ON THE DEVELOPMENT OF VERTEBRAE IN GYMNOPHIONE AMPHIBIANS

by

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The concept that the living amphibians form a monophyletic group (Lissamphibia) was first examined in detail by Parsons and Williams (1963), who supported this view. Despite the equivocal nature of most of the evidence, there has been wide-spread acceptance of the concept. Developmental patterns of vertebrae have played an important role in arguments about amphibian relationships, and Wake (1970) re-examined available information concerning the three living orders. In addition he examined developmental series of species in each order. His conclusion was that each order differed substantially from the other, and from amniotes, in many aspects of vertebral development, and that nothing in the vertebral column of modern amphibians supports the concept of the Lissamphibia. While distinctions between the three orders are great, Wake (1970) argued that they had been over-emphasized by some workers and under-emphasized by others. Subsequently, Wake and Lawson (1973) studied the development of the vertebrae in the plethodontid salamander Eurycea bislineata. They concluded that it was futile to attempt to discuss homologies of parts of amphibian vertebrae given the data at hand.

In 1977, Verbout re-examined the question of whether resegmentation occurs in vertebral morphogenesis, and concluded on the basis of a detailed study of sheep that there was no resegmentation. This was in direct conflict with the ideas of Williams (1959), who had argued that resegmentation was one of the few fundamental features of amniote vertebral development, and that it was probably also characteristic of vertebral development in lissamphibians. Wake (1970) and Wake and Lawson (1973) accepted the arguments of Williams (1959) that resegmentation occurs in amniotes, but found the evidence for resegmentation in all amphibian groups to be equivocal. In particular, Wake and Lawson (1973) argued that the sclerotome of salamanders was so scanty that resegmentation could not be demonstrated, and that even if it did occur its significance was questionable.

Recently Gardiner (1983) has again raised these questions. Although he has reported no new data, he presented a detailed analysis of the literature and a novel interpretation: the arcualia postulated by early authors were present primitively, and they contributed to the complex centra of labyrinthodont amphibians, but the centra of tetrapods have formed independently at least twice and the arcualia do not contribute
to the adult vertebrae of living tetrapods. Not only did he support the idea that the Lissamphibia are a monophyletic group, but he also argued that no resegmentation took place in any vertebrates. He failed to cite the work of Verbout (1977), who had argued that there is no resegmentation but on different grounds.

Is it possible that such a seemingly well founded phenomenon as resegmentation, which is in nearly every textbook of embryology and comparative anatomy, and which has been studied directly by generations of students examining serial sections of vertebrate embryos, is but a figment of the imagination of earlier workers?

Gardiner's argument is far too long and complex to outline here. He has returned to elements of the arcualia theory of Gadow and Abbott (1895) and Gadow (1896), and stands apart from most modern workers. However, it is crucial to his argument that the so-called basidorsals form in an intersegmental position, in the clefts between the somites. It is also important that the sclerocoel be a feature of limited extent which does not extend so far as the mesenchymatous perichordal sheath.

Gymnophiones are, we believe, a key taxon in this entire debate. Whereas both urodeles and anurans have scanty sclerotomes which make it difficult to distinguish sclerotome halves and virtually impossible to detect a sclerocoel even if one is present, gymnophiones have an abundant sclerotome (Marcus and Blume, 1926; Wake, 1970). Thus it is in theory possible to detect the phenomena of interest in gymnophiones. Another feature that makes the gymnophiones especially attractive is the very large number of segments in the body - as many as 285, far more than any other vertebrate. Further, there is a very strong developmental gradient in a given embryo, with very many stages in vertebrogenesis represented in a single individual.

We have had available for study a number of embryos taken from the reproductive tracts of Dermophis mexicanus, Gymnophis multiplicatus, Typhlonectes compressicaudus, and Geotrypetes seraphini and embryos taken from eggs deposited by Hypogeophis rostratus (the latter prepared by Ronald Lawson, see Lawson, 1966). We are in the process of preparing a detailed manuscript which will describe vertebral development in these species (and in particular, in Dermophis mexicanus), and will only mention a few relevant highlights here.

In embryos as small as 7 mm of Dermophis mexicanus clear evidence of differentiated somites can be found near the head. The somite is cell-rich, but compared with our material of salamanders the far more numerous cells of gymnophiones are much smaller and more densely packed. Furthermore, there is a clear division of the sclerotome into more dense posterior sclerotomites and less dense anterior sclerotomites. The myocoel is readily apparent, and we now can confirm the presence of a distinct sclerocoel that is continuous with the myocoel. This observation confirms the report of Marcus and Blume (1926), working with Hypogeophis rostratus.
It is the posterior sclerotomites which give rise to the neural pedicle rudiment (of Wake and Lawson, 1973; apparently equivalent to the basidorsal of Gadow, 1896). In resegmentation theory these are thought to fuse with cells from the anterior sclerotomite of the following segment and to give rise to the neural arch in an intersegmental position. We can trace the general fate of the cells of the posterior sclerotomite from the point where they are exactly opposite the posterior part of the myotome to a time when they are in an intersegmental (using the position of the myotomes as the marker) position and becoming cartilaginous, forming the neural arch. We believe that it is highly likely that some cells from the anterior sclerotomite following and even from the anterior sclerotomite preceding this posterior sclerotomite join the developing neural arch rudiment, but this simply cannot be determined using only observational techniques. Development is a very dynamic process, not a static event involving discrete blocks of tissues. The individual cells are discrete to be sure, and it is important to know the fate of specific cells. Certainly there is some repositioning of the myotome and the sclerotomites relative to one another, but there has been no crisp and clear resegmentation. But we believe that the developing neural arch is composed of cells derived from adjacent segments, so that in a technical sense there is a resegmentation. This somewhat ambiguous position is similar to that of Wake (1970) and Wake and Lawson (1973), which led Ver bout (1977) to comment on the apparent confusion concerning this issue. To us it is not a matter of confusion, but of data. But it is also a matter of expectations. Thus, for us resegmentation is a subtle phenomenon of no great importance, either developmental or phylogenetic, while to Ver bout (1977) it is a matter of what one can actually see happen to large blocks of tissue during development and to Gardiner (1983) it is a question intimately linked to the phylogeny of the vertebrate centrum.

Development of the vertebral column in gymnophiones is important because of the much closer resemblance of the developmental process in this group to that of amniotes relative to that of other modern amphibians. The gymnophiones will be a key group in any attempt to determine whether there is a general pattern of vertebral development in terrestrial vertebrates, or whether the modern amphibians do have a vertebral structure that differentiates them from living amniotes, as Gardiner (1983) claims.

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References


N.B. En raison du manque d'homogénéité dans les usages en cours ainsi que dans les manuscrits qui nous ont été envoyés, les bibliographies de ce colloque comportent quelques imperfections, notamment dans les titres des articles (emploi irrégulier des majuscules) ou dans les titres des ouvrages (omission des caractères gras). Nous avons dû renoncer à les corriger toutes pour ne pas retarder la parution de ce fascicule. Nos lecteurs voudront bien nous en excuser.