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Aspects of vertebral Evolution in the modern Amphibia ¹⁾

Betrachtungen zur Stammesgeschichte der Wirbel bei rezenten Amphibien

Aspects de l'Evolution vertébrales chez les Amphibiens modernes

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Abstract: Vertebral development in frogs, salamanders and caecilians follows a basic tetrapod pattern, but each group is highly distinctive. Evidence for segmentation and then a resegmentation of the sclerotome is not good for these groups, but caecilians do resemble amniotes to a greater degree than do the others in this regard. The pattern of vertebral development gives no useful information concerning homologies of elements. Homologies of lower tetrapod vertebrae are considered, and the general conclusion, although not the specific arguments, of PANCHEN (1967) is accepted. The centra of modern amphibians are considered to be broadly homologous to each other and to those of other tetrapods, be they monospondylous or diplospondylous. Without fossil evidence, identification of the centrum of modern amphibians with the pleurocentrum of fossil forms is not warranted. Nothing in the vertebral column of modern amphibians supports the concept of the Lissamphibia, and, in fact, the vertebral evidence offers no suggestion of relationship of the living amphibian orders. At the same time, the basic differences in the mode of ossification of the vertebrae of caecilians and salamanders on the one hand, and frogs on the other, have been overemphasized. The distinctions are great, but are less fundamental than an examination of the literature would suggest.

Vertebral development in terrestrial salamanders is summarized, and factors which lead to radically different centrum morphology in related groups are discussed. Modern salamanders are used as a system of analysis, which can provide insights into the relation of behavior, ecology, function and morphogenesis in the evolution of vertebral structure. Convergence in living salamanders produces similar centrum configurations in separate lineages. Morphogenesis of the centra in these convergent groups may be relatively similar, or markedly different. Based on these and similar examples, caution is advised in interpreting vertebral structure for phylogenetic purposes without information concerning morphogenesis and function.

Zusammenfassung: Die Entwicklung der Wirbel bei Fröschen, Salamandern und Blindwühlen folgt einem grundsätzlichen Vierfüßer-Plan, ist aber bei jeder Gruppe deutlich verschieden. Es gibt keinen klaren Beweis für die Segmentierung und dann folgende Resegmentierung des Sklerotoms für diese Gruppen, aber die Caecilia ähneln den Amnioten in dieser Hinsicht deutlicher als die anderen. Der Ablauf der Wirbelentwicklung bietet keine nützlichen Aufschlüsse hinsichtlich der Homologiefrage. Probleme der Homologie der Wirbel bei niederen Vierfüßern werden diskutiert, und die Schlüsse von PANCHEN (1967) werden übernommen. Die Wirbelzentren der modernen Amphibien dürften zueinander und zu denen der anderen Vierfüßer homolog sein, seien sie nun mono- oder diplospondyl.

¹⁾ Dedicated to Professor ALFRED SHERWOOD ROMER on the occasion of his 75th birthday.

Ohne fossile Beweise läßt sich eine sichere Identifizierung des Zentrums der modernen Amphibien mit dem Pleurozentrum der fossilen Formen nicht durchführen.

In der Wirbelsäule der modernen Amphibien gibt es nichts, das das Konzept Lissamphibia stützen könnte, und der Wirbelbauplan liefert auch keinen Hinweis auf Verwandtschaftsbeziehungen der lebenden Amphibien-Ordnungen. Auf der anderen Seite sind die grundlegenden Unterschiede in der Art der Wirbelverknöcherung bei Blindwühlen und Salamandern gegenüber den Fröschen überbetont worden.

Die Wirbelentwicklung bei terrestrischen Salamandern wird zusammengefaßt dargestellt, und einige Faktoren, die zu grundsätzlich verschiedener Zentrum-Morphologie bei verwandten Gruppen führten, werden diskutiert. Die heutigen Salamander sind eine brauchbare Gruppe zur Analyse der Frage, wie die Evolution der Wirbelmorphologie zusammenhängt mit dem Verhalten, der Ökologie, der Funktion und Morphogenese. Konvergenzerscheinungen liefern ähnliche Zentrum-Konfigurationen bei getrennten stammesgeschichtlichen Gruppen der heutigen Salamander. Bei solchen konvergenten Gruppen kann die Morphogenese der Zentren relativ ähnlich oder deutlich verschieden verlaufen. Aus diesen Gründen sollte man bei der Interpretation von Wirbelstrukturen zu phylogenetischen Zwecken Zurückhaltung üben, wenn man nicht nähere Informationen über die Morphogenese und Funktion in der Hand hat.

Résumé: Le développement vertébral chez les grenouilles, les salamandres et les Apodes, s'est fait selon le plan fondamental suivi chez les tétrapodes, mais de façon nettement distincte dans chaque groupe. S'il n'apparaît pas clairement qu'il y ait eu dans ces groupes une segmentation des sclérotomes suivi d'une resegmentation, on note cependant qu'à ce propos, les Apodes se rapprochent d'avantage des Amniotes que ne le font les autres Amphibiens. Le plan du développement vertébral ne fournit pas d'indications permettant une homologie des éléments. En considérant les homologies vertébrales chez les tétrapodes inférieurs, les conclusions générales de PANCHEN (1967), sinon ses arguments spécifiques, peuvent être acceptées. D'une façon générale, il existe une homologie des centrams, tant entre les différents Amphibiens modernes, qu'entre ceux-ci et les autres tétrapodes, qu'ils soient monospondyles ou diplospondyles. En l'absence de preuves paléontologiques, l'assimilation du centrum des Amphibiens modernes au pleurocentrum des formes fossiles est problématique.

Rien dans la colonne vertébrale des Amphibiens modernes ne peut servir de base au concept de Lissamphibiens, et, de fait, la structure de leurs vertèbres ne suggère pas de relations entre les Amphibiens actuels. A ce sujet, on notera que si des différences très marquées s'observent dans le mode d'ossification vertébrale des Apodes et des salamandres, d'une part, des grenouilles, d'autre part, elles sont cependant moins fondamentales que ne pourrait le faire croire la littérature.

Le développement vertébral chez les salamandres terrestres est ensuite résumé, et les facteurs qui mènent à une morphologie du centrum radicalement différente dans des groupes apparentés, sont discutés. Les Salamandres actuelles se prêtent à une analyse qui peut éclairer les relations entre le comportement, l'écologie, la fonction, la morphogenèse et l'évolution des structures vertébrales. Un phénomène a conduit à des centrams de même configuration dans des lignées distinctes, toutefois, leur morphologie peut être, ou assez comparable, ou nettement différente.

A partir de ces exemples et de quelques autres, il apparaît qu'en l'absence de données sur la morphogenèse et sur la fonction, on ne doit utiliser les structures vertébrales dans la phylogénie qu'avec une certaine prudence.

Much has been written concerning vertebral development, structure and evolution. Yet, information from fossils and studies of living groups continue to provide fresh insights. These, in turn, require reevaluation of prevailing theories. In this paper I focus attention on several aspects of vertebral evolution in the living members of the Class Amphibia. This group has been particularly difficult to interpret. Hopefully, data presented here will provide new perspectives for future studies of vertebral development and evolution in the group.

By the mid-1950 s, the volume of literature relating to vertebral development and evolution had reached enormous proportions. Separation of facts and theories was becoming nearly impossible. Then, a decade ago, WILLIAMS (1959) published a critical review of great value. He looked anew at facts, freed himself from the intellectual constraints of earlier theories, and presented a new theory of the development and evolution of tetrapod vertebrae. The reader's familiarity with this important work is assumed.

I will consider just two questions. First, are the vertebrae of modern amphibians comparable, in terms of morphogenesis, among the three orders and with other tetrapods? Second, what are the major patterns of centrum evolution in a living amphibian order, the salamanders?

Work reported here is a review of several long-term projects. Reports of these are in manuscript or in preparation, and will be published elsewhere. Some of these have been written in collaboration with colleagues, and I would especially like to acknowledge the contributions of RONALD LAWSON. I enjoyed many long discussions with him concerning centrum homologies in salamanders and several of the ideas here are extracted in part from our joint paper on vertebral development in the plethodontid salamander *Eurycea bistineata* (WAKE and LAWSON, 1970). MARVALEE H. WAKE and RICHARD J. WASSERSUG have offered many constructive criticisms. Finally, I am indebted to ERNEST E. WILLIAMS, who disagrees with several of my interpretations, for his careful review of an earlier draft of the manuscript. This work has been supported by the National Science Foundation (Grants GB 3868, GB 6423 X, GB 17112).

A. Historical Perspectives

The three living orders of modern amphibians, Caudata (salamanders), Gymnophiona (caecilians), and Anura (frogs), have long posed difficulties for those attempting phylogenetic analyses of vertebrates. Even recent workers have differed greatly in their treatment of the groups. JARVIK (1968) thought that the three orders evolved separately from three different groups of fishes. PARSONS and WILLIAMS (1963) considered them to form a natural group (Lissamphibia), and BOLT (1969) has recently suggested that a common ancestor might have been a specialized Paleozoic rhachitome.

It is generally acknowledged that each order is distinctive in regard to adult vertebral structure. However, developmental data have been interpreted in diverse ways. MOOKER-JEE (1936) saw no great differences of patterns in vertebral morphology, but GADOW (1933) envisioned fundamental ones. WILLIAMS (1959) recognized differences but did not emphasize them. A commonly encountered treatment, especially following ROMER (1945), has been to compare the caecilians and salamanders with Paleozoic lepospondyls,

based on the common presence of spool-shaped centra presumed to be membranous ossifications. Frogs, with extensive preformation of the centra from cartilage, have usually been viewed as closer to amniotes in vertebral construction. With the publication of the reviews of WILLIAMS (1959) and PARSONS and WILLIAMS (1963), amphibian relationships have been reconsidered. For example, ROMER (1966) recognized the Lissamphibia in marked contrast to his earlier views.

There is no real question concerning the distinctiveness of the vertebral columns in the three orders of living amphibians, relative to each other and to other living and fossil vertebrates. The basic problem is rather to determine whether the vertebrae are truly comparable within the Tetrapoda, and especially the Amphibia, and to discover the factors that are responsible for the various conditions in different groups. The differences are great, but are the similarities sufficient to provide evidence of phylogenetic relationship?

B. Early Patterns of Morphogenesis and their Result

I. Amniotes

WILLIAMS (1959) has presented an admirably concise summary of knowledge concerning vertebral morphogenesis in amniotes. Although I will not attempt to repeat his summary here, a thorough understanding of his work is assumed. However, it is essential to emphasize that his major point relates to the formation of vertebral centra from perichordal tissue originating from adjacent somites (sclerotomal parts), but not from arcualia in the sense of GADOW (1933). Evidence was presented that a common pattern is found in amniotes, with the main centrum being formed from a resegmentation. Caudal and cranial sclerotomites (essentially half-sclerotomes) of adjacent segments unite to form the centrum proper, while the intervertebral discs and other centrum elements (e. g. chevron bones) are formed basically from tissue originating from a single somite. A major landmark is the sclerocoel, a space or cavity separating the generally more dense caudal sclerotomite from the generally less dense cranial one and marking the approximate limits of the adult vertebrae. On paleontological grounds, the primary centrum of amniotes is identified as a homologue of the element which has been named the pleurocentrum in labyrinthodont amphibians. WILLIAMS essentially redefined the term pleurocentrum so that it applies to that part of the total centrum complement that arises from a resegmentation of sclerotome material. Since he thought that the fundamentals of vertebral development in living amphibians and amniotes were identical, he identified the unitary centrum of amphibians as a pleurocentrum. While one cannot challenge WILLIAMS' identification of the dominant amniote centrum as a pleurocentrum, based on paleontological evidence, his attempt to use embryological evidence to establish centrum homologies is specifically questioned (see below).

II. Amphibia

Knowledge of vertebral development in the modern amphibians, based on a review of the literature, was summarized by WILLIAMS (1959). He concluded that neither the centra nor the arches seemed to differ in terms of sclerotome components from those of

amniotes. Living amphibians were said to be very similar to amniotes in fundamentals of vertebral development, and he states (p. 16) "*The centra, though aberrant as compared with those of Amniota (in a somewhat different way in each of the orders) are intersegmental in place of origin as in amniotes and, again as in amniotes, are formed from perichordal tissue independent of the arches*". However, mention was made of the ways in which the amphibians differed from amniotes, a) lacking certain developmental structures (sclerocoel poorly developed, or not present at all, in salamanders and frogs), and b) deviating sharply from the amniote condition in later stages of development (centrum ossification in the various groups). As WILLIAMS notes, his conclusions were based on his interpretation of the literature rather than original work with amphibians.

My discussion is restricted by space considerations to aspects of segmentation, centrum development, and the craniovertebral joint. Other aspects of development will be considered in future papers.

1. Salamanders

Despite the work of numerous individuals, no clear evidence of a segmentation, then resegmentation, of the sclerotome has been presented for salamanders. The only evidence of a sclerocoel or of a division of a single sclerotome into dense and less dense parts is that presented by DE GAAY FORTMAN (1918) in embryos of unspecified size of the Japanese Giant Salamander, *Andrias japonicus* (= *Megalobatrachus maximus*), and by MAURER (1904) in *Ambystoma mexicanum*. In both instances, the somite is still in a scleromyotome (no distinct sclerotomal masses) stage, and neither the figures nor the textual accounts convinces me that they found sclerocoels. Figures 1 and 2 of DE GAAY FORTMAN are quite clearly of myotome. MAURER was illustrating the organization of the trunk musculature, and does not mention the sclerocoel. It was SCHAUINS-LAND (1905) who first called attention to MAURER's Figure 19, as possibly illustrating a sclerocoel. MAURER's is a diagrammatic and stylized drawing, and the plane of section does not permit interpretation as far as location in the segment is concerned. No differentiation of the segmental tissue is illustrated. Since MAURER did not present any discussion of this point, and in the absence of corroboration by others who have studied the same species without finding a sclerocoel (TEEGER, 1956), it is best ignored. One cannot deny that a sclerocoel is present in the species, but the evidence is not good and is not now subject to interpretation. The comprehensive studies of urodele vertebral development by MOOKERJEE (1930) failed to reveal segmentation of the sclerotome or sclerocoel development. The sclerocoel is simply a landmark, but its presence could be used to support the concept of a resegmentation, as in the arguments of WILLIAMS (1959). The only recent study of salamander vertebral development is by MAUGER (1962) who seems to accept resegmentation as a fact, without further discussion (MAUGER did not cite WILLIAMS' paper and seems unaware of the controversy concerning resegmentation and the presence or absence of a sclerocoel).

The sclerotome in salamanders is very scanty in volume and low in cell density during early stages of somitic differentiation. Sclerotomal cells are derived from the ventromedial borders of the myotomal units, below the level of the myocoel. The cells migrate

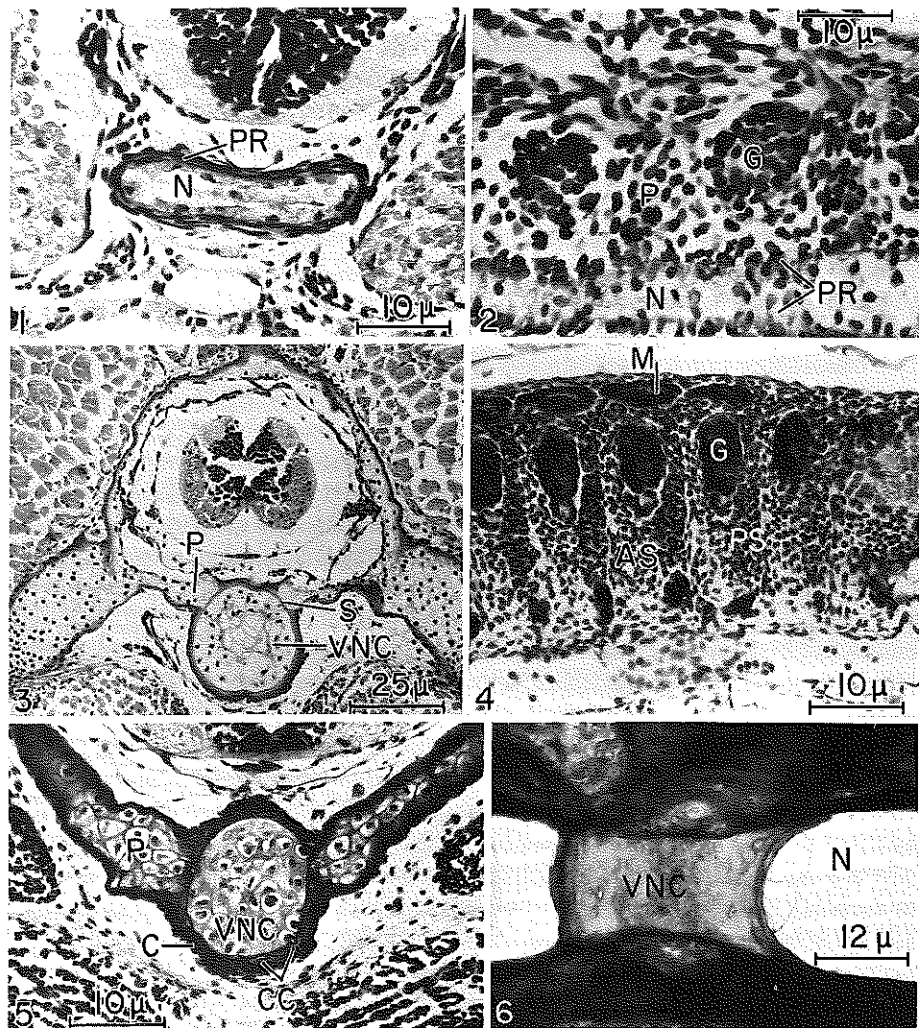
medially at first, then dorsally. An indistinct layer results in which the cells are not clearly organized into segmental units, although one can find segmental boundaries by locating myotomal boundaries and segmental blood vessels, assuming that these have as yet not been displaced. Among other derivatives of the cells is the continuous and excessively thin perichordal tube which surrounds the notochord. In forms such as the plethodontid *Eurycea bislineata* it consists of no more than one, or at most, two cell layers, and these are very closely applied to the notochord (Fig. 1). The perichordal rings are only slightly differentiated from the rest of the perichordal tube and consist of but two or three layers of elongated cells. At slightly later stages these are aligned with their long axes surrounding the notochord. The perichordal rings, which give rise to the intervertebral cartilages, are at approximately midsegmental positions, but this varies from species to species. In *Eurycea*, for example, the rings are very near the posterior margins of the segments, while in *Pseudoeurycea*, *Ambystoma* and *Notophthalmus* they have a midsegmental position. Ganglia of the spinal nerves appear before any concentrations of sclerotomal cells are in the vicinity. When the sclerotomal cells migrate dorsally into this region, they tend to be concentrated in the intermyotomal recesses. It is these areas which give rise to the neural pedicels, and on strictly topographic grounds they seem to lie in a position which corresponds to the caudal part of a sclerotome. This can be most clearly seen in sections (Fig. 2) of a moderately advanced embryo of *Pseudoeurycea juarezi*, a species that has direct development (see McDIARMID and WORTHINGTON, 1970). Differentiation is much delayed in *Pseudoeurycea*, relative to generalized species with aquatic larvae. The embryo is larger when vertebral development is initiated, with more mesenchymatous cells. Yet, even in *Pseudoeurycea* the perichordal tube is scanty.

Spinal nerve ganglia generally lie in the cranial part of a given trunk segment, as in amniotes, but in the neck region the ganglia arise in the caudal part of a segment. This does not, of course, interfere with the development of the neural pedicel in the area of the intermyotomic recess, which is the only logical site for its development. It is rather an indication of the general flexibility of the developmental pattern in salamanders and the absence of a stable, uniform pattern.

Much of the developing and adult centrum consists of cartilage which may be converted to bone in the definitive centrum. Generally this is ignored, for this ossified material is derived exclusively from the hypertrophied intervertebral cartilage and that cartilage found within the notochord in mid-vertebral and intervertebral areas (see section on salamander centrum, below). The intervertebral cartilage itself is formed from the perichordal tube (especially the perichordal ring) and extends virtually to the center of each centrum. It may be continuous from one intervertebral area to the next along the entire centrum length on anterior vertebrae. SCHMALHAUSEN (1958, 1968) has argued that the husk-like centrum of salamanders is a perichondral ossification. This is certainly the case at the ends of the centra, where they surround the intervertebral cartilage. Only near the center of the centrum is bone formed which is clearly independent of cartilage. This perichondral pattern of ossification is not substantively different from that which occurs in reptiles, as SCHMALHAUSEN notes, but there are certainly differences in the degree to which the

perichondrium contributes to the adult ossification. At the center of each centrum, the cartilaginous core of the neural pedicel rests directly on the notochord (except on the atlas and, in some species, a few of the anterior vertebrae), and this condition persists throughout life. At this small spot no bone forms, but a cartilaginous plug within the notochord acts as the supporting base (Fig. 3). This observation is in agreement with SCHMALHAUSEN (1958), but not with MOOKERJEE (1930), who held that the pedicel rudiment (his basidorsal) did not rest directly on the notochord, but on the perichordal tube. This is really an academic question. In the later stages, that perichordal tube tissue, if any, which lies between the pedicel and the notochordal sheath becomes converted to cartilage. The cartilage formed is indistinguishable from that of the pedicel. It consists of no more than a single thin layer of cells in a mesenchymatous state at any stage. The situation on some of the anterior vertebrae, especially the atlas, is slightly different. Here a distinct cartilage layer underlies the pedicel, and this cartilage is converted to bone in the adult centrum. Also, in some salamander groups (ambystomatids and others) the pedicel may have a somewhat broader base than in others. However, there is no evidence for a cartilaginous base for the dorsal arch in the centrum. Because the perichordal tube is so thin, it is impossible to recognize, even in the most technical sense, any indication of a neurocentral suture in salamander vertebral development.

The cranio-vertebral joint of salamanders is highly distinctive. Salamanders have a well developed tuberculum interglenoideum ("odontoid" of authors). In early development the notochord extends continuously from the basal plate of the skull into the vertebral column. In the area from just before its emergence from the skull to the center of the atlas, it is filled with cartilage. This cartilage has relatively large amounts of matrix and has a hyaline consistency. In generalized groups (hynobiids, ambystomatids) anterior extensions of the mesenchymatous mass which will form atlantal cotyles and occipital condyles appear. These extensions hypertrophy on either side of the notochord ventromedial to the bases of the occipital pedicels. In derived groups (e. g. plethodontids), these masses form as independent centers. Each mass chondrifies to form a small condyle, which articulates with a cup-like depression in the cartilage of the occipital pedicel. Bone forms around the margins of the small condyles and around the notochord, forming the tuberculum interglenoideum. The tuberculum is formed more or less in continuity with the bone of the front of the atlas. In one larval *Notophthalmus viridescens* a separate center of ossification has been found for the tuberculum, near its eventual tip at the level of the occipital arch. Possibly this is an indication of a more ancient pattern in which tissue at the base of the occipital arch gave rise to an ossified vertebral centrum unit, but this may simply be an aberrancy that has no phylogenetic significance. In early embryos a large volume of mesenchymatous tissue is found between the atlas rudiment and the occipital pedicels. This tissue is impossible to trace with conventional techniques, but it must be derived from several segments. For example, presumptive cells of a perichordal ring between the atlas and the occipital arch may be involved (cf. MOOKERJEE, 1930). However, there is no evidence that the atlas of salamanders consists of more than one vertebra.



Abbreviations see p. 57

Figure 1. Transverse section through notochord and perichordal ring in 7.4 mm (body length) embryo of *Eurycea bislineata*. Van Gieson stain

Bild 1. Querschnitt durch Chorda und perichordalen Ring bei einem Embryo von *Eurycea bislineata* von 7,4 mm Länge. Van-Gieson-Färbung

Figure 2. Parasagittal section through trunk of advanced embryo of *Pseudoeurycea juarezi*. The neural pedicels and perichordal rings are in early states of development. Anterior to left. Van Gieson stain

Bild 2. Parasagittaler Schnitt durch den Rumpf eines älteren Embryos von *Pseudoeurycea juarezi*. Neuralknospen und perichordale Ringe in frühem Entwicklungszustand. Kopfende nach links. Van-Gieson-Färbung

Figure 3. Transverse section through midvertebral region of large larval *Ambystoma opacum* (32.1 mm, body length). Note support of cartilaginous neural pedicels on notochordal sheath and intravertebral notochordal cartilage. Van Gieson stain

Bild 3. Querschnitt durch die mittlere Wirbelregion einer großen Larve von *Ambystoma opacum* von 32,1 mm Körperlänge. Beachte das Abstützen der knorpeligen Neuralknospen auf der Chorda-Scheide und dem intravertebralen Chorda-Knorpel. Van-Gieson-Färbung

Figure 4. Parasagittal section through trunk of embryonic *Gymnopsis proxima* (10 mm, body length). Note clear segmentation of the cell rich sclerotome to form dense posterior sclerotomites and less dense anterior sclerotomites. Anterior to left. Van Gieson stain

Bild 4. Parasagittaler Schnitt durch den Rumpf eines 10 mm langen Embryos von *Gymnopsis proxima*. Beachte die klare Segmentierung des zellreichen Sklerotoms mit der Bildung dichter posteriorer Sklerotomiten und weniger dichter anteriorer Sklerotomiten. Kopfende nach links. Van-Gieson-Färbung

Figure 5. Transverse section through midvertebral region of 30 mm embryo of *Gymnopsis proxima*. Note incorporation of cartilage cells into bone of the definitive centrum. Azan stain

Bild 5. Querschnitt durch die mittlere Wirbelregion eines 30 mm langen Embryos von *Gymnopsis proxima*. Beachte die Inkorporierung von Knorpelzellen in den Knochen des definitiven Zentrums. Azan-Färbung

Figure 6. Frontal section through midcentrum region of adult *Caecilia occidentalis* (427 mm, body length), illustrating persistence of large notochord and presence of mineralized plug of intravertebral notochordal cartilage. Anterior to left. Safranin O and Mayer's hematoxylin stain of plastic embedded tissue

Bild 6. Frontalschnitt durch die Zentrum-Region bei erwachsener *Caecilia occidentalis* von 427 mm Körperlänge. Die Persistenz einer großen Chorda und die Anwesenheit eines mineralisierten Pfropfens intravertebralen Chorda-Knorpels sind deutlich. Kopfende nach links. Safranin O und Hämatoxylin nach Mayer

2. *Caecilians*

The only comprehensive paper that has been written concerning the early development of caecilians is that of MARCUS and BLUME (1926), who worked with *Hypogeophis*. Other papers (MARCUS, 1937; RAMASWAMI, 1958; LAWSON, 1966) deal with later stages. The caecilians are reported to be more like amniotes in early stages of development than are other amphibians, and I agree fully with this view. We (D. WAKE and M. WAKE) have had embryos of several stages of two live-bearing caecilians (*Gymnopsis proxima* and *Typhlonectes compressicauda*) and of the oviparous *Hypogeophis rostratus*. This material tends to corroborate the pattern outlined by MARCUS and BLUME (1926), though I would not like to validate their conclusions concerning homologies of elements. The sclerotomal cells are metamericly arranged and the sclerotome is very cell-rich relative to other amphibians (Fig. 4). I have seen no sclerocoel, but MARCUS and BLUME (1926) present diagrams which have been interpreted by WILLIAMS (1959) as representing a well developed sclerocoel. MARCUS and BLUME call it a "Urwirbelhöhle" and state that it is continuous with the nephrocoele. It appears to me to be the myocoel

rather than the sclerocoel, and the separation of sclerotome halves which they show in their diagrams is likely the result of the formation of the spinal ganglia in a midsegmental position. Perhaps this is all that can be expected of a sclerocoel in the Amphibia; but I remain unconvinced, on the basis of my investigations of new material, that a sclerocoel occurs in caecilians.

In most other respects, the sclerotome of caecilians is very much like that of amniotes. It produces a relatively thick perichordal tube with clearly demarcated, segmentally arranged perichordal rings. Two distinct sclerotomites are evident in each segment, a cell-rich, dense, deep-staining caudal half and a less dense, light-staining cranial half which has fewer cells. The caudal half gives rise to the bulk, if not all, of the cartilaginous neural pedicel, save for dorsal parts and the zygapophyseal connections which develop relatively late. The centrum is clearly a trans-segmental structure and fulfills the requirements of resegmentation as set forth by WILLIAMS (1959).

Caecilians have cartilaginous parts that are converted to bone in the centrum during development, although the great bulk of the bony centrum is formed from membranous additions. Parenthetically one might add that in amniotes, too, much bone is added to the cartilaginous model and this is often in the form of perichondral ossification. In particular, near the middle of the centrum of *Gymnopsis* embryos (Fig. 5), cartilage cells undergoing ossification may be found [see also MARCUS and BLUME, 1926]. Neural pedicel development is similar to that in salamanders, but much less of the centrum is formed from intervertebral and notochordal cartilages. The adult caecilian vertebra has a large cavity filled by a greatly dilated notochord in which the sheath has become fragmented (Fig. 6). The intervertebral cartilage is reduced and forms a joining ligament between adjacent centra. However, its cells have contributed bone to the ends of the centrum (see LAWSON, 1966). The only notochordal cartilage found in trunk vertebrae is the intravertebral notochordal cartilage which lies under the cartilaginous rudiments of the neural pedicel. PARSONS and WILLIAMS (1963) refer to this as a rudimentary cartilage core of the centrum, which they identify as dermal bone. As has been shown, the centrum consists of more than dermal bone. Rather than being a cartilaginous core, the bit of cartilage which is retained in a highly mineralized form is a derivative of the notochord and is characteristic of salamanders and lizards as well as of caecilians (see also comments of LAWSON, 1966).

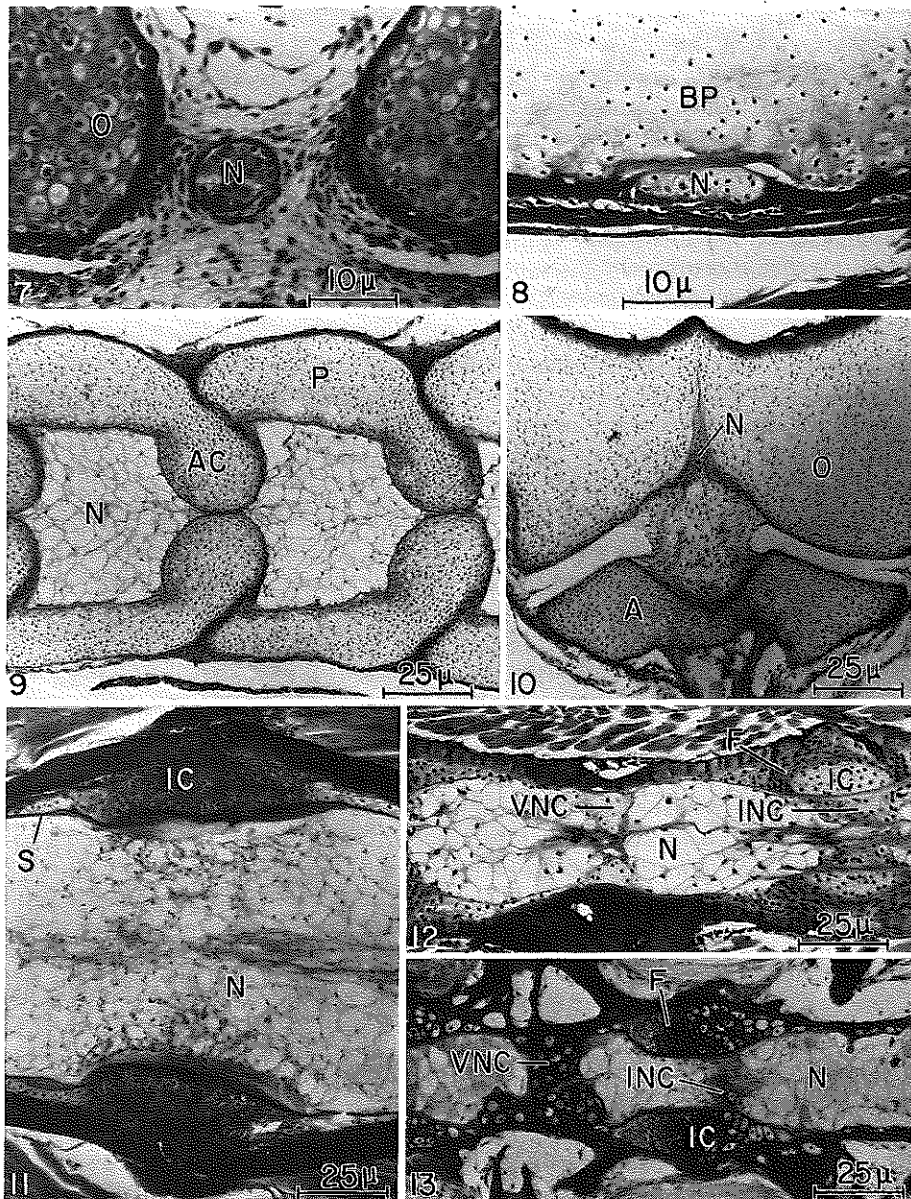
Caecilians have a peculiar craniovertebral joint that features medially located atlantal cotyles. The cotyles extend a considerable distance anteriorly, between the occipital condyles. At first these are well separated from each other, and from the continuous, cartilage-filled notochord that lies between them (Fig. 7), but with growth they are forced together where they obliterate the notochord and end in a point. This is a different organization scheme than is seen in the salamanders, where development of the tuberculum interglenoideum is initiated medially, and is more like the situation in frogs. GADOW (1933) seems to have missed this point in a curious fashion, for he calls the cartilage-filled notochord of caecilians the "odontoid". This may have been the result of his ignorance of the existence of a cartilage-filled notochord in the craniovertebral region in all groups of living amphibians, which is reported for the first time in this paper.

3. Frogs

Sclerotome tissue is scanty in anurans and to date no sclerocoel has been reported. SMIT (1953) notes that the sclerotome is at first segmented (see also MOOKERJEE, 1931), and that a resegmentation occurs, but neither author has seen a sclerocoel. Early stages of only pipids, hylids and bufonids have been available to me, and I have not seen any clear indication of sclerotomal metamerism or of a sclerocoel. The Anlagen of the neural pedicels arise at segmental borders and the intermyotomal septa attach to them. Work is badly needed on very early stages of such primitive frogs as *Ascaphus* and *Leiopelma*. The latter should be a particularly good subject since it is both primitive and has direct development. Hence it can be expected to have relatively large amounts of sclerotome cells. WILLIAMS (1953) reported a "normal neurocentral suture" in *Leiopelma* embryos, the only recorded instance of such a feature in amphibians. I have seen no evidence of such a structure in my sections of other species.

In frogs, a variety of patterns of vertebral development is found, but they may be viewed in very broad terms as falling into two general categories. The first is perichordal, where the cartilage model ossifies around the notochord, eventually reducing its size and often obliterating it. Secondly, epichordal, where tissue dorsal to the notochord ossifies and the cells lateral and ventral, as well as the notochord itself, degenerate and disappear (DUGES, 1834; MOOKERJEE, 1931; KLUGE and FARRIS, 1969). No notochordal cartilage is found in frogs except in the intervertebral joint region of *Ascaphus* (Fig. 8). In the trunk region the bases of the neural pedicels are greatly expanded and anteriorly extended at an early developmental state (Fig. 9), and the notochord is relatively very large. The presence of notochordal cartilage in the basal plate of the skull and the anterior part of the atlas of *Ascaphus* suggests that the notochordal cartilage in the vertebral column behind the atlas is a feature that has been eliminated during the phylogeny of frogs. Much of the centrum of frogs with perichordal development is essentially a membranous ossification, especially along its lateral margins. In many groups, especially those with epichordal development, most of the originally cartilaginous material around the notochord disappears. The notochord becomes discontinuous at a very early age, and the rudiment of it is pushed ventrally. Dorsal parts of the centra are always preformed in cartilage.

The occipital condyles are very wide-spread and the anteromedial tip of the atlas, while it may be produced forward to an extent, has no special articulation facets such as occur in salamanders (Fig. 10). The evidence for an intercalated arch or vertebra between the occipital and atlas arches is not convincing, despite the arguments for one presented by GANGULY and SINGH-ROY (1966). These authors find a structure in *Rana tigrina* which has some characteristics of a tuberculum interglenoideum. However, from the illustrations presented, it appears more like a secondarily specialized condition in these highly derived frogs. Such a structure may be produced as a result of the relative great ventromedial development of the atlantal cotyles. Production of a process may result from union of parts of the two cotyles on the ventral midline.



Abbreviations see p. 57

Figure 7. Transverse section through craniovertebral joint region of 30 mm embryo of *Gymnopsis proxima*. The notochord is filled with cartilage in this region and has no contact with either the occipital condyles or the atlantal cotyles. Azan stain

Bild 7. Querschnitt durch die craniovertebrale Gelenkregion bei einem 30 mm langen Embryo von *Gymnopsis proxima*. Die Chorda ist in dieser Region mit Knorpel erfüllt und hat keinen Kontakt mit den Occipital-Condylen bzw. den Atlantal-Cotylen. Azan-Färbung

Figure 8. Transverse section through basal plate in skull of 35 mm (body length) juvenile *Ascaphus truei*. The notochord is filled with cartilage in this region. Van Gieson stain

Bild 8. Querschnitt durch die Schädelbasisplatte bei einem 35 mm langen jugendlichen *Ascaphus truei*. In dieser Region ist die Chorda mit Knorpel erfüllt. Van-Gieson-Färbung

Figure 9. Frontal section through developing vertebral centra of newly metamorphosed *Bufo boreas* (18,8 mm, body length). The bases of the neural pedicels are greatly expanded and are continuous with the developing articular condyles. The large notochord contains no cartilage. Anterior to left. Van Gieson stain

Bild 9. Frontalschnitt durch sich entwickelnde Wirbelzentren einer neu metamorphosierten *Bufo boreas* von 18,8 mm Länge. Die Basen der Neuralpedikeln sind stark expandiert und hängen mit den sich entwickelnden Artikular-Condylen zusammen. Die große Chorda enthält keinen Knorpel. Kopfende nach links. Van-Gieson-Färbung

Figure 10. Frontal section through craniovertebral joint of newly metamorphosed *Bufo boreas* (18.8 mm, body length). Note absence of accessory articulation processes. Anterior at top. Van Gieson stain

Bild 10. Frontalschnitt durch das craniovertebrale Gelenk eines neu metamorphosierten *Bufo boreas* von 18,8 mm Länge. Beachte das Fehlen akzessorischer Gelenkfortsätze. Kopfende nach links. Van-Gieson-Färbung

Figure 11. Frontal section through intervertebral joint region of adult *Hynobius dunni* (64 mm, body length). The notochord is very large and the intervertebral cartilage is relatively small. Anterior to left. Hematoxylin and eosin stain

Bild 11. Frontalschnitt durch die intervertebrale Gelenkregion eines adulten *Hynobius dunni* von 64 mm Länge. Die Chorda ist sehr groß, der intervertebrale Knorpel aber relativ wenig ausgedehnt. Kopfende nach links. Hämatoxylin-Eosin-Färbung

Figure 12. Frontal section through centrum and intervertebral joint of subadult *Ambystoma laterale* (35 mm, body length). The notochord is relatively smaller and the intervertebral cartilage is relatively larger than in *Hynobius*. Cartilage is present in the notochord at both midvertebral and intervertebral levels. Anterior to left. Van Gieson stain

Bild 12. Frontalschnitt durch Zentrum und Intervertebralgelenk einer subadulten *Ambystoma laterale* von 35 mm Länge. Die Chorda ist relativ kleiner, der intervertebrale Knorpel aber relativ größer als bei *Hynobius*. Knorpel findet sich in der Chorda sowohl in der Mitte der Wirbel wie auch im intervertebralen Raum. Vorderende nach links. Van-Gieson-Färbung

Figure 13. Frontal section through centrum of large larval *Taricha granulosa* (23.5 mm, body length). The notochord is relatively large and contains both midvertebral and intervertebral cartilage. The intervertebral cartilage is large and moderately differentiated in the joint region. Anterior to left. Methylene blue stain of plastic embedded material

Bild 13. Frontalschnitt durch das Zentrum einer 23,5 mm langen Larve von *Taricha granulosa*. Die Chorda ist relativ groß und enthält Knorpel im vertebralem wie auch im intervertebralen Bereich. Der intervertebrale Knorpel ist in der Gelenkregion groß und mäßig differenziert. Vorderende nach links. Methylenblau-Färbung

4. Comparisons

The three orders of living amphibians have unique features of vertebral development that separate them from each other and from amniotes. Caecilians are the only living amphibians that closely resemble the amniotes in aspects of early morphogenesis, yet unequivocal evidence of a sclerocoel and of resegmentation is lacking for them as well as for the other amphibian orders. A perichordal tube, of varying thickness, forms in all tetrapods, and it bears perichordal rings. These rings mark the site of intervertebral joints, and, between the rings, the neural pedicels will attach to the future centrum. The adult vertebral column does not have the same segmentation pattern as the somites. These are about the only features of fundamental significance that bind the tetrapods together.

In order to demonstrate resegmentation in modern amphibians one should be able to observe a metamERICALLY arranged sclerotome. Parts of each sclerotome segment should separate, with the separation point marked by a space or gap (the sclerocoel), and the parts of adjacent sclerotomes should merge across segmental borders, giving rise to an intersegmental or trans-segmental centrum element. This complete sequence has not been directly observed in any amphibian. However, as WILLIAMS (1959) has pointed out, evidence that amphibian centra develop in intersegmental positions is good. This might imply a resegmentation, with contributions to the centrum by cells derived from adjacent somites. On the other hand, it might simply be an indication of a realignment, for in the production of the perichordal tube the original segmentation of the sclerotome, if any, is lost. The centrum is formed directly from the nonsegmental perichordal tube, which is already one developmental step removed from the sclerotome. In producing centra in intersegmental positions, differentiation of the perichordal tube appears to be following the simplest and most direct developmental route. Thus development of centra in intersegmental positions can hardly be taken as evidence, in and of itself, of resegmentation. It is necessary, of course, for intermyotomal septa to attach to vertebrae. The clear resegmentation which occurs in amniotes is an efficient mechanism for attaining this end. One can also conceive of other pathways, which might involve many similarities with the amniote pattern without being identical. In any one of these, intersegmental development of the principal or sole centrum is to be expected, and cells which contribute to the centrum might well be derived ultimately from two different segments. Resegmentation may occur in amphibians, but whether or not it does seems to me to be neither very interesting or important, considering the functional constraints imposed on the system. Rather, the significant problem is to discover what selective factors are responsible for the varied kinds of perichordal tube differentiation patterns and centrum structures seen in fossil and living vertebrates.

Centrum ossification is very different in frogs, salamanders and caecilians, but in all some cartilage is converted to bone and some bone forms in membrane. This also occurs in amniotes. The differences are matters of degree and reflect the long, separate histories of the groups. While the patterns of ossification do not differ in fundamental ways on the cell and tissue level, the adult vertebral centra are distinctly different among the amphibian orders. Further, each group contrasts sharply with amniotes in several features of centrum anatomy.

Cranio-vertebral joints of the three groups of amphibians have been shown to differ in seemingly basic ways. Salamanders have a distinct tuberculum interglenoideum, but, despite literature reports to the contrary, no identical structure is found in either frogs or caecilians. No "proatlas", "intercalated arch" or other extra elements occur during development between the occipital and atlas arches. While more research is needed on diverse groups of living amphibians, it is evident that the nature of the cranio-vertebral joint is not a basis for close association of the orders. This point is discussed in greater detail by WAKE and LAWSON (1970).

III. Vertebral Homologies

In most of the Paleozoic labyrinthodonts the centrum typically was divided into two or more parts (see ROMER, 1966). Rhachitomes had a single large intercentrum and a pair of smaller pleurocentra per vertebra. The intercentrum was in the anterior and ventral part of the centrum area, and the pleurocentra were in a more posterior and dorsal position. The neural arch was a separate bone. This is generally considered to represent the primitive labyrinthodont condition (WILLIAMS, 1959; ROMER, 1966). Much diversity occurred within the labyrinthodonts in vertebral centrum conformation. In some groups (e.g. stereospondyls) the pleurocentra were eliminated, while in others (e.g. advanced anthracosaurs) they fused to form a single bone that was the dominant centrum element. The fossil evidence is good that the principal centrum of amniotes is a pleurocentrum (CARROLL, 1969 a), but the homologies of the modern amphibian centrum have remained controversial.

Attempts to determine homologies of vertebral parts have been numerous, and a general review cannot be undertaken here. Since the work of WILLIAMS (1959) represents a landmark, it is a natural point of departure for this discussion.

By combining data from embryology and paleontology, WILLIAMS (1959) developed a general theory of centrum homologies in tetrapods that was clear, concise, internally consistent and factually based. His arguments should be studied directly and in detail, but I shall attempt to summarize them in the following sentences. Amniotes share a common pattern of vertebral development. They are clearly derived from labyrinthodonts, who likely shared this developmental pattern, although it is not clear how far back, in a phyletic sense, this particular pattern extended. Those parts of labyrinthodont centra called pleurocentra seem homologous, on paleontological grounds, with the principal centra of amniotes, which therefore are pleurocentra. Finally, since the centra of modern amphibians share developmental similarities with amniotes, they, too, are pleurocentra.

WILLIAMS (1959) felt that evidence was good that the amphibian centrum develops intersegmentally, as it does in amniotes, where resegmentation is clearly demonstrable. Explicit is the idea that all pleurocentra develop in the same manner, viz. by resegmentation. Therefore, WILLIAMS reasoned, amphibian centra are pleurocentra. Note that paleontology alone is used to identify amniote centrum homologies, while embryology alone is used in the case of the modern amphibians.

I cannot accept identification of the amphibian centrum as a pleurocentrum. The neural arch is fused to the centrum in all amphibians, and clearly the segmentation of the musculature must differ from that of the vertebral column if the organism is to be capable of sinusoidal movement. The initial appearance of vertebral ossification in amphibians is in the intermyotomal recess, that is, intersegmental. There is no other developmental possibility. In a situation such as this, where functional mechanisms impose a design constraint, reliance on developmental patterns for homologies is very risky. Developmental processes are sufficiently plastic that bone will be produced where required for functional reasons, without regard to homologies.

Strict adherence to the developmental criterion of pleurocentrum identification would require that the centrum of most teleost fishes be considered a pleurocentrum homologue. WILLIAMS (1959) specifically refrained from extending his arguments to living fishes. FRANCOIS (1966, 1967) has shown, however, that the complex centra of teleosts arise in trans-segmental positions. While many features indicate compositional differences in teleost and tetrapod centra, it seems evident that tissue from areas equivalent to parts of two adjacent segments must contribute to those skeletal structures which span two segments. This, it would seem, satisfies WILLIAMS' criterion of resegmentation. FRANCOIS (1966) and SCHAEFFER (1967) reported that the sclerotomic tissue of the perichordal tube in teleosts shows no evidence of metamerism, and SCHAEFFER therefore denied that any direct evidence of resegmentation, in his sense of the term, existed. As discussed previously, many amphibians also fail to show sclerotomic metamerism. Technically, therefore, one cannot speak of resegmentation in these groups, but rather of a vertebral segmentation that is out of phase with the myotomic segmentation. Certainly the simplest and most direct developmental solution to the problem of production of such an out-of-phase segmentation is intersegmental development of the vertebrae. Regardless of the true homologies of vertebral centrum parts in tetrapods, one would predict intersegmental development when each vertebra has a single centrum which is fused, essentially throughout development, to the neural arch.

Pleurocentra and intercentra are identified according to their relative positions in labyrinthodonts. That appears to be the only logical criterion. Paleontological sequences and not embryology identify the centrum of amniotes as the homologue of the labyrinthodont pleurocentrum. In the development of his theory, WILLIAMS (1959) reasoned that as far back as one could trace clear homologues on paleontological grounds, one could also make predictions about the embryology of those elements based on knowledge of living amniotes. He traced pleurocentra and intercentra as far back as *Eusthenopteron* and the ichthyostegids, spanning the fish-tetrapod transition. He therefore suggested that the embryology of all tetrapods was similar, and felt confident in using embryology within the tetrapods to establish homologies when fossil sequences were lacking, as in the modern amphibians. While I deny that this last step can be taken, even granting the correctness of the paleontological comparisons which WILLIAMS makes, it now appears that the homologies suggested for the earliest groups are not correct. *Eusthenopteron*, other rhipidistians, and ichthyostegids are now thought to have had monospondylous centra (SCHAEFFER, 1967; THOMSON and VAUGHN, 1969), and

the homologues of pleurocentra and intercentra can be traced no further back in time than to the earliest rhachitomes. This further weakens the embryological argument for homology, for it is possible that each of the modern amphibian groups might have been derived from monospondylous ancestors which diverged from early tetrapod lineages before the first appearance of diplospondyly. This may seem unlikely, but various groups of early, monospondylous amphibians have been suggested as possible ancestors of modern amphibian groups by numerous workers in the past (for example, see review by PARSONS and WILLIAMS, 1963; also GREGORY, 1965). It seems evident that while the centrum of modern amphibians may conceivably be the homologue of the labyrinthodont pleurocentrum, this can neither be proved nor disproved by embryology.

Some other recent views must also be considered. Most lepospondylous amphibians had unitary centra and CARROLL (1967) suggested that they represented intercentra; one could extend his reasoning to the modern orders as well, but the reasons cited for rejection of the pleurocentrum homology also apply here.

THOMSON and VAUGHN (1968) attempted to show that the large primary centrum of rhipidistian fishes might not be the homologue of the tetrapod intercentrum. They tried to reconcile GADOW's arcualial theory (1933) with their data, and reconstructed the centrum of *Eusthenopteron* with the primary centrum being formed from the "interventral" and "basiventral" of the same segment. They suggested that non-resegmented holospondyly occurred in rhipidistians, and denied that either rhipidistians or ichthyostegids had a true pleurocentrum (see also SCHAEFFER, 1967). Resegmentation and the patterns of diplospondyly seen in tetrapods were thought to have evolved on the amphibian side of the fish-amphibian transition (see also THOMSON, 1967). One is then stimulated to search for selective factors in the environment which might have led to the evolution of diplospondyly in early amphibians; the recent efforts of PARRINGTON (1967) are admirable in this regard.

Despite the positive features of their work, THOMSON and VAUGHN (1968) do the field a disservice in resurrecting the gadovian embryological terminology. WILLIAMS (1959) has admirably disposed of the arcualial theory as far as tetrapods are concerned, and it seems nonproductive to now revive the terminology for fossil groups for which there is not one shred of embryological supportive evidence.

SCHMALHAUSEN (1958, 1968) did not discuss WILLIAMS' (1959) views on vertebral evolution, but formulated his own distinctive theory. His paleontological knowledge was both limited and dated, and he incorrectly assumed that embolomeric vertebrae were structurally the most generalized tetrapod vertebrae. This assumption led him to identify the "basiventral" with the caudal half-sclerotome derivatives, which he considered to be the equivalent of the intercentrum of embolomeric vertebrae. The term "interventral" was applied to the cranial half-sclerotome derivatives, which he considered to be equivalent to the pleurocentrum of embolomeres. His theory involved resegmentation in modern amphibians with fusion of inter- and pleurocentra. He thought the neural pedicel (his basidorsal) was incorporated into the centrum, so that three "arcualia" contribute to the centrum of modern amphibians. It is difficult to analyze this modification of gadovian theory, for like GADOW (1933), SCHMALHAUSEN relied on nonexistent rudiments.

PARSONS (1965) criticized WILLIAMS' (1959) view concerning identification of the amphibian centrum as a pleurocentrum. But in emphasizing the point that muscle attachments require intersegmental adult centrum positions, he misinterprets WILLIAMS, who clearly stresses intersegmental development (see comments in ESTES, 1965). In PARSONS' view, fusion of the intercentrum and pleurocentrum to form the amphibian centrum was possible, although he admitted that no evidence existed. This is a suggestion that is similar to the more detailed theory of SCHMALHAUSEN. In my view, the best feature of it is the recognition that the amphibian centrum is the equivalent of the labyrinthodont centrum, but I see no reason to postulate fusion of parts.

Recently PANCHEN (1967) presented a theory of vertebral evolution in labyrinthodonts. He suggested that the whole labyrinthodont centrum is homologous with that of amniotes, and that the division between the intercentrum and pleurocentrum represents, in effect, a "split" within the body of the centrum. One should, according to his view, seek explanations for the varying conditions of the centra in terms of functional and mechanical adaptations to environmental selective pressures. I find PANCHEN's suggestions concerning homology to be acceptable, but his attempts to deduce embryological patterns from fossils are not convincing.

Several evolutionary routes might have been followed in the evolution of monospondylous centra, including the possibility of independent derivation from different ancestral stocks with diplospondylous centra. CARROLL (1968) found that the Permian microsauro *Pantylus* had one centrum per vertebra in the trunk, but two in the tail. This is significant because it shows that no major developmental change is required to derive monospondylous from diplospondylous types (or presumably vice-versa). More recently CARROLL (1969) has suggested that the monospondylous centra of microsaur and lysorophids were derived from apsidospondylous (diplospondylous) ancestors. BOLT (1969) described a dissorophoid rhachitome, *Dolesempeton*, which had a very large pleurocentrum and a very small intercentrum. It is only a short step from this kind of centrum to a monospondylous one, in structural terms. BOLT questioned the statement by PARSONS and WILLIAMS (1963) that an ancestor of modern amphibians should be expected to have had a pleurocentrum as the dominant or sole centrum element. Rather, the centrum should be monospondylous, or nearly so.

Why must a monospondylous tetrapod centrum be either a pleurocentrum or an intercentrum? Modern amphibians show many signs of the influence of heterochronic modes of evolution, especially paedomorphosis. Perhaps ancestral differentiation patterns have been so modified that the homologues of these centrum parts have been eliminated from the ontogeny of one or more groups. Direct ossification from the perichordal tube, such as occurs in all modern amphibians to a degree, may have been substituted, in an evolutionary sense, for a more elaborate ancestral condition.

Regardless of their ancestry, centrum development takes distinctive forms in each of the modern amphibian orders. Possibly caecilians, with their relatively cell-rich, metamericly arranged sclerotome, retain more ancestral developmental features than do salamanders and frogs. Apart from the fact that they are exclusively monospondylous, the vertebrae of the modern amphibian orders bear little similarity to each other. Further, despite BOLT's

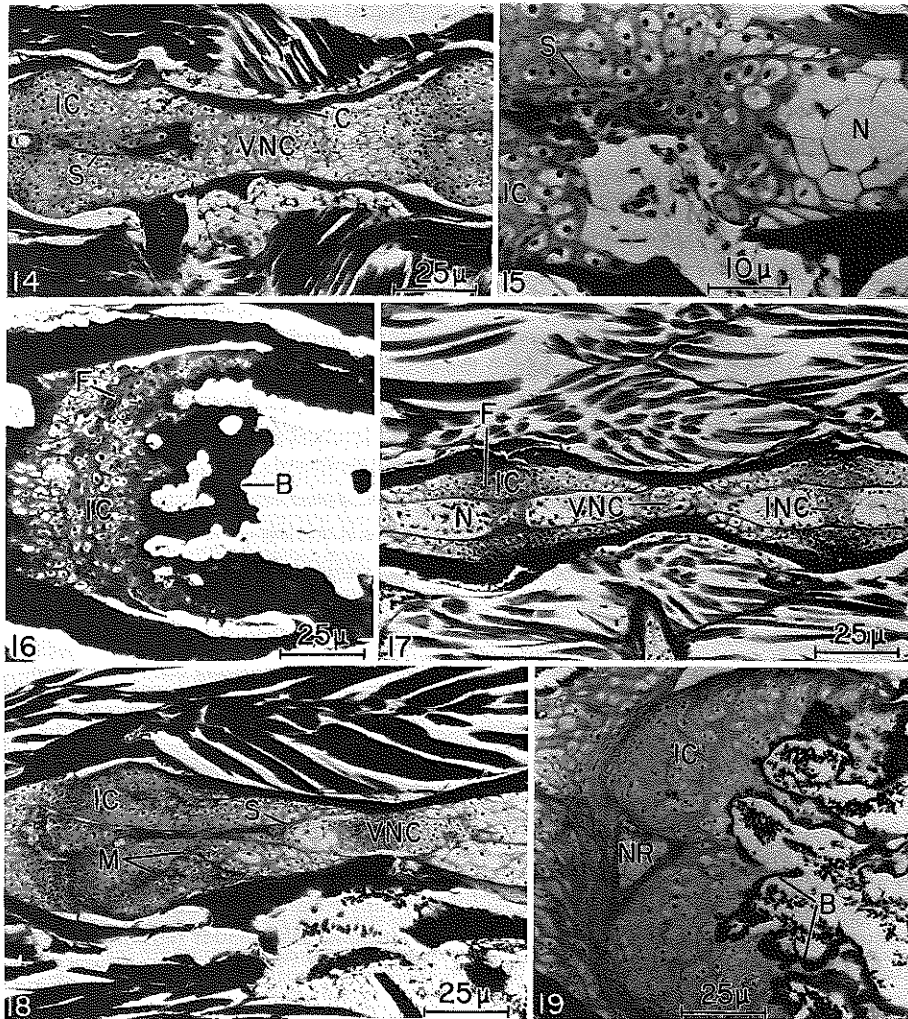
(1969) discovery of *Dolesempeton*, there is no unequivocal evidence of ancestry of any of the modern orders from any Paleozoic group. The concept of the Lissamphibia (PARSONS and WILLIAMS, 1963) receives no support from vertebral characters, which instead tend to emphasize the differences between the groups.

The only solution to the controversy concerning centrum homologies is to consider the entire centrum of modern amphibians to be the homologue of the entire centrum of all tetrapods, living and fossil, and of fishes. All share a developmental perichordal tube which is formed either from metamericly arranged sclerotomes which lose their segmentation during the production of the tube, or from non-metamerized sclerotomic tissue. Differentiation of the perichordal tube produces vertebrae which, at least in adult tetrapods, are necessarily intersegmental or trans-segmental. The simplest embryological pattern for the production of such vertebrae is one in which the ossification of the primary or solitary centrum is intersegmental, and such is the case in all living tetrapods, and most fishes. Paleontology seems to offer the only hope for tracing vertebral evolution in the modern amphibians, but the fossil record is as yet inconclusive. To discuss homologies of centra in living groups without fossil evidence is fruitless, for it appears that the only criterion for the identification of parts of diplospondylous centra is relative position. The only defensible conclusion from embryological data is that tetrapod centra, regardless of their patterns of development, are homologous.

C. Centrum Evolution — The Salamander Vertebral Column as a System for Analysis

Some results of my work on the evolutionary morphology of the salamander vertebral column are presented in the following paragraphs. I hope to correct some misconceptions concerning salamander vertebrae, and to show how the study of a living group might provide insights into the analysis of centrum evolution on a broader scale. For this discussion only a brief summary of work with terrestrial salamander families is reported. These include the families Hynobiidae, Ambystomatidae, Salamandridae and Plethodontidae, which account for about ninety per cent of living salamander species. More detailed analyses of salamander vertebral evolution will be presented in future publications.

Generalized terrestrial salamanders as well as many of the specialized aquatic ones have notochordal vertebrae, in which the popular view of the salamander vertebra as a bony husk surrounding a notochordal remnant is not far wrong. The notochord is much more than a remnant, however. It is an integral, highly functional, differentiated part of the column, and comprises a very large proportion of the centrum (Fig. 11). In larvae, this notochord acts as an axial spring, and bits of cartilage appear in it at regular intervals, beneath the rudiments of the neural pedicels. In *Ambystoma* and in more derived groups among the salamandrids and plethodontids, additional cartilage appears in the notochord later in ontogeny. The production of cartilage occurs early, before vertebrae are well established, and the early bony pieces serve for little more than sites of attachment of



Abbreviations see p. 57

Figure 14. Frontal section through centrum and intervertebral joint of subadult *Notophthalmus viridescens* (28.7 mm, body length). The centrum is largely filled with cartilage, and the notochordal sheath is badly disrupted. The intravertebral notochordal cartilage is large, and the intervertebral cartilage is very large and highly differentiated in the joint region. Anterior to left. Azan stain

Bild 14. Frontalschnitt durch Centrum und Intervertebral-Gelenk eines subadulten *Notophthalmus viridescens* von 28,7 mm Länge. Das Centrum ist zum großen Teil mit Knorpel ausgefüllt, und die Chordascheide ist deutlich aufgerissen. In der Gelenkregion ist der intravertebrale Chorda-Knorpel groß, der intervertebrale Knorpel sehr groß und hoch differenziert. Vorderende nach links. Azan-Färbung

Figure 15. Frontal section through centrum of subadult *Notophthalmus viridescens*, illustrating vascular erosion of the intervertebral cartilage and notochordal cartilage. Erosion is initiated from the lateral margin of the centrum. Ossification of the inner centrum cartilage follows. Anterior to left. Azan stain

Bild 15. Frontalschnitt durch das Zentrum eines subadulten *Notophthalmus viridescens*, der die vaskuläre Erosion des intervertebralen und Chorda-Knorpels zeigt. Die Erosion beginnt vom lateralen Rand des Zentrums. Die Ossifizierung des inneren Knorpelzentrums folgt. Vorderende nach links. Azan-Färbung

Figure 16. Frontal section through intervertebral joint of adult *Taricha granulosa* (72 mm, body length). Most of the cartilage of the inside of the centrum has been converted to bone. Only a small amount of highly differentiated intervertebral cartilage remains to function as a joint. Anterior to left. Azan stain

Bild 16. Frontalschnitt durch das intervertebrale Gelenk einer adulten *Taricha granulosa* von 72 mm Körperlänge. Der Knorpel des Centrum-Inneren ist schon fast ganz zu Knochen umgewandelt worden, nur ein kleiner Betrag hochdifferenzierter intervertebralen Knorpels bleibt zur Gelenkfunktion erhalten. Vorderende nach links. Azan-Färbung

Figure 17. Frontal section through centrum and intervertebral joint of subadult *Plethodon jordani* (31.6 mm, body length). Note relative sizes of the intervertebral cartilage and the two kinds of notochordal cartilage. Anterior to left. Van Gieson stain

Bild 17. Frontalschnitt durch Centrum und Intervertebral-Gelenk eines subadulten *Plethodon jordani* von 31,6 mm Länge. Beachte die relative Größe des intervertebralen Knorpels und der beiden Arten von Chorda-Knorpel. Vorderende nach links. Van-Gieson-Färbung

Figure 18. Frontal section through centrum and intervertebral joint of adult *Desmognathus ochrophaeus* (39.8 mm, body length). Note large amounts of cartilage. Mineralization is proceeding at the base of the intervertebral cartilage. Anterior to left. Azan stain

Bild 18. Frontalschnitt durch Centrum und Intervertebral-Gelenk eines adulten *Desmognathus ochrophaeus* von 39,8 mm Länge. Beachte die großen Knorpelmassen. Die Mineralisierung schreitet an der Basis des intervertebralen Knorpels fort. Vorderende nach links. Azan-Färbung

Figure 19. Frontal section through intervertebral joint of adult *Phaeognathus hubrichti*. The intervertebral cartilage is highly differentiated and forms a condyle-cotyle complex. Cartilaginous contents of the notochord and parts of the intervertebral cartilage have been converted to bone, which forms a stout base for the articular condyle. Anterior to left. Van Gieson stain

Bild 19. Frontalschnitt durch das Intervertebral-Gelenk eines adulten *Phaeognathus hubrichti*. Der intervertebrale Knorpel ist hoch differenziert und bildet einen Condylus-Cotylus-Komplex. Die Knorpelbestandteile der Chorda und Teile des intervertebralen Knorpels sind in Knochen umgewandelt worden, der als derbe Basis des Gelenk-Condylus dient. Vorderende nach links. Van-Gieson-Färbung

the trunk muscles in flexing the notochord. This system is retained throughout life in many of the more primitive species in the various families. One is tempted to speculate that the ancestors of the salamanders were very small, semi-terrestrial tetrapods with paedomorphic tendencies which included a notochordal vertebral column. Under such conditions, one might visualize a situation in which selection for notochordal flexing takes precedence over selective pressures for other mechanical demands (in the sense of PARRINGTON's suggestions, 1967).

In the vertebral column of a generalized salamander such as *Ambystoma*, the notochord is retained throughout life and plays important functional roles. In the two areas of greatest stress, the site of attachment of the neural pedicel rudiments to the notochordal sheath and the center of the articular condyle on the anterior end of the centrum, the notochord is filled with cartilage (Fig. 12).

Ambystomatid notochords are somewhat smaller than are those of hynobiids. In adults, there is a well developed intervertebral cartilage, much more elaborated than in the presumably more primitive hynobiids. This cartilage is primarily hyaline, but immediately in front and in back of the ring of hyaline cartilage are found slightly differentiated cells which are a kind of fibrocartilage. The zone of flexion is the anterior fibrocartilage ring.

Salamandrids and plethodontids are somewhat more derived than ambystomatids. They have increased amounts of inter- and intravertebral notochordal cartilage. Some adult plethodontids, and juveniles of both salamandrids and plethodontids, resemble ambystomatids in notochordal dimensions. The notochord is badly disrupted in adult salamandrids and certain adult plethodontids.

Typical salamandrid larval vertebrae are similar in terms of organizational plan to those of adult *Ambystoma* (cf. Figs. 12, 13). As development proceeds in postmetamorphic salamandrids, the notochord becomes nearly completely filled with cartilage. The intervertebral cartilage becomes highly differentiated (Fig. 14) and a distinct zone of fibrocartilage marks the articular region. The posterior (major) part of the intervertebral cartilage is produced into a condyle, which contains a crushed and partially mineralized notochordal remnant in its center. Although the notochordal sheath is partially disrupted, the route of the structure is relatively clear and it is still a major, functionally important component of the vertebral column. Ossification of the mineralized columns of cartilage cells begins in the base of the intervertebral cartilage (Fig. 15). As the centrum grows, the course of the vertebral artery is impressed in the side of the vertebra in the vicinity of the base of the ventral rib bearer. Vascularization invades the inner core of the cartilage-filled centrum, eroding the cartilage and laying down a thin layer of bone in the remodeling process. Remodeling is extensive in salamandrids, and eventually results in the destruction of most of the central cartilage, including the intravertebral notochordal cartilage. Finally, only the bulk of the cartilaginous articular condyle of one vertebra, and the cotyle of the vertebra in front remains (Fig. 16). The cartilage of the articular condyle consists mainly of columnar, mineralized cartilage, with some articular fibrocartilage distally. The region of the joint is mainly fibrillar, not synovial (cf. MOOKERJEE, 1930). The production of these fibers is seemingly carried on by cells which differentiate from the original perichordal ring. This differentiation occurs anterior to the main part of the

intervertebral cartilage of early forms. The articular condyle is formed from the bulk of the intervertebral cartilage. Most salamandrids have a distinct terrestrial stage. Locomotion is of the "walking-girder" type and the vertebral column reflects the extensive transmission of forces through it.

Most generalized plethodontids resemble the ambystomatid condition. Usually more notochordal and intervertebral cartilage is present. This is particularly evident in the plethodontines (Fig. 17) *Aneides*, *Plethodon*, and *Ensatina*. In *Eurycea* and its relatives the articular condyle enlarges enormously. It is produced into a well developed structure that is much more condylar in form than its counterpart in *Plethodon*. Intervertebral notochordal cartilage is present, but it tends to be less well developed than in *Plethodon* and the notochord is soon squeezed and obliterated by the growing intervertebral cartilage. The condyle in *Eurycea* becomes heavily mineralized in old age. *Eurycea* and its allies (most of the tribe Hemidactyliini, WAKE, 1966) often use vigorous, sinuous locomotion, while *Plethodon* and its allies (tribe Plethodontini) rely more on limbs in locomotion.

Desmognathines are short, stocky plethodontids which are characterized by very strong, spring-like movements of the body in locomotion. Generalized members of this group have vertebrae that resemble those of *Eurycea* but with more cartilage, especially in the notochord in the intervertebral region (Fig. 18). They tend to have even more heavily mineralized intervertebral cartilages than *Eurycea* (see WAKE, 1963). I have not as yet seen ossification in *Desmognathus* or *Leurognathus* (WAKE, 1965), but it would not be surprising to find it in old adults. In *Phaeognathus*, a giant terrestrial relative of *Desmognathus*, ossification of the cartilage within the centrum occurs (Fig. 19), in a manner that at least roughly approximates that seen in salamandrids (WAKE, 1969). Invading blood vessels enter the centrum from the side, branching from the vertebral artery.

Neotropical plethodontids display a variety of centrum structure. Many of the more generalized species have relatively unspecialized vertebrae, similar in a broad sense to those of *Plethodon*. Curious developmental patterns are seen in diminutive members of the genera *Thorius*, *Lineatriton*, *Chiropterotriton*, and *Parvimolge*. MOOKERJEE (1930) first showed that the neural canal of *Triturus* increases in diameter during growth by a remodeling process. The inner margins of the neural arch are gradually resorbed, with new bone being added to the outer margins. *Thorius* is very small (adults may be less than 30 mm, standard length) and the bone of the centrum is thin. Resorption is sufficiently extreme that it obliterates the floor of the neural canal (i. e., the dorsal part of the centrum) in the midvertebral region, exposing the inside of the cartilage-filled centrum to vascularization. The bulk of the centrum is quickly resorbed, leaving only a faint scar of the notochordal remnant in the new floor of the neural canal (Fig. 20). However, this process also has the effect of producing a strengthened intervertebral joint which is probably a very important and highly selective feature. In other respects, *Thorius* is a slender and relatively weakbodied form, strongly affected by paedomorphosis (WAKE, 1966). Possibly the vertebral articulation is a compensatory adaptation. Much variation occurs within the vertebral column of a single individual in *Thorius*. For example, in vertebra N (Fig. 21)

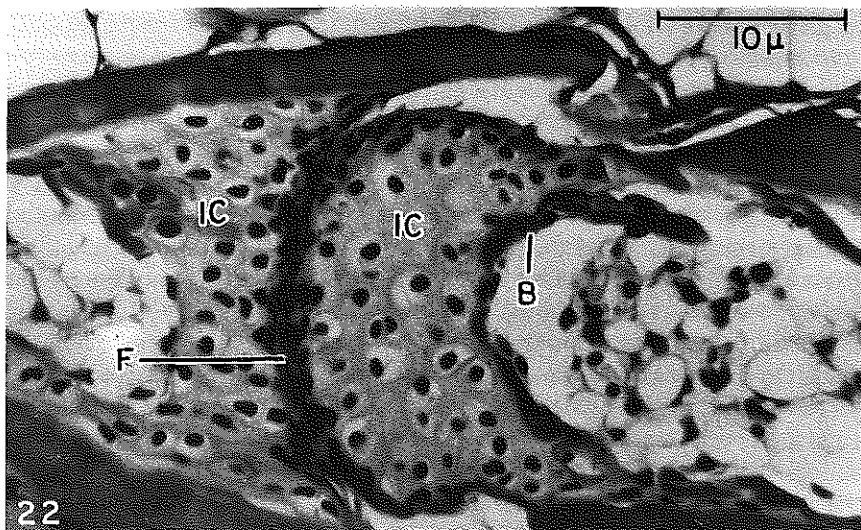
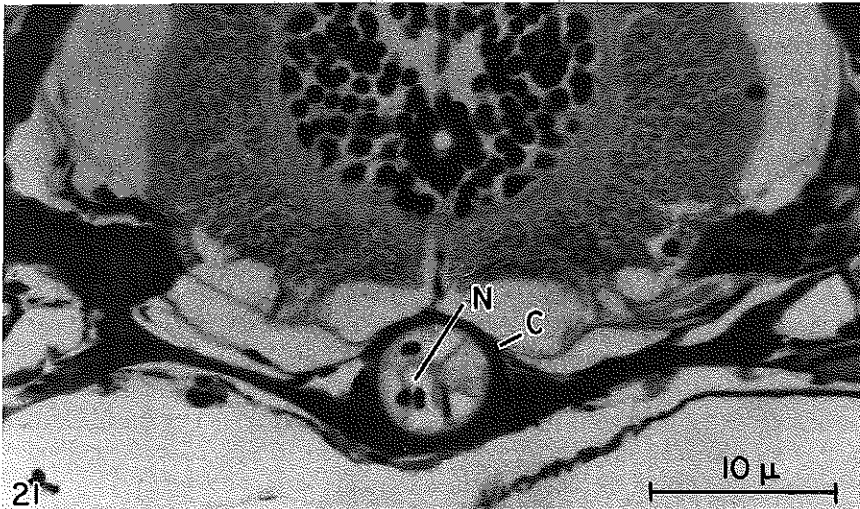
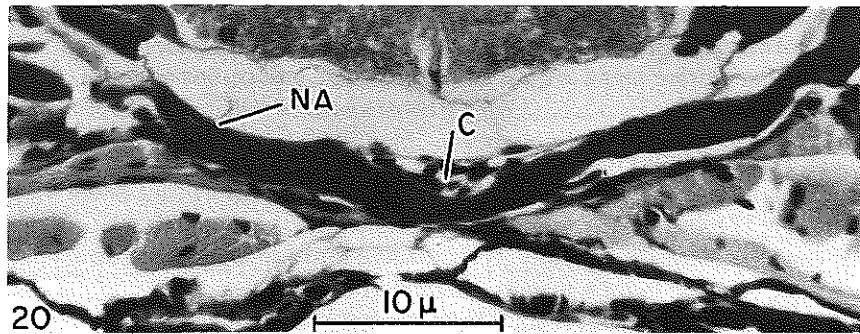


Figure 20. Transverse section through trunk vertebra N + 1 of adult *Thorius dubitus* (20.4 mm, body length). The dorsal and lateral surfaces of the centrum have been resorbed, exposing the contents to the inside of the neural canal, and the centrum is incorporated into the neural arch. Van Gieson stain

Bild 20. Querschnitt durch den Rumpfwirbel N + 1 eines adulten *Thorius dubitus* von 20,4 mm Länge. Die dorsale und laterale Oberfläche des Zentrums ist resorbiert und exponiert den Inhalt zum Innern des Neuralkanals, und das Zentrum wird in den Neuralbogen inkorporiert. Van-Gieson-Färbung

Figure 21. Transverse section through trunk vertebra N of adult *Thorius dubitus*. The centrum of this vertebra has not been resorbed at the midvertebral level, but the centrum is very small and is almost completely enclosed within the neural canal. Van Gieson stain

Bild 21. Querschnitt durch den Rumpfwirbel N eines adulten *Thorius dubitus*. Das Zentrum dieses Wirbels ist nicht resorbiert, aber sehr klein und fast ganz vom Neuralkanal umschlossen. Van-Gieson-Färbung

Figure 22. Frontal section through intervertebral joint of adult *Thorius dubitus*. The centra in this region have been eroded at the midvertebral level, and the notochord and cartilaginous contents of the centra have been replaced by bone and vascular tissue. The highly differentiated intervertebral cartilage forms a condyle-cotyle articular complex. Condyles and cotyles are supported by bony bases. Anterior to left. Van Gieson stain

Bild 22. Frontalschnitt durch das Intervertebral-Gelenk eines *Thorius dubitus*. Die Zentren dieser Region sind erodiert, die Chorda- und Knorpelbestandteile der Zentren sind durch Knochen und Gefäße ersetzt. Der hochdifferenzierte intervertebrale Knorpel bildet einen Condylus-Cotylus-Gelenk-komplex. Condylen und Cotylen werden durch Knochenbasen gestützt. Vorderende nach links. Van-Gieson-Färbung

Abbreviations:

A atlantal cotyle; AC developing articular condyle; AS anterior sclerotomite; B bone; BP basal plate; C centrum; CC cartilage cells; F area of flexion in the intervertebral joint region; G dorsal root ganglion; IC intervertebral cartilage; INC intervertebral notochordal cartilage; M myotome; N notochord; NA neural arch; NR notochordal remnant; O occipital condyle; P neural pedicel; PR perichordal ring; PS posterior sclerotomite; S notochordal sheath; VNC intravertebral notochordal cartilage

Abkürzungen:

A Atlas-Cotylus; AC sich entwickelnder Gelenk-Condylus; AS anteriorer Sklerotomit; B Knochen; BP Basalplatte; C Zentrum; CC Knorpelzellen; F Biegezone der intervertebralen Gelenkregion; G Dorsal-Wurzelganglion; IC Intervertebral-Knorpel; INC intervertebraler Chorda-Knorpel; M Myotom; N Chorda; NA Neuralbogen; NR Chorda-Rest; O Occipital-Condylus; P Neuralpedikel; PR perichordaler Ring; PS posteriorer Sklerotomit; S Chorda-Scheide; VNC intravertebraler Chorda-Knorpel

the integrity of the centrum is maintained and the outer bony cylinder is filled with cartilage. The notochordal sheath is largely disrupted and tends to be mineralized, but remnants of the cartilage-filled notochord, now almost completely surrounded by hypertrophied intervertebral cartilage, are plainly visible. The intervertebral joint region is well differentiated, with a distinct ball and socket arrangement. In vertebra N + 1 (Fig. 20) the floor of the neural canal (which is also the dorsal part of the bony centrum) is resorbed near the middle of the vertebra. The inside of the centrum is exposed for a distance that is about one-third to one-half of the total vertebral length. Over much of this distance the centrum has been incorporated in the neural arch, forming a circle of bone around the spinal cord. Near the ends of each vertebra, the centrum is separated from the neural canal by a thin layer of bone. The cavity of this area of the centrum, which is in broad continuity with the neural canal, is filled with haemopoietic tissue. Cartilage of the condyle (Fig. 22) is underlain by a thin layer of bone. The nature of the intervertebral articulation is structurally similar to the situation seen in salamandrids and in *Phaeognathus*, but in miniature. All are structurally opisthocoelous. However, the mechanisms responsible for this convergence are basically different in the groups. In the larger species vascularization of the inner parts of the centrum occurs from outside the vertebra. In the diminutive tropical species, vascularization of the centrum occurs from within the vertebra, via the neural canal.

Selection for increased strength of the centrum and of the intervertebral articulations has occurred in separate lineages of salamanders. In some groups, the addition of notochordal cartilage in areas of stress is the result, while in others the intervertebral cartilage hypertrophies and mineralizes. In still others, the notochordal sheath mineralizes in areas of stress, although the intervertebral cartilages remain relatively small. Finally, different lineages have independently converged on a kind of structural opisthocoely. This has occurred by two distinctive morphological modes in organisms that have very different structural plans and face different environmental selective pressures. The vertebral column can be highly instructive when one knows something about the total biology of the organism. However, interpretation of details of centrum morphology without reference to ontogeny, behavior and ecology is likely to provide little useful phylogenetic information within the salamanders and probably other groups as well. It is hoped that these findings will have broad significance in understanding evolutionary patterning in the sense of structural diversity and "richness" during the phylogeny of groups of vertebrates.

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