and A. M. Smith (Canberra, Australia) on sex ratios and survivorship in the Australian freshwater *Crocodylus johnstoni*.

The study seems to me a model of careful naturalist work spanning from extensive field surveys to theoretical computations, *via* histological gonad analysis. It is clear, however, that the "advantages" (if any), in terms of classical selective/evolutionary theories of "epigenetical" sex determinism, still seem far from being clearly understood.

V. Lance's (New Orleans, USA) paper on endocrinology of reproduction in male reptiles seems to me to be a clear, up to date, synthesis review of an interesting problem, much more orientated, however, towards histo-endocrinology than towards physiological ecology itself. My only reservation is that, perhaps, not enough emphasis is put on the relationships between reproductive cycles and the various environmental ones, such as climatic cycles, that male reptiles find in their actual environments.

The next paper, by H. R. Bustard (Alyth, Scotland) reviews the captive breeding behaviour of the gharial. This is part of a major UN and Government of India conservancy project, the aim of which is to save the Ganges gharial from extinction. This lively report is a true piece of natural history, full of practical experiences, political, managerial and ethological. It happily ends with reasonably optimistic prospects for gharial survival.

Thermoregulation, energetics, metabolism and growth are interrelated fields which pervade modern researches on reptiles, and have far-reaching consequences for our understanding of vertebrate evolutionary biology in general. It is thus not surprising that these themes are touched upon by at least five papers, spread under chapters on physiological ecology and evolution.

R. A. Avery's (Bristol, England) paper on the role of thermoregulation in lizard growth, as exemplified by *Lacerta vivipara*, is a case in point. The experiments reported show that thermoregulation *per se* has no influence on growth physiology, growth rates being increased under behavioural thermoregulation only because this allows an increase in food intake. This seems to be a reasonable conclusion but the paper amply demonstrates the difficulties in getting experimental results with good statistical reliability in such kinds of researches.

R. A. Coalson's (New Orleans, USA) contribution, on how metabolic rate and anaerobic glycolysis

determine the habits of reptiles, is an intriguing paper, worth studying in detail. This work encourages controversy as some definitions and physiological interpretations offered would probably not match those used by other specialists.

Next comes a paper on thermoregulation in the Nile crocodile by J. P. Loveridge (Harare, Zimbabwe). It is surprising that this common species among crocodylians had not been subjected to modern analysis in terms of its ecological physiology. This paucity of data is now ending, thanks to these detailed field studies, which bring new results, for instance on the significance of evaporative cooling by gaping.

I have little to comment on F. E. Russell's (Tucson, USA) paper on snake venoms. It seems to me that this paper may be an excellent and helpful general introduction to the subject, notably for clinicians. The paper is deeply pervaded by the author's personal experience and overall humanistic feeling for the subject, rather than being really an in-depth technical-analytical review of it. Some acid comments on the current state of the art "gadgetisation" of research are excellent. I would have liked to find more in-depth discussions in this work on venom chemistry as possibly interesting biochemical "trade marks" of snake phylogeny.

The last section, on evolution, opens with G. Underwood's (London, England) work on scleral ossicles of lizards: an exercise in character analysis. The title of the paper expresses admirably the aim of the work. Explicit statements and formalisation at all steps of the analysis are provided. This kind of approach is exceedingly useful because the procedures, both intellectual and practical, are crystal clear and encourage possible "tests" and discussions. However, I have the feeling that what is *not* explicit in the paper are basic "philosophical" issues on relationships between classifications and phylogeny, between phenetics and cladistics, even if both turn-out to be quantitative; hence, perhaps, an overall feeling of "stoic, lucid, desperation" in the general discussion.

O. Rieffel (Zurich, Switzerland) gives an excellent account on miniaturisation of the lizard skull and on its functional and evolutionary implications. D. B. Norman (Oxford, England) starts the more palaeontological section of the book with an account on cranial morphology and evolution of dinosaurs. This is essentially a progress report which provides, nevertheless, a clear introductory account of the current concepts on interrelationships in this important group. The paper offers one of the very few cladograms found in the whole book.

Next contribution is J. W. Osborn's (Edmonton, Canada) on the evolution of dentitions from reptiles to mammals, with emphasis on tooth attachment. This paper proposes a very detailed evolutionary scenario, trying to encompass the various changes required, starting from a plesiomorphic acrodont, haplodont, polyphriodont dentition, to reach the highly derived thecodont, plexodont diphodont condition found among most mammals. I found some difficulty in following the details encompassed into the numerous, small and complex sketch drawings. Is the task involved in making such detailed evolutionary

scenarios worth the work? I think that, in this actual case, the answer may be yes, because the scenario can be tested. Indeed detailed comparative palaeohistological analyses of teeth and dentigerous bones among the full array of pelycosaurs and therapsids may constitute an effective test of the scenario. It would practically involve, however, at least a several-year full time programme by an experienced palaeohistologist, always provided the material was available.

M. J. Benton's (Oxford, England) paper on the relationships and early evolution of the Diapsida, certainly an up-to-date and useful overview of a most important and complex theme of reptilian phylogeny. An especially original contention of the work is that *no* competition need be invoked to explain the substitution of therapsids by archosaurs from the most prominent terrestrial niches during the mid-upper Triassic.

This very point is taken up as the subject of the next contribution, by A. Charig (London, England), which deals with competition between archosaurs and therapsids during the Triassic, with a review and synthesis of the current theories. In this paper, which is in substantial disagreement with the preceding one by Benton, a competition phenomenon is clearly advocated. Charig's overview is a most interesting and useful one, as it makes the debate clear, proposes a taxonomy of opinions and reviews many contributions.

Last but not least, R. E. H. Reid's (Belfast, Ulster) paper on the histology of dinosaur bone, and its possible bearing on dinosaurian physiology will be commented upon here as it so obviously deals with this reviewer's favourite studies. Dr. Reid with this paper, offers the most modern analytical review of dinosaurian bone histology, with a great number of new and interesting data. To what extent do these new data change the functional interpretations of dinosaur bone histology? Briefly, even though the issue of thermal and metabolic physiology of dinosaurs must remain an open one, I regard Reid's contribution as definitely one of the most careful, reliable and fairly balanced ones published in this "hot" field.

The closing address, by Professor d'A. Bellairs (London, England) deals with the organ of Jacobson, intermandibular connection and evolution of squamates. This paper aptly describes and comments on rather complex structures, which may be importantly involved in discussions on squamate evolution. They are dealt with by Professor Bellairs in his usual pleasant style.

After these analytical comments, some sort of synthetic overview on the book should be finally added. First, it might be felt that the crocodylian part of the book (five papers and relatively more in terms of pages), relative to turtles (one paper) and squamates, is on the heavy side, but this feeling is not warranted and the balance between various topics, and various reptilian groups, is, by and large, a good one. The book will be of interest to all kinds of herpetologists and to biologists more generally.

Second, there is a feeling of healthy excitement and enthusiasm to discover in this book; vertebrate evolutionary biology is fresh and alive, perhaps more so than some other fields of "classical" biology. Especially commended are the apparently good

interrelationships between various approaches devoted to different levels of biological integration. From molecular biology, gene products, genetics and chromosomes through cytology, histology, developmental biology, descriptive embryology, functional and comparative anatomy, physiology, ethology, ecology to systematics, phylogeny and evolution, the whole array of approaches is there, happily cooperating and interacting towards, at the same time, a more precise and a more general understanding of reptilian evolutionary biology.

For the scientists of some countries, where it appears that progress in a given scientific field can be achieved only if other fields are first killed for good, the apparent healthy situation of cooperation and open-mindedness conveyed by the book between various "classical" and "modernist" approaches in Biology will appear as a most refreshing and encouraging hope. But on the gloomy side, and even if, as a Festschrift, and hence dedicated to one outstanding scientist by his friends and former students, I regret that a book of such importance and magnitude has not better

conveyed the truly international aspects of current researches on reptiles. It seems to me hard to believe that major scientific countries like the Soviet Union, Italy, Germany, Spain (which is currently performing a dramatic scientific come back in vertebrate evolutionary biology), South American countries, and many others, not to mention my own, should not have contributed more, at least at the level of cited bibliography, to the exciting content of this book.

To conclude, the Editor, Professor Marc Fergusson should be congratulated for a splendid job well done. This massive volume is a fitting monument dedicated to the scientific and teaching achievements of Professor d'A. Bellairs. It is obviously a "must" for the libraries of all universities, museums and similar institutions actively working in vertebrate evolutionary biology, and not only on reptiles. Shelves should be emptied again, for this magnificent book to secure a place proudly with such classics as C. Gans' *Biology of the Reptilia* and *Morphology and Biology of Reptiles* of B. Cox and . . . A. d'A. Bellairs.

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GARDEN PONDS AS AMPHIBIAN BREEDING SITES IN A CONURBATION IN THE NORTH EAST OF ENGLAND (SUNDERLAND, TYNE AND WEAR)

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ABSTRACT

A survey of the distribution of amphibians was carried out in Sunderland (Tyne and Wear). Five species were present in the area, but *Triturus cristatus* and *T. helveticus* were uncommon. All the amphibian species were declining or apparently extinct in wild ponds. Garden pools were less common than in other parts of England that have already been surveyed, and as a result of the low density of ponds many had not been colonised by amphibians. There was an encouraging number of colonies that had been started by deliberate introduction however. *Rana temporaria* and *T. vulgaris* were the only species that had colonised the ponds to any great extent. Both were found to be very susceptible to fish predation, and mechanisms for surviving in fish ponds are discussed. Another danger was the destruction of garden ponds which was astonishingly common.

INTRODUCTION

It is a well known fact that while amphibian breeding sites have been declining in the countryside, garden ponds have increased in popularity and are becoming important refuges for some species (Mathias, 1974; Beebee, 1979 and 1981; Cooke and Scorgie, 1983). In particular the common frog *Rana temporaria* and the smooth newt *Triturus vulgaris* seem to have been the most successful in this respect, while the common toad *Bufo bufo* has been less adaptable.

The palmate newt *T. helveticus* has also been recorded in garden ponds, although Cooke and Scorgie stated that it was less common in these habitats by virtue of its being most common in areas that are less susceptible to urbanisation. The crested newt *T. cristatus*, however, has not been very successful in colonising this relatively new habitat.

Mathias reported a recent increase in the number of garden ponds being built, while Beebee found that 16.5 per cent of gardens in Brighton had one or more. In Scotland, according to Cooke and Scorgie, the idea