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On the Evolution of the Vertebral Column of Fishes

Hans Gadow and E. C. Abbott

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IV. *On the Evolution of the Vertebral Column of Fishes.*

By HANS GADOW, *M.A., Ph.D., F.R.S., and Miss* E. C. ABBOTT, *Bathurst Student, Newnham College, Cambridge.*

Received June 20,—Read June 21, 1894.

INTRODUCTORY REMARKS.

THE importance of the problems attempted in the present communication needs no special comment, but I have much pleasure in expressing my thanks to generous friends for kind assistance.

Mr. ADAM SEDGWICK put at my disposal his probably unique and comprehensive collection of well-preserved embryos and prepared slides, illustrative of the development of *Scyllium*, *Acanthias*, and *Acipenser*.

Professor W. N. PARKER lent the original sections which had been prepared by himself and F. M. BALFOUR for their work on *Lepidosteus*. He also agreeably surprised me with the loan of a well-assorted selection of slides of a young *Protopterus*.

Last, not least, I gratefully acknowledge the donation of £50 from the Royal Society, "for investigations into the anatomy of Elasmobranch fishes," May, 1892, which I therefore was able to collect and to study on the spot, namely, on the coast of Portugal.

In an investigation like the present it was absolutely necessary to learn the amplitude or range of variation, generic, specific, and individual, of the numerous, and therefore all the more variable, constituents of the axial skeleton. Thus alone true abstractions could be arrived at, instead of mistaking for essential that which, with more extensive experience, revealed itself as an unimportant departure from the general drift of evolution.

Miss ABBOTT'S share in this work is by no means merely manual. She not only prepared a great number of sections of *Petromyzon*, *Acanthias*, *Centrophorus*, and *Amia*, and "looked through" a total of several thousand sections, sorting, following up and sketching long series illustrative of the various points in question (the accom-

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panying figures being a mere selective fraction of those originally prepared), but she also went through the wearisome task of studying the involved literature bearing upon the subject.

The all-important overlapping of the various parts of successive protovertebræ was first traced by her, and caused an unforeseen long, but most fruitful, departure from the original plan of the work. Moreover, it is only fair to her to mention that she had found and satisfactorily traced the origin of the cartilage in the chordal sheath, when KLAATSCH's admirable work appeared in the spring number of the 'Morpholog. Jahrbuch,' 1893. Although we were clearly anticipated by him, both in this paper and in a second which followed in the summer of 1893, I thought it advisable to continue our line of research (being fortunately able to corroborate the points found by KLAATSCH), and not to publish disjointed results, but to wait until the whole work could be presented in a rounded-off form.

H. GADOW.

June 19*th*, 1894.

CONTENTS.

To prevent misunderstandings a number of technical terms used in this communication require some definition. Although apparently well known, and used by the morphologist almost like household words, their occasional promiscuous use has led to a surprising amount of uncertainty, fruitful of errors and misconceptions.

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*The Skeletogenous Layer** is a mass of cells derived from the protovertebral plates for the formation of the inner skeletal framework. We dismiss here the gratuitous hypothesis concerning mesenchyme.

The skeletogenous layer surrounds the chordal sheath, the spinal cord, and in the tail the principal blood-vessels, and extends peripherally in the shape of the inter-muscular septa. So long as and wherever this skeletogenous layer remains membranous it corresponds with the "membrana reuniens" of REICHERT.

The *Chordal Sheath* is originally the cuticular product of the chorda, which it surrounds; later on it is in many cases invaded by skeletogenous cells. The chordal sheath is surrounded by an outermost layer, the *Elastica Externa*, which, itself genetically part of the sheath, forms the original boundary between the latter and the skeletogenous layer.

* *Synonyms.*

Skeletogenous Layer.	STANNIUS.	Aeussere Scheide der Chorda or Zweite Gewebeschicht.
	GEGENBAUR.	Skeletbildende Schicht, Skeletogene Scheide.
	SCHEEL.	Skeletogene Schicht.
	KLAATSCH.	Skeletoblast.
		Perichordales Gewebe.
Elastica Externa.	Name invented by KÖLLIKER.	HASSE, SCHEEL, and most other authors.
	GEGENBAUR.	Aeussere elastische Lamelle der Chordascheide;
		Membrana limitans externa.
	WIEDERSHEIM.	In *Protopterus*: Aeussere Scheide der Chorda (of STANNIUS).
	KLAATSCH.	Elastica.
	HASSE.	In *Elasmobranchs*: Elastica or Cuticula Skeleti.
		In Ganoids: Elastica.
Elastica Interna.	Name invented by KÖLLIKER, 1860, both in Elasmobranchs and Teleostei.	
	J. MÜLLER.	*Holocephali*: Fibroese Scheide.
	STANNIUS.	Eigene Scheide der Chorda.
	GEGENBAUR.	Innere Lamelle der Chordascheide.
		Membrana limitans interna.
		Cuticulare Membran.
		Cuticular-Schicht.
	HASSE.	Ganoids: Cuticula Chordæ, Faserschicht.
		Elasmobranchs: Elastica Interna.
	SCHEEL.	*Teleostei*: Chorda-Scheide.
Chordal Sheath invaded by skeletogenous cells, or Cellular Chordal Sheath.		
	KÖLLIKER.	Elastica interna mit fibroeser Mitte.
	GEGENBAUR.	Binde-substanz-schicht, Bindegewebs- oder Knorpellage in der Chorda-Scheide.
	WIEDERSHEIM.	*Protopterus*: Innere Scheide der Chorda.
Chordal Sheath in general.		
	GEGENBAUR.	*Lepidosteus*: Ganze Chorda-Scheide.
	BALFOUR.	Chordal Sheath.
	KLAATSCH. } SCHEEL. }	Chorda-Scheide.

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We distinguish, therefore, between several conditions and parts of the chordal sheath as follows:—

Elastica Interna = chordal sheath in its original condition.

Cellular Chordal Sheath = chordal sheath containing also skeletogenous cells.

Elastica Externa = outermost boundary of the whole chordal sheath.

Concerning the segmentally arranged mesodermal products (omitting nephrotomes and gonotomes) the following subdivision is adhered to:—

Protovertebra divides into { Myotome, which produces { Cutis. / Myomere. } / Two sklerotomes, two of which produce one skleromere. }

Considerable uncertainty exists about the use or application of the terms: Muscle plates, Myotomes, Wirbelkörper, Ursegmente, &c.

REMAK clearly meant by Platte or Tafel the whole layer from head to tail, which, by transverse splitting or segmentation, changed into "die Urwirbel," or protovertebræ. In the same way, REMAK'S Muskelplatte is the sum total of all the future muscular mass regardless of segmentation.

GOODSIR ('Brit. Ass.,' 1856; 'Edin. New Phil. Journ.,' vol. 5, 1857, p. 122), proposed the terms myotome and sclerotome for segments of the muscular and of the skeletal system. These terms, originally invented without reference to embryology especially, have gradually been more and more adopted in embryological parlance. As pointed out by VAN WIJHE (see footnote, p. 7), the tendency has made itself felt to assign to the compounds of *tome* a somewhat different meaning to those of *mere*. HIS, apparently in 1868, was the first to introduce a new meaning for the expression Muskelplatte, and thereby to cause confusion. He used it, namely, as the equivalent of the outer half (Urwirbelrinde) of *one* Urwirbel, in a transverse instead of a horizontal direction. This has led to confusion whenever "Urwirbelplatten" and "Muskelplatten" are used. The same mistake, or carelessness, was committed by KÖLLIKER. Instead of one right and one left head-to-tail Muskelplatte, there are now as many as there are segments!

FOSTER and BALFOUR were misled by this changed application of the term Muskelplatte. Another most unfortunate mistake is that KÖLLIKER speaks of the lower, or ventral, or inner half of the Urwirbel (Protovertebra) as the "*eigentliche Urwirbel.*" REMAK'S term, "primitive Wirbel," is infinitely better and clearer.

HATSCHEK'S *Ursegmente*, applied to cases in which, as in Amphioxus, the whole of the mesoblast is segmented (not yet differentiated into Urwirbelplatten and Seitenplatten, although segmented), are the same as some of the anterior head *somites* of VAN WIJHE.

It will be observed that the *Somites*, as used by BALFOUR ('Comp. Embryol.,' vol. 2), and the *Ursegmente*, as used by HATSCHEK, in 1888, are not completely segmental successive parts because they include the non-segmented lateral plates

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besides the protovertebræ. Moreover MINOT'S primitive segments are not at all the same as either Ursegmente or Somites. They are, in reality, the same as RUECKERT'S Mesoblastsegmente.

A fruitful source of error, and of vagueness, is the Mesenchyme hypothesis. Since the gratuitous assumption was once made that the skeletal parts were produced out of "Mesenchyme," it followed that there was no longer any room for the Sklerotomes (which produce the whole of the skeletogenous cells) within, or as part of, the protovertebræ. Consequently, the "Ursegmente" assumed a third meaning, hitherto undefined.

Lastly, whilst MINOT considers myotome as equivalent to protovertebra, MARSHALL used myotome as synonymous with muscle segment in the adult, consequently, as different from muscle plate.

Although most authors are probably aware of the degree of imperfect correspondence of the technical terms as used by them, with those of other authors, this does not necessarily apply to their readers unless they have, perhaps, spent a considerable amount of labour in trying to arrive at the exact equivalent of the various terms. To mitigate the prevailing uncertainty, I make the following suggestions :—

The term *Myotome* is to be restricted to the whole remainder of the protovertebra after the skeletogenous cells have been given off for the production of the *Sklerotomes.*

The sum total of the Sklerotomes makes up the Skeletogenous Layer.

The ending *tome* to indicate the primary, or earlier, less differentiated,

the ending *mere* to signify the final condition or product.

Hence, each *Myotome* produces (1) one Myomere, or segment, of the general mass of trunk muscles; (2) Cutis (out of the "aeussere Lage," or Rindenschicht, KÖLLIKER, p. 208).

Of *Sklerotomes,* there are two to each protovertebra, namely, a ventral and a dorsal Sklerotome; two Sklerotomes combine to form one *Skleromere, i.e.*, a vertebra in the widest sense, in fact, a skeletal trunk segment.

The sum total of the Sklerotomes forms the so-called membranous vertebral column, extending upwards and downwards as the "Membrana reuniens" of REICHERT, and outwards in the shape of the intermuscular septa.

The ventral sklerotomes correspond exactly with the sklerotomes of VAN WIJHE and RABL. The dorsal sklerotomes have hitherto been neglected. BALFOUR stated correctly that in Stage L of his *Elasmobranchs* there appear four thickenings, namely, two dorsal and two ventral; they are, according to him, not segmented, but form four ridges along the sides of the spinal cord; correctly, again, he interpreted these ridges as the indications of, or material for, the future "neural and hœmal arches."

REMAK, 1851 . . . . . . ('Untersuchungen')	Urwirbelplatte (in opposition to Seitenplatte) zerfällt in *Urwirbel*	Rueckentafel oder *Muskelplatte*	Wirbelkernmasse, consisting of *primitive Wirbel*

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GOODSIR, 1856	. . . .	Myotome	Sclerotome
GEGENBAUR, 1862 ('Wirbelsäule')	Urwirbel		Primitive Wirbelkœrper und *Bogen*
OWEN, 1866* ('Comparative Anatomy')	. . . .	Myocomma	Scleromere
HIS, 1868 ('Untersuchungen')	Urwirbelplatten und Urwirbel	Urwirbelrinde . . . P. 118. "Rueckentafel oder Muskelplatte scheidet sich vom uebrigen Urwirbel ab"	Urwirbelkern
LANGERHANS, 1873	. . . .	"Muskelplatten" are used in a new and confused sense	
HAECKEL, 1874 ('Anthropogenie')	Urwirbelstrang und Seitenplatte		
FOSTER and BALFOUR, 1874	*Protovertebra* . . .	P. 136. Outer half, or "muscle-plate"	"Rest still called Protovertebra"
SCHENK, 1874 ('Vergl. Embryologie')	Urwirbel	P. 74. Peripherischer .	Centraler Theil
BALFOUR, 1876 ('Elasmobranchs')	P. 86. The protovertebræ constitute the vertebral plate. P. 105. The vertebral plates are split up into series of segments (Protovertebræ)	P. 107. After the separation of the vertebral bodies from the Protovertebræ *the remaining parts of the Protovertebræ may be called the muscle-plates*	Vertebral bodies
QUAIN, 1876 ('Anatomy.' 1.)	. . . .	P. 185. The muscles of the trunk being subdivided into zones or myotomes by partitions, or	Sklerotomes. [These partitions are, in fact, the primitive Wirbelbogen of GEGENBAUR]
KÖLLIKER, 1876 ('Entwicklungsgesch.,' 1st ed.)	Urwirbel	"Oberer Theil des Urwirbels ist die *Muskelplatte*, von REMAK." 2nd ed., p. 804. "Aeussere Lage [Cutis, &c.] und innere laengsfaserige Schicht der Muskelplatte"	Unterer Abschnilt den *eigentlichen Urwirbel* darstellend

* OWEN, in a footnote to p. 203, vol. 1 of his 'Comp. Anat. Vert.,' gives rise to the impression that he had invented the term "myocomma" already in 1849 (namely, in his work "On the Nature of Limbs"), before GOODSIR, in 1856, proposed the term "myotome."

In the essay "On the Nature of Limbs," however, only *osteocomma*, meaning a complete "skeleton segment," but nothing approaching myocomma, is mentioned.

In the same footnote, the terms *osteomere*, *scleromere*, and *neuromere* are suggested as more appropriate than GOODSIR's sclerotome and neurotome.

In the text-book, 1866, *myocommata* are spoken of as divided by the aponeurotic septa. Myocommata are identical with myotomes in GOODSIR's sense, or myomeres of later authors, but the fact that the term

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HASSE, 1879	Urwirbel		*Vorwirbel*
HATSCHEK, 1881 ('Amphioxus')	*Ursegmente*, including the whole segmental mesoblast		
v. WIJHE, 1882* ('Mesoderm Segmente . .')	Somit	*Myotom* oder Muskelsegment	Sklerotom oder Skelettsegment besser Bindesubstanz - segment
H. JACKSON, 1888 ('Forms of Animal Life')	"Primitive division into Somites or Myomeres"!		
RABL, 1888	. . . .	Seitenrumpfmuskulatur und Cutis	Sklerotom
RUECKERT, 1888 ('Excretionsorgane')	Dorsaler Abschmitt der Mesoblastsegmente = P. 254. Ventraler Abschnitt =	Myotom . . . . + Nephrotom	Sclerotom
DUVAL ('Atlas d'Embryologie')	Prévertèbres. (Lame prévertébrale)	Partie périphérique (Lame musculaire)	Partie centrale
O. HERTWIG ('Entwicklungsgesch')	. . . .	Muskelplatten in the sense of muscular segments	[Anything corresponding with sklerotome has been eliminated out of the protovertebra through the Mesenchyme hypothesis]
MINOT ('Embryology')	Primitive segment = I. "Myotome or Protovertebra of authors"! This produces . . . II. Nephrotome	{ 1. . . . . 2. True muscle plate [our myomere] 3. Conversion of the outer wall into Mesenchyma to form the dermal layer.	Mesenchyma from the inner wall of the Myotome [our Sklerotome]
MARSHALL ('Embryology')	Protovertebra . . .	P. 323. Muscle plate (dorsal half of the divided protovertebra) P. 119. "Muscle segments or myotomes" in the adult.	

myocomma as expressive of no new meaning had become superfluous, may justify the now rather common use of the word myocomma in the sense of intermuscular septum.

* WIJHE, p. 7, footnote. "Die Worte Myomer und Scleromer sind von verschiedenen Autoren für die Muskeln und die Bindesubstanz der Kœrpersegmente angewendet. Es gehœren zu den Myomeren sowohl die Muskeln welche aus den Somiten als diejenigen welche aus den Seitenplatten stammen. Ein Myotom ist demnach nur ein Theil eines Myomeres. In gleicher Weise ist ein Sklerotom nur ein Theil eines Skleromeres."

H. v. JHERING ("Peripher. Nervensyst. d. Wirbelthiere," 1878, p. 222) seems to be the first who used the terms Myo- Neuro-Sklеromere for "Muskel- Nerven und Skeletsegmente" of the adult vertebrate.

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The names of the Cartilaginous pieces which form one Skleromere or Vertebra, inclusive of appendages.

I propose the use of the following terms :—

Arcualia	Basalia	Basidorsalia	Supradorsalia	Dorso	Spinalia.
		Basiventralia	Ribs	Ventri	
	Interbasalia	Interdorsalia	Supra-inter-dorsalia.		
		Interventralia	Infraventralia.		

The term "arches" is liable to confusion if we take into consideration that the distal portion of a ventral arch when differentiated off constitutes a rib, and that ribs are as much ventral trunk "arches" as there are branchial and visceral "arches."

The distinction between "arches" and intercalary pieces is arbitrary. In many cases the intercalaries are more of the nature of "neural arches" than the neighbouring pieces or supposed true arches.

Frequently it is stated (for instance in WIEDERSHEIM'S "Text-book") that the "dorsal arch" is perforated by the motory root, the intercalary by the sensory root of the spinal nerves. In reality, this is no criterion whatever, not holding good even in closely-allied genera of *Elasmobranchs.* Nor is the statement that the "dorsal intercalaries" take up an intervertebral position of any practical use.

JOH. MÜLLER'S account ('Vergl. Anat. Myxinoiden,' pp. 151 and 155) of these various cartilages is most confusing.

Most of OWEN'S (Arche-type) names proposed for the ideal constituents of a vertebra are inapplicable, because they cannot be defined (being based upon preconceived theoretical notions), or because they have been used by various authors in different senses.

Arcualia seems to be a suitable term for all the cartilaginous paired pieces both on the dorsal and on the ventral side of the chordal sheath; they are distinguished as *dorsalia* and *ventralia.*

The Dorsalia consist of :—

1. *Basidorsalia.*—The cartilages produced by the dorsal halves of the sklerotomes, and resting chiefly around the spinal cord and above the chorda. They are frequently pyramidal, resting with their bases on the chordal sheath, often perforated by the motory root of the spinal nerve, generally carrying the dorsal spinous processes or pieces if such are present.

Synonymous terms :—

Obere Wirbelstücke welche die Bögen bilden } J. MÜLLER.
Knorpelbogen oder Knorpelige Schenkel . . }

Genuine Bogenschenkel, cartilagines crurales. STANNIUS.

Dorsal, upper, neural-arches.

Neurapophyses. Neuralbögen, obere Bögen der Neurapophysen.

Cruralstücke. JHERING.

Intercalaria-neuralia. HASSE in *Acipenser.*

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2. *Interdorsalia* produced by those cell masses of the ventral halves of the Sklerotomes which have grown dorsalwards, and have there founded cartilages which now lie between two successive basidorsalia.

Frequently these interdorsals are pyramidal or wedge-shaped, with the apex directed down towards the chordal sheath, which they may or may not reach. Often, but by no means in the majority of cases, these interdorsals assume an intervertebral position, hence the name assigned to them by MÜLLER.

Synonyms.

Intercalaria corporum s. intercalaria superiora. MÜLLER.
Schaltstücke; dorsal intercalaries.
Intercalaria neuralia.
Intercalarstück. ROSENBERG, JHERING.
Neurapophysen. HASSE, occasionally.

Supradorsalia.—By this term I propose to distinguish a second system of paired cartilages, which are carried by the primary series, namely, by the basalia and inter-basalia, and are genetically their separated-off distal portions. Their ventral counterparts are the ribs, as the free portions of the basiventralia. Supradorsalia are in fact, the true representatives of "Diapophyses" in OWEN's arche-type vertebra,* just as in reality the ribs are the "Hæmapophyses." These supradorsals are generally present as separate pieces, when basi- and inter-dorsalia do not meet above the spinal cord, in which case the Supra-inter-dorsals fill the gaps and complete the roofing-in of the spinal canal. Their position is always below the dorsal longitudinal ligament, which is so prominent in all cartilaginous fishes, less in the osseous Ganoids, vestigial in Teleostei.

It is necessary to distinguish between two kinds of supradorsalia, in order to be absolutely correct when necessity requires their being mentioned.

3. *Supra-basi-dorsals.*—Double paired cartilages in larva and young of *Lepidosteus*; *na'*, in fig. 81 of BALFOUR-PARKER; *a''* 'Fortsätze der Bögen,' GEGENBAUR, Lit. (p. 57) No. 8, figs. 3 and 4. Present as double cartilages also in the young *Protopterus*, where they are actually connected by a thin string of cartilage with the broad top of the low basidorsalia (fig. 13). GRASSI described them as present in young *Teleostei*, and as developed out of the "upper arches." Frequently they are fused with the tops of their basi-dorsals, and this may be either a primary or a secondary feature, *e.g.*, in the tail of many Rajidæ. In most bony fishes these supra-basi-dorsals lose their independence by ossifying together with the basalia, forming there the unpaired neural spine, the right and left halves being likewise fused together.

4. *Supra-inter-basals.*—Double, paired cartilages, situated behind the previously described pairs. Mentioned by BALFOUR as intercalated cartilaginous elements of the neural arches (*ic.* in his figures). GEGENBAUR's 'Schluss-stücke' (*a'* in his figures).

* In reality, not in the scheme of the arche-type, because OWEN considered vertebral (or dorsal portion of) rib + sternal (ventral portion of) rib = pleurapophysis + hæmapophysis.

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GRASSI describes them as paired cartilages, which, later on, fuse across, and then grow downwards with their free ends grasping like a semi-ring half way round the spinal canal (tegola in some of his illustrations).

Present as paired cartilages in the young of *Amia* (S.I.B. in figs. 8 and 12), and in *Lepidosteus* (S.I.B. in figs. 9–12); in young *Protopterus* they are represented by a mass of connective tissue.

In Elasmobranchs these supra-inter-dorsals are fused into an unpaired piece, which forms a little bridge across the spinal cord, filling the gap between the tops of two successive supradorsals.

In the literature these supradorsals are mentioned promiscuously as Intercalaria spinalia. MÜLLER, HASSE (?).

'Schluss-stücke,' Cartilagines impares: STANNIUS, GEGENBAUR, ROSENBERG. 'Obere-Schluss Knorpel.' HUBRECHT.

5. *Dorsospinalia.*—Unpaired prolongations of the dorsalia lying in the middle vertical plane. They may each consist of several superimposed systems of cartilaginous rods, *e.g.*, Ceratodus, or they may form the ordinary "dorsal spinous process."

Synonyms:—

'Schluss-stücke.' HASSE (sometimes in Elasmobranchs).

Intercalaria accessoria. HASSE.

The *Spinalia*, the same applying to both dorsals and ventrals, often carry the fin rays proper. Fusion with them may render distinction difficult, although they are fundamentally different, the spinalia being outgrowths, or direct continuations of the endoskeletal elements, while the fin rays proper are ectoskeletal, no matter if epidermal, mesodermal, or both. It is very probable that the spinalia were originally paired, as, indeed, most, if not all, bilateral organs; *cf.* the condition of these spinalia in the *Cyclostomes*.

The *Ventralia* consist of—

6. *Basiventralia.*—The cartilages produced by the ventral halves of the sklerotomes, and chiefly resting below and laterally upon the chordal sheath. These basiventrals carry the *ribs*, if such be normally present. Sometimes the basiventrals, or the interventrals, are mistaken for ribs.

Synonyms:—

Basilarstücke, untere Wirbelstücke. MÜLLER.

Ventral, lower, hæmal arches.

Untere Bogen. Blutbogen! HASSE.

Hæmapophyses (not OWEN).

Pleurapophyses. OWEN (sometimes).

Costa, Rippe. ROSENBERG.

Parapophysen. OWEN, GEGENBAUR (sometimes), SCHEEL.

Basal stumps. Basalstümpfe. WIEDERSHEIM (sometimes).

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7. *Interventralia.*—Produced by the apices of the dorsal halves of the sklerotomes which have grown ventralwards, and have there founded cartilages which now lie between two successive basiventrals.

Synonyms :—

Ventral Intercalaries.
Intercalaria hæmalia.
Untere Schaltstücke. HUBRECHT.
Parapophyses. ROSENBERG, ZITTEL.

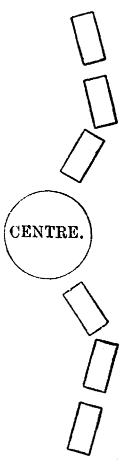
8. *Infraventralia* seem to occur in Elasmobranchs and cartilaginous Ganoids, especially in the tail, corresponding with the supra-inter-dorsalia.

9. *Ventrispinalia.*—Unpaired prolongations of the ventralia in the middle plane. They either consist of several systems of rods, or they form the ordinary ventral spinous process. In the tail they are frequently carried by, and often fused with, the ribs, *e.g.*, *Amia.*

To complete the account of an entire skleromere, we have to mention the centre or body, namely, that mass of tissue which, after deduction of the chorda itself, holds the basal portions of the arcualia together. This vague definition is, nevertheless, the only true one which is applicable in all cases.

It is much to be regretted that OWEN'S terms of the constituent parts of his ideal vertebra cannot be applied. The confusion resulting from the wilfully arbitrary application of almost every one of his terms to one or more different elements renders hopeless any attempt to revive their original meaning.

For comparison I append the following scheme :—



Neurapophysis = dorsospinals, paired or unpaired, consisting of one or more superimposed rods of cartilage.

Diapophysis = supradorsals.

Neurapophysis = basidorsals and interdorsals.

Pleurapophysis = basiventrals and interventrals.

Hæmapophysis = rib and infraventrals.

Hæmal spine = ventrispinals.

The nine (with ribs, ten) different sorts of arcualia mentioned above, are, strictly speaking, not all of the same morphological value. The basalia and interbasalia are of primary rank, while the supradorsals and dorsospinals are of secondary rank only. It can be proved by the comparative method that these supradorsals and dorsospinals are the distal portions which are separated off from the basalia. They are extremely

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variable in size, position, and number, sometimes fusing with neighbouring cartilages, and then apparently absent, sometimes wedged in; either very insignificant, and only functioning as stop-gaps, or developed into high and large fin-supporting rods or blades. Their amplitude of variation can be studied in the vertebral column of *one* individual, for instance, in a grown up *Carcharias glaucus*.

It is not always easy to recognize these extra cartilages, and this accounts for their perplexing synonymy. In most cases they are ignored; occasionally their existence has been noticed, but they are summarily dismissed in such terms as the ventral arch (or dorsal arch, as the case may be) is broken up into several little pieces. In most, although not in all Elasmobranchs, these intradorsals and dorso-spinals attain greater size and significance in the tail, frequently growing downwards so as to assume an intercalated position between the principal basalia and inter-basalia. In such cases the number of arcualia standing upon the centre or body of a vertebra is increased or doubled within the extent of a complete segment.

Elasmobranchi.

Development of the Chorda and its Sheath.

In the tail of embryos of *Scyllium catulus* 7 millims. in length, the chorda consists of protoplasm with nuclei aggregated in the central position. Further forward, in the trunk, corresponding with later stages of the tail, the nuclei are scattered throughout the chorda, and are connected with each other by protoplasmic strands. Still further forwards, the central portion of the chorda is composed of a very loose network of protoplasm, while the nuclei are gone, and are restricted to the peripheral zone, forming there the so-called chordal epithelium. No outlines of cells can be distinguished in this zone, but only a few nuclei, imbedded in a somewhat denser ground substance, which, probably owing to shrinkage, appears as an irregular zone against the inner meshwork. In later stages the strands of the meshwork disappear in the centre, while the thickness of the peripheral zone increases, together with an increased number of nuclei (see figs. 22–28 on p. 176). Ultimately, when cartilaginous arches and centra of the vertebræ are already well advanced, the zone of epithelium disappears, and only radiating strands remain, as shown in fig. 29, on p. 176.

Very early the chorda becomes surrounded by a membrane or sheath, which, at its earliest appearance, begins to differentiate itself into two layers of different physical and chemical properties, namely (1) an inner layer, henceforth called the *chordal sheath proper*, or *Elastica interna*, which ultimately assumes a considerable thickness and initiates what is frequently spoken of as the membranous vertebral column; (2) an outermost layer, the *Elastica externa*, always very thin and highly refracting. The origin, formation, and nature of this Elastica externa has given rise

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to many misconceptions. HASSE (Lit. 14) originally went so far as to deny its existence as a membrane; he explained it as a circular system of slits within the skeletogenous layer at a variable distance from the chorda. However, in Dipnoi it forms a thin but completely solid ring, not of interstices or slits, but of an apparently dense and highly refracting membrane, proving thus its existence as a separate layer. On the other hand, in Elasmobranchs, this Elastica externa, even in its earliest stages appears as a broken line, which is in direct contact with the chordal sheath, as depicted in figs. 17–19.

The chordal sheath itself makes its beginning as a very thin line only, being then easily confounded with the Elastica externa, fig. 18; soon however, between the latter and the chordal epithelium appears a membrane, at first very thin and hyaline, then continuously increasing in thickness and being composed of an ever increasing number of concentric lamellæ, or fibrillæ in sections. This *Chordal sheath* or *Elastica interna*, or Membrana limitans interna, is not a membrane of cells, but a cuticular product of the chorda itself. This is now the generally accepted view, first propounded by GEGENBAUR.

According to HASSE, however, it is fundamentally different from the chordal sheath, being produced by the cells of the skeletogenous layer, either as a system of lymph spaces, or as a structureless, cuticular membrane, hence called by him Cuticula skeleti in Ganoids.

KLAATSCH (Lit. 21, I.) considers the Elastica externa likewise as genetically different from the chordal sheath, being probably derived from his perichordal tissue (our skeletogenous cells), it being in his opinion unlikely that the chorda should produce two layers chemically and physically different.

However, both the Elastica interna and externa occur in very early stages, even before the skeletogenous cells have separated themselves from the "muscle plates," and are moreover always in closest contact with each other, before any of the skeletogenous cells have appeared in the vicinity of the chorda.

Lastly, the elastica externa is also very early formed on the dorsal side, where the chorda touches the spinal cord, while there are not yet any but chordal cells to form the Elastica.

We have, therefore, to assume that the Elastica externa owes its existence to an early differentiation of the originally extremely thin entire chordal sheath into highly refracting elements which arrange themselves peripherally, and into an inner, at first likewise hyaline transparent cuticular layer which soon thickens and grows concentrically. The concentrically fibrillar appearance of the Elastica interna itself, which is never absent, is caused simply by the alternation of denser and less refracting layers with each other.

This view of the chordal origin of the Elastica externa is supported by some further observations:—(1) The Elastica externa nowhere, not even in Dipnoi, assumes any appreciable thickness, appearing in embryonic fishes at best as a colourless silky

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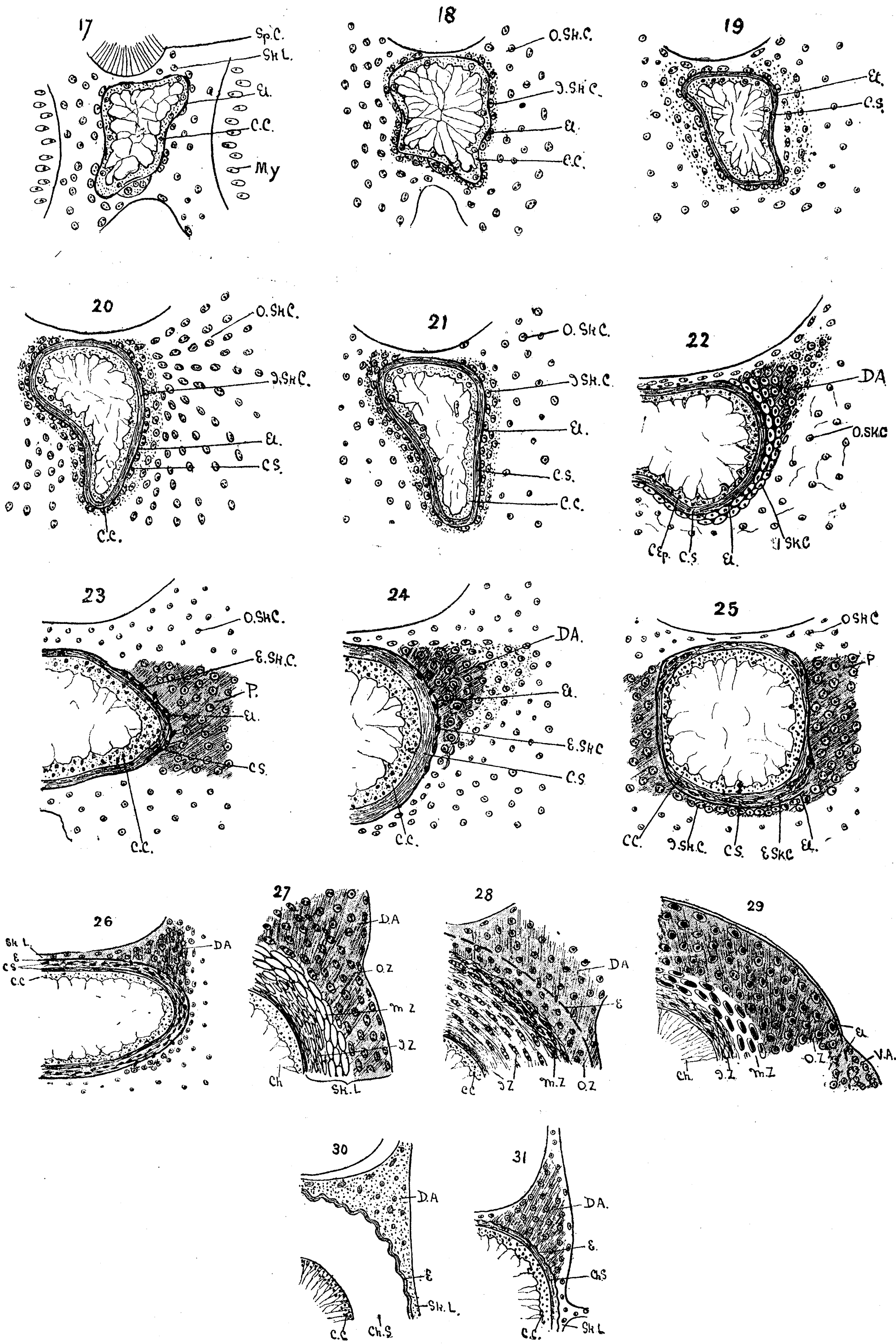

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Figs. 17–29. Transverse sections through *Scyllium catulus*, *Acanthias vulgaris* and *Centrophorus granulosus*. Showing the aggregation of skeletogenous cells round the chordal sheath and their entrance into the sheath.

Fig. 17. *Scyllium*, 7 millims. Trunk. Elastica externa as a broken membrane; skeletogenous cells not yet aggregated round the chorda, but scattered uniformly through the whole space between chorda and myotome.

Fig. 18. *Scyllium*, 8 millims. Trunk. Formation of an innermost zone, *I.Sk.C.*, and an outermost, much broader zone of the skeletogenous layer.

Fig. 19. *Scyllium*, 9 millims. Behind the head. Chordal sheath visible as a thick hyaline membrane, bounded by the elastica externa. In this section a refracting line is seen also on part of the *inner* side of the chordal sheath. The inner zone of the skeletogenous layer now consists of two rows of cells round the chordal sheath, and forms a layer which stains deeply.

Fig. 20. Same embryo as fig. 19. Anterior portion of trunk. The cells of the outer zone assume a radiating arrangement.

Fig. 21. Same embryo. Posterior portion of trunk, resembling section, fig. 19.

Fig. 22. *Acanthias vulgaris*, 11 millims. Anterior portion of trunk. Accumulation of cells for the formation of dorsal arcualia.

Fig. 23. *Acanthias*, 14 millims. Posterior portion of head. P = lateral mass of cells which are about to form the parachordals. Some of the skeletogenous cells are beginning to make their way through the elastica externa into the chordal sheath.

Fig. 24. Same embryo. Trunk. The dorsal arcualia are becoming cartilaginous, especially near the elastica. Cells have passed through the latter and are flattening out against the inside of the elastica.

Fig. 25. *Acanthias*, 15 millims. Head. Flattened skeletogenous cells are now in the chordal sheath, which has become fibrous.

Fig. 26. Same embryo. Trunk. The inner zone of the chordal sheath is still free from invading cells. The invasion is most marked in the region of the basis of the arches.

Figs. 27, 28. *Centrophorus granulosus*. Nearly ripe embryos. Showing the three zones of the chordal sheath.

Fig. 29. *Scyllium*. Nearly ripe embryo.

Fig. 30. *Petromyzon fluviatilis*. Young. The thick chordal sheath is bounded by a thick elastica externa. On the outside is a partly cartilaginous dorsal arch, which is continued ventrally into the indifferent skeletogenous layer or membrana reuniens.

An example of an acentrous axial skeleton.

Fig. 31. *Salmo salar*. Just hatched. The chordal sheath is very thin; it receives no skeletogenous cells through the elastica externa, which is only about 1·5 μ in thickness. Centra of vertebræ are about to be formed by the fusion of the dorsal and ventral arcualia with each other; the arcualia remain in the skeletogenous layer and chondrify, calcify or ossify, as the case may be.

An example of an arco-centrous vertebral column, in opposition to the chordo-centrous type shown by figs. 28 and 29.

Explanation of Lettering to Figs. 1 *to* 30.

BV. = Blood-vessel.
Ch. = Chorda.
C.C. = Chordal cells.
C.S. = Chordal sheath.
D.A. = Dorsal arcuale.
D.R. = Dorsal root of spinal nerve.
E. = Membrana elastica externa.
S.Z. = Inner zone of metamorphosed chordal sheath.
L.Sk.C. = Lower skeletogenous cells from ventral half of sklerotome.
M.P. = Myotomic portion of a Protovertebra.
M.Z. = Middle zone of metamorphosed chordal sheath.
N. = Nerve.
O.Z. = Outer zone of cartilaginised chordal sheath.
Sp.C. = Spinal cord.
Sk.L. = Skeletogenous layer.
Up.Sk.C. = Upper skletogenous cells; cluster from dorsal half of skelerotome.
V.R. = Ventral root of spinal nerve.

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thread of perhaps 1 to 2μ in thickness; it does not seem to grow much in thickness, but frequently breaks up in numerous irregular places, independently of the perforations by the invading skeletogenous cells to be mentioned hereafter. (2) The following peculiarity is sometimes seen in sections: The refracting membrane lies in part of one section on the inner side of the chordal sheath; that is, the right side of one section shows the Elastica externa on the inside of the chordal sheath, while the left side shows it on the outer surface. This may in some cases be due to oblique or similarly disturbed sections, but in the trunk of Acanthias (fig. 13) a refracting line has been observed both inside and outside the chordal sheath for a great part of the circumference. This, although exceptional, tends to show that the chordal sheath can occasionally secrete refractive elements on either side.

Aggregation of Skeletogenous Cells round the Chordal Sheath.

After the completion of the chordal sheath, the skeletogenous cells (themselves derived from the inner halves of the protovertebræ) begin to arrange themselves round the chordal sheath. As the tail generally shows earlier stages than the trunk, a forward gradation can be made out in each embryo in passing from the tail towards the head.

When first formed, the skeletogenous cells do not yet appear in the vicinity of the chorda, but are scattered uniformly through the whole space between the chorda and the myotomes, but in the embryos of Acanthias and Scyllium of about 7 millims. in length, some of the innermost cells come close to, and flatten themselves against the chordal sheath (fig. 17). This process continues so that soon a ring of flattened cells is formed, and thus an outer and an inner zone of skeletogenous cells can be distinguished (fig. 18). The inner zone increases in thickness, being composed of two or three layers of cells, a few more in the bases of the future arcualia, while the cells of the outer much broader zone arrange themselves in radiating rows (fig. 20).

Invasion of the Chordal Sheath by Skeletogenous Cells.

The formation of a mantle of skeletogenous cells round the chordal sheath ushers in a new stage in the history of the axial skeleton, namely its conversion from the membranous into the cartilaginous stage. This means a strengthening by means of cartilaginous blocks within the skeletogenous layer. Such blocks, at first irregular and ill-defined in shape, arise first in the region of the parachordals and bases of the arcualia, earlier on the dorsal, later on the ventral side, latest in the "centre."

The centra or bodies of the vertebræ of Elasmobranchs are formed out of the whole thickness of the chordal sheath, the latter being converted into cartilage and becoming segmented. The mode of development of the centra, and especially the

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question of the origin of the necessary cartilaginous cells within the elastica externa has led to much discussion and has caused some differences of opinion.*

BALFOUR ("Elasmobranchs") held that while the arches were being formed by two dorsal and two ventral concentrations of skeletogenous cells a layer of tissue appeared between the elastica externa and the chordal cells. This layer, in a position corresponding with our chordal sheath proper, or elastica interna, was stated to stain deeply, and to contain flattened nuclei, but he said he could not, to his satisfaction, prove its origin, and considered it as probably derived from the previously existing mesoblastic investment of the notochord.

HASSE, in one of his later papers ("Entwicklung der Wirbelsäule der Elasmobranchier," 1893) came to the startling conclusion that the Elasmobranchs possess two cuticulæ, the one formed by the chorda (Chorda-scheide), the other, the elastica externa, produced by the skeletogenous layer, and that between these two cuticulæ grows a layer of cells, the "Intercuticulare Schicht or Scheide."

This latter, according to him, is derived from the inner layer of skeletogenous cells and forms the centra or vertebral bodies.

In the same year, KLAATSCH, in two lengthy papers (Lit., No. 21), showed that the cells which form the centra do not pass from the outside between the two existing layers (namely, the elastica externa, and the elastica interna or chordal sheath proper), and consequently are not *inter*cuticular, but that they break through the elastica externa, from the outside and become embedded in the chordal sheath itself. He was able to show satisfactorily (1) the immigration into, and the pervasion of the chordal sheath by skeletogenous, future cartilaginous, cells; (2) that these cells do not reach the innermost zone of the chordal sheath, leaving there a cell-less zone, which retains its concentric fibrillar appearance; and (3) that this inner zone is what HASSE considered a separate membrane, and called the cuticula chordæ or elastica interna. Our own investigations fully confirm the results of KLAATSCH.

The invasion of the chordal sheath by skeletogenous cells begins in *Acanthias* from the bases of the arches, just after these have become cartilaginous. Even in the early stages the elastica externa does not form a continuous ring, but is a broken line before any cells pass through it (figs. 17 and 18). The cells concentrate round the outside of the elastica and flatten against it; some of them pass through the gaps, and others through the membrane itself.

* GEGENBAUR ('Untersuch. Vergl. Anat. d. Wirbelsäule,' 1862, Part 63), "Die eigentliche Chordascheide als eine durch die Gesammtheit der Wirbelthiere hindurchlaufende Bildung ist die Elastica interna der Selachier, Ganoiden, und Chimœren. Die sogenannte mittlere Schichte [layer or zone] der Chordascheide, in der bei Chimœra und bei den Selachiern Verknöcherungen (Knorpelknochen) [calcified cartilage in *Chimæra*] auftreten, halte ich für einen sehr frühzeitig von der skeletbildenden Schicht sich abtrennenden und dann durch eine äussere duenne Lamelle [elastica externa] davon geschiedenen Theil."

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Arrived within the elastica externa they form a deeply stainable layer of much flattened nuclei in the outer zone of the chordal sheath, and force parts of the elastica externa outwards* (figs. 23 and 24), while the inner zone which they have not yet entered, still remains undisturbed in its concentrically fibrillar condition. In this stage certain sections give indeed the wrong impression, as if the invading cells formed a layer between the two cuticulæ, namely between the elastica externa and the chordal sheath proper.

But in the trunk of embryos of about 15 millims. in length, when more cells have entered, they are seen to be embedded in the deeply stainable fibrillar substance itself, while nearer the head the cells have already penetrated almost as far as the chorda itself (fig. 25). In such cases or regions, therefore, there no longer exists an inner zone which could be regarded as a separate membrane. The invaded chordal sheath thickens in proportion as the invading cells multiply and new cells enter. This is the case especially near the bases of the arches.

In sections of nearly ripe *Centrophorus* (fig. 28) the immigration of cells through the gaps in the elastica externa is shown clearly. The whole chordal sheath is divided into three zones (fig. 27). The outer consists of cells which have just entered, and are beginning to assume an elongated shape, least so at the basis of the arch whence they have entered.

These cells lie in a prechondral matrix, through which they are scattered in much the same proportion as in the arches.

The middle zone consists of closely packed cartilage cells, and is that portion of the sheath in which calcification first takes place.

In the inner zone the hyaline matrix preponderates over the likewise elongated but less numerous cells; moreover, we observe that the ground substance becomes less hyaline and more concentrically fibrillar as we approach the chorda itself. This means, of course, that no skeletogenous cells have penetrated into the innermost portion of the chordal sheath, but also that the bulk of the inner zone is filled with those skeletogenous cells which were the first to enter and have become most modified. They have namely produced a ring of hyaline matrix, while the concentrically arranged fibrillar original material of the chordal sheath has been either destroyed or has been used up, and become converted into cartilage. It need scarcely be mentioned that a series of successive sections of the same individual shows a somewhat variable grouping of the cells, and different proportions of these zones. For instance, in the intervertebral region there are no calcifying, and scarcely any cartilaginous, cells. The extent and intensity of calcification likewise influence the appearance of other-

* Exactly the same had already been observed by HASSE, but it was wrongly interpreted; *cf.* his fig. 5, Plate 1, in "Beiträge zur allgemeinen Stammesgeschichte der Wirbelthiere," 1883. In this figure of *Acipenser* a cell is actually represented in the act of slipping through the "elastica chordæ" into the "Faserschicht" [true elastica interna].

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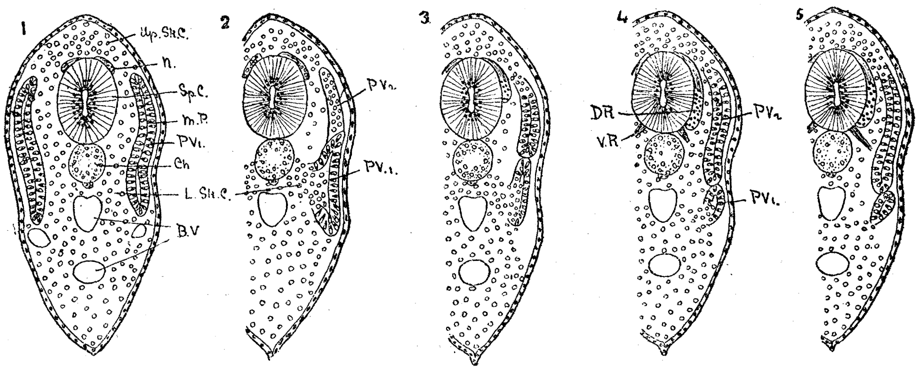
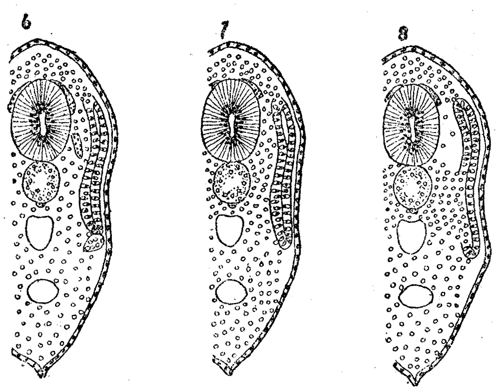
wise essentially similar sections (compare fig. 29 of *Scyllium* with figs. 27 and 28 of *Centrophorus*).

Origin and Metamerism of the Skeletogenous Layer.

The sum total of the skeletogenous cells forms the skeletogenous layer. In an embryo of *Scyllium* of 7 millims. in length, the skeletogenous cells can be followed up distinctly in the tail only, as the tail of embryonic Elasmobranchs generally shows more primitive conditions or stages than the trunk. In later stages—sections through the trunk of the same embryo (figs. 9 to 13), the clusters of cells show no connection with the myotomes, and lose their segmental arrangement, so that metamerism is then shown only by the nerves and by the cavities in the dorsal portion of





Figs. 1 to 8. Series of sections through one segment of the *tail* of *Scyllium catulus*, 7 millims. in length, showing the formation of skeletogenous clusters from the dorsal and ventral parts of each protovertebral plate. These sections follow from head to tailwards.

Fig. 1. This section passes through *one* protovertebra only. The skeletogenous cells are scattered uniformly through the space between protovertebra and chorda.

Fig. 2. Owing to the slope of the protovertebræ this section passes also through the dorsal edge of Pv_2, while the ventral half of Pv_1 gives off cells which extend to the top of the chorda, leaving a space above with a few scattered cells only.

Fig. 3. The dorsal half, Pv_2, gives off cells.

Fig. 4. The ventral half, Pv_1, is nearly exhausted, but still gives off cells, which, however, extend only half-way up the aorta. It is probably owing to such sections that the hypothesis of the mesenchymatic or parablastic origin of the skeletogenous cells has given rise to the following surprising statement: "Die skeletogene Schicht, wie die Bindesubstanz überhaupt, entsteht zuerst durch Auswanderung von embryonalen Blutzellen aus der Aorta" (HASSE, 'Lit.,' No. 15, p. 3).

Fig. 5. Pv_1 is exhausted. The dorsal and ventral roots of the spinal nerve are cut.

Fig. 6. Only the dorsal root remains.

Fig. 7. Only Pv_2 remains, still giving off cells from its dorsal end. This section approaches that of fig. 1.

Fig. 8. Pv_2 gives off cells from its ventral half.

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the myotomes, because the help is lost which was previously afforded by the successive giving off of skeletogenous cell clusters from the protovertebræ.

In tracing a series of sections through the *middle of the tail of Scyllium* (figs. 1 to 8) (total length about 7 millims. corresponding with BALFOUR's Stage L, the end of the tail still representing Stages F and E), the formation of skeletogenous cells in each segment is as follows:—

That part of the protovertebral block where the cells are coming off has no inner boundary; the skeletogenous cells are small with round nuclei, while the nuclei of the remaining cells of the protovertebra are characterised as growing muscle cells by their spindle shape. The cells are at first given off from the whole of the lower half of the protovertebra, and extend as a cluster to the top of the chorda (fig. 8), but as the sections are traced onwards the clusters sink lower and lower, leaving a space above with a very few scattered cells in level of the spinal cord (fig. 3).

Clusters of cells are also given off from the dorsal end of each protovertebral plate, and these dorsally created clusters alternate with the ventral clusters.

In some sections the dorsal clusters of skeletogenous cells are not different from those which remain in the protovertebra (figs. 3 and 4), but in other sections the remaining mass of the protovertebra has a distinct upper and inner boundary, the nuclei of its cells being quite different from those of the skeletogenous cells. This means that the original protovertebræ are now differentiated into *sklerotomes* (*i.e.*, the mass of skeletogenous cells) and into *myotomes* (that which remains of the protovertebral plates after the skeletogenous cells have been given off). These myotomes consist of two separate layers of cells, both layers having the characteristic spindle-shaped nuclei, and the whole myotome has now a definite inner boundary, resembling again fig. 1.

The spinal nerve arises in the front part of the protovertebra; the dorsal root with its ganglion lies just where the upper cluster of skeletogenous cells is growing downwards; the course of the dorsal nerve is very short, and it ends in the same plate in which it arises.

The ventral root appears in the same section which cuts through the middle of the dorsal root and goes to the same myotome (figs. 4 and 5).

In the trunk of the same embryo the arrangement of the skeletogenous cells is more difficult to trace, as here the two dorsal and ventral clusters have met and joined, so that the chorda is now surrounded by a continuous sheath of cells (figs. 9 to 13). Thus it is not clear how much of the skeletogenous layer is derived from the dorsal, and how much from the ventral half of the sklerotomes. The dorsally-formed clusters seem to extend only to the top of the chorda in fig. 13, while in the tail they surround the chorda. The protovertebræ, especially the myotomes, are curved, the middle part and the ventral end looking headwards, the dorsal end tailwards (figs. 14, 15, and 16). The dorsal and ventral nerves come off alternately (compare figs. 10 and 13).

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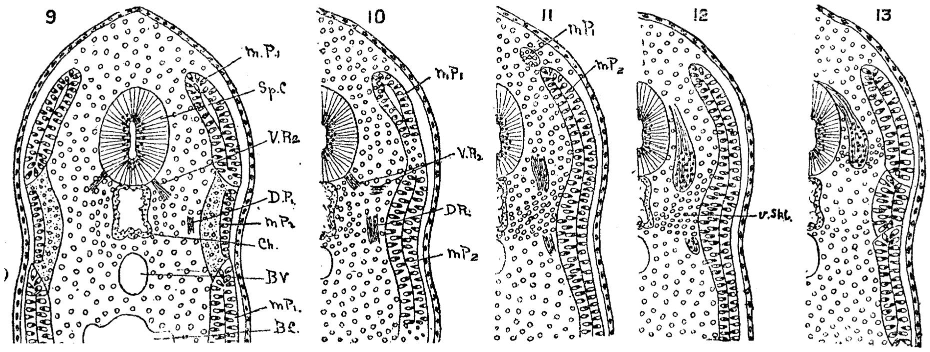

Figs. 9 to 13. Sections through one segment of the *trunk* of *Scyllium catulus*, of 7 millims. in length, showing the relations of the skeletogenous clusters (sklerotomes) to the nerves and muscles (myotomes).

Fig. 9. Section passing through the dorsal and ventral parts of *one* protovertebra (MP_1), and the middle part of the next one behind (MP_2). The origin of the ventral root is cut, also the middle part of the dorsal root.

Fig. 10. Section passing mostly through MP_2 into which the ventral nerve is seen to pass.

Fig. 11. Section passing almost entirely through MP_2, only a small bit of MP_1 remaining. *V.Skl.* = the belt described below, mentioned in the diagram on p. 188 as BV_2.

Fig. 12. Section through the spinal ganglion, showing, in comparison with Sections 11 and 10, the forward-curved course of the sensory root.

Fig. 13. The dorsal and ventral portions of protovertebra MP_2 are cut through; between them appears the foremost (middle) portion of MP_3.

In tracing a series of transverse sections backwards, as we cut through a new protovertebra MP_2, just at its forward-bulged curve, we also cut the ventral nerve VR_2, and the dorsal cluster of cells seems to extend down to the chorda (fig. 9). At the point where the ventral root enters the myotomes (fig. 10), the dorsal root is hit in about the middle of its course and in a section a little further back (fig. 11) its ganglion and peripheral end are cut. The dorsal nerve obviously bends slightly forwards. The reason of this disturbed course is a broad belt of skeletogenous cells, which extends transversely from the myotome towards the aorta. This belt fills the space which is later on to be occupied by the ventral arcualia. It is the first clear indication of the ventral half of the sklerotome. The dorsal nerve-root forms a loop, bending headwards round this dawning arch; it then emerges between the dorsal and ventral clusters of skeletogenous cells of the same protovertebra, while the ventral root issues between two successive myotomes and goes into the one behind.

Sagittal sections of Acanthias embryos of 7 millims. in length. Fig. 16 represents a sagittal section through twenty-five segments of the posterior region of the trunk and the beginning of the tail. The section has cut the first and the last segments more laterally than segments 9 to 22, while 3 to 8 are cut nearest to the chorda, consequently, the whole of the two myotomes is visible only in segments 23 to 24, in segments 1 and 2 only the dorsal half, in the other segments only the dorsal ends of the myotomes.

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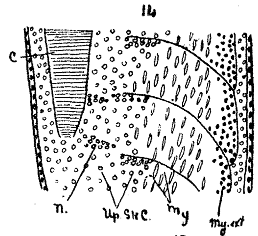

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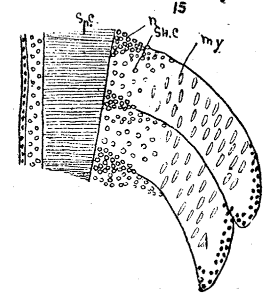

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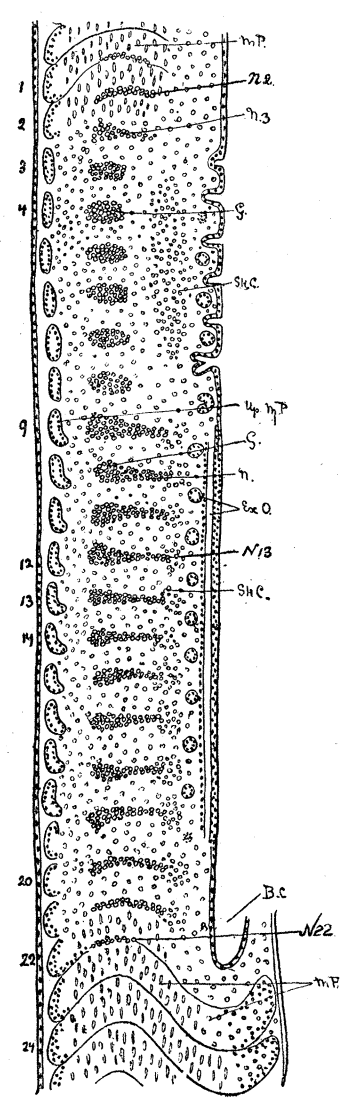

Figs. 14 and 15. Sagittal sections near the middle line, *Scyllium catulus*, embryo of 7 millims. in length.

Sp.C. = Spinal cord.

Sk.C. = Skeletogenous cells, clusters of the sklerotomes.

My. = Myotomes; *My. ext.* = their outer cutaneous layer.

Fig. 16. Sagittal section through 25 segments of a 7 millims. embryo of *Acanthias vulgaris*. This section represents a plane considerably more lateral than figs. 14 and 15. The description is given in the text, p. 183–185. *Ex.O.* = Excretory organs.

The myotomes, and the same applies to the whole protovertebræ, are curved in S-shape, the top end curving tail- and inwards, the ventral end and the middle portion bulging headwards; the amount of curvature is so great that a transverse plane will cut through the dorsal and ventral third of one, but through the middle of the next following segment.

The skeletogenous cells are seen on the inner side of the myotomes, most numerous in the vicinity of the chorda, and also just above the neural ridge of nerves, scarcest in level of the spinal cord. In segments 9 to 21 they are seen as clusters, indicating the material collected for the formation of the future ventral arcualia. In the district of segments 4 to 7, that is, nearer the middle line, the clusters are fused into one continuous mass; this means, they have lost their metameric arrangement. The latter would, however, still be visible towards the end of the tail of the same embryo.

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The spinal nerves arise and lie in the middle or their protovertebræ, the ganglion slightly in front of its nerve. At first, the course of the sensory roots is truly transverse and downwards, the nerve remaining in its myotome, but then it assumes a slight tailward direction, and comes out in the intermuscular septum on the hinder side of the myotome to which it belongs. Thus it comes to pass that in a more lateral sagittal plane the nerves lie in the septa behind their corresponding myotomes (for instance, N. 2 and N. 22), while in a plane nearer the chorda the nerves lie inside their myotomes, but owing to the strong forward curve of the latter each nerve seems to arise in level of the dorsal portion of the next previous myotome; for instance, Nerve 13 belongs to myotome 13, although placed in level of the dorsal half of myotome 12.

The S-shaped curving and overlapping of the protovertebral plates is of fundamental importance for our understanding of the formation of the vertebral column, because it explains, (1) the so-called new segmentation of the axial column; (2) the almost universal occurrence of more than one dorsal and one ventral pair of arcualia, namely, basalia and interbasalia, in each of the later vertebral segments or skleromeres.

Obviously, the metamerism of the myomeres does not correspond with that of the skleromeres, at least not in position, although in numbers. In the new segmentation the relation of the various parts is the following. The blocks of the myomeres alternate with, or rather overlap, the blocks of the skleromeres, the intermuscular septa abutting upon the middle of the underlying skleromeres.

The nerves, certainly their motory portions, are essentially myomeric; the ribs, like the intermuscular septa, are skleromeric but intra-myomeric.

The necessity for such an alternating or overlapping arrangement has long been understood (*c.f.* BALFOUR's 'Embryology,' Part 2, p. 453).

REMAK (Lit., No. 32) was the first to draw attention to this "Neugliederung der Wirbelsäule." According to him, out of each "Urwirbelkern" or skleromere were developed, (1) Head portion of a vertebra with its arches; (2) Intervertebral ligament; (3) Tail end of the next previous vertebra.

GEGENBAUR, in 1862 (Lit., No. 7). In the chick, during the fifth day of incubation, the chorda is surrounded by a uniform continuous mass of primitive cartilage, without any segmentation being indicated except by a series of dorsal outgrowths which surround the spinal cord and are the first appearance of arches. The portions between these successive arches were called "Intervertebral-Stücke." Within these archless portions there appears a transverse slit separating the whole into a longer anterior mass which remains with the archbearing portion next in front, and a shorter posterior mass which joins the archbearing portion next behind, and was supposed ultimately to be converted into a meniscus. It was stated, further, that this meniscus was formed by the posterior half of the "primitive Wirbel," and that the spinal ganglion attaches itself to (ordnet sich zu) the vertebra next in front.

No further progress was made for nearly thirty years, the question as to the detailed

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products of the respective halves of the sklerotomes being generally left untouched or slurred over with some obscure phrases.

EBNER, in 1888 and 1892 ('Lit.,' Nos. 5 and 6), and CORNING, in 1891 (Lit., No. 4), studied embryos of *Tropidonotus* and of *Anguis*. Their chief conclusions are: The sklerotomes show a transverse slit, which seems to be continuous with (or at least to lie in the same level as) the slit or cavity in the dorsal portion of the protovertebra or myotome.

According to EBNER, this slit, called Intervertebral-Spalte, initiates the vertebral segmentation. He thought he was able to show (es liess sich nachweisen) that the halved sklerotomes recombined with the adjoining halves of the neighbouring sklerotomes and consequently formed metameres, which alternate with the myomeres. This is, of course, the usual vague statement. In his second paper, EBNER stated, amongst other controversial points with CORNING, that his Intervertebral-Spalte was totally different from the future intervertebral cavity (Gelenkhöhle), that the slit disappears and makes room for intervertebral cartilage.

CORNING'S results seem to be :—

The arch and anterior half of vertebra x is produced by the posterior half of sklerotome x.

The archless body portion of vertebra x is produced by the anterior half of sklerotome $x + 1$.

The arteries lie in level of the myocommata, *i.e.*, they are interprotovertebral.*

The nerves lie in level of the myotomes, *i.e.*, they are protovertebral.

Later on, nerve XXI. belongs to vertebra X., *i.e.*, lies behind its vertebra.

It is easily seen that the results arrived at by REMAK, GEGENBAUR, and CORNING are all different, and cannot be reconciled with each other.

In fact, it had long been felt that there was something unsatisfactory in this generally-accepted expression "neugliederung," or new segmentation. O. HERTWIG ('Lehrbuch der Entwicklungsgeschichte der Menschen und der Wirbelthiere,' Jena, 1888, p. 473) pointed out that the expression is not correct, because, as long as the axial column is still in the membranous stage, there is no segmentation in it, and it is only when cartilage makes its appearance that "gliederung" makes its appearance. This argumentation does not quite meet the point.

However, it is misspent energy to seek the solution of the mystery of resegmentation in birds and reptiles. The necessity of overlapping of contractile and passive segments has been met with before any Amniota came into existence, even long before there was anything like a segmented vertebral column; it is ready in *Dipnoi* and *Holocephali*, which have no segmented centra in their axial skeleton, ready in Cyclostomes even before they show any cartilaginous arches. In fact, the

* The protovertebræ cease to exist as such after they have given off the skeletogenous material, henceforth there exist only myotomes and sklerotomes. It is, therefore, confusing to speak of the interprotovertebral position of the myocommata.

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overlap began with the earliest Vertebrate, which did not progress by peristaltic motion.

The overlap, the alternation to the extent of one-half, dates back to the stage where the protovertebral plate has differentiated itself into myotomes and sklerotomes.

I have no hesitation in stating categorically that nobody has ever seen a transverse splitting within a sklerotome, dividing the latter into two successive halves, and that nobody has ever observed a healing up or recombination of these halves. The assumption of such a split and fusion offered itself as a theoretical necessity, simply in order to explain the actually-observed overlap of myomeres and skleromeres. That which was crudely observed to take place in the axial cartilage of comparatively late stages of Sauropida was, so to say, projected by mental reflexion upon the progenitors of this cartilage, namely, upon the sklerotomes.

The explanation is the following :—

Reconstruction of the sections through the tail (figs. 2 to 8 and 16) shows that—

1. The dorsal half of sklerotome 2 grows downwards to lie behind ventral sklerotome 1.

2. The ventral half of sklerotome 2 lies in front of and below the dorsal half of sklerotome 3.

3. The formation of a physiological unit is effected by the combination or fusion of the unequally numbered sklerotomic halves, so that the dorsal half lies behind and above the ventral half.

The new skleromere I. (dorsal sklerotome 2, ventral sklerotome 1) stands now in the following relation to the myomeres :—The dorsal broad end of skleromere I. coincides with myomere I., the septum between myomeres I. and I.–1 passes between the dorsal sklerotome 2 and ventral sklerotome 1—that is to say, right across the new skleromere I. In other words, this skleromere lies within the influence or range of action of two successive myomeres. Taken as a whole, the skleromere is interprotovertebral, more correctly bi-protovertebral, because it is composed of two successive sklerotomes, namely, the ventral half of one and the dorsal half of a second.

Reconstruction of sections through the trunk (figs. 9 to 13 and 16) gives similar results, but the conditions are not so clear as in the tail, owing to the advanced mixing up of the dorsal and ventral clusters.

Ventral half of sklerotome 2 lies behind and below dorsal sklerotome 2 ; the ventral half of this sklerotome 2 remains situated within the domain of myotome 2, whose spinal nerve-ganglion lies truly intraprotovertebral, and the sensory nerve runs likewise intraprotovertebral, curving round in front of the ventral sklerotome 2, and ultimately coming out in the septum between myomeres II. and III. The ventral root arises a little in front of the dorsal root and ganglion.

Reference to the accompanying diagrams will render these somewhat intricate conditions clearer than long descriptions. It should always be borne in mind that

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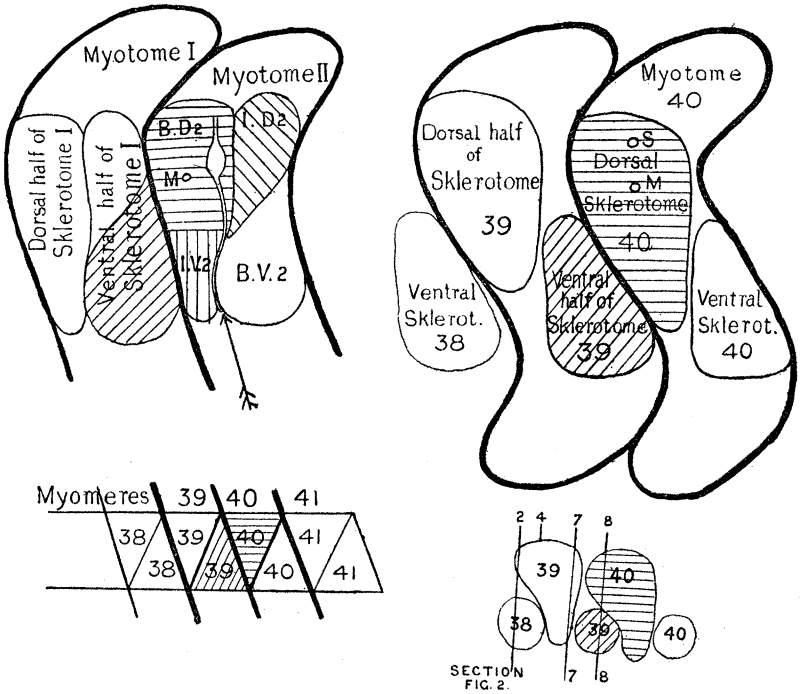
the Arabic index numbers indicate parts or offspring of the same numbered protovertebra; that the numbers are counted from head to tail; that the Roman index numbers refer to the finished physiological units, namely, the myomeres and the skleromeres.



Left upper diagram.—Two protovertebral segments in the trunk, *after* establishment of the interbasalia. Imaginary numbers 1 and 2.

B.D. = Basidorsal. B.V. = Basiventral.

I.D. = Interdorsal. I.V. = Interventral.

M. = Position of the motory root.

The arrow indicates the plane of the section of fig. 9 on page 183.

Right upper diagram.—Two protovertebral segments in the tail, *before* establishment of the interbasalia. Imaginary numbers 39 and 40.

Left lower diagram, illustrating that "unequally numbered sklerotomic halves combine to form new skleromeres." Dorsal behind, ventral in front, *e.g.*, 40 dorsal and 39 ventral = one new skleromere, which is govered by myomeres 39 and 40.

Right lower diagram, indicating the planes of the sections shown in figures 2, 4, 7, 8, on page 181.

We have consequently to give up the time-honoured notion that the protovertebræ split and recombine to form new segments, the hard products of which overlap with the contractile portion. It is true that each skleromere (but not the whole segment, the myotome remaining undisturbed) results from the combination of two half-skleromeres, but in a way fundamentally different to that which hitherto was supposed to have taken place.

If A and B mean two successive sklerotomes, a and b their dorsal, α and β their respective ventral halves, then the new skleromere is composed of

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$b + \alpha$, and not of $\frac{A + B}{2}$, because $b + \alpha$ is the same as $\frac{\text{B dorsal}}{2} + \frac{A}{\text{ventral } 2}$.

This formation of a skleromere by combination of dorsal and ventral alternating halves of sklerotomes explains also the presence of eight (four pairs) of cartilages, namely, basalia and interbasalia, to each complete segment. For the sake of shortness we call the pyramidal mass of skeletogenous cells which grows out from the ventral half of a sklerotome simply the ventral sklerotome or ventral pyramid, &c.

Each ventral pyramid extends with its apex above the chorda, and founds there (separated from the ventral mass by the subsequent rapid growth of the chorda and its sheath) a cluster of cells, which remains henceforth behind the basal mass of the dorsal pyramid; this latter, through its downgrowing apex, founds a colony of cells but below the chorda and in front of the basal ventral mass. Thus are produced the basalia and interbasalia.

Each colony of cells retains its potentiality of developing into a separate independent piece of cartilage; the basidorsal does not fuse with its interdorsal because both are the offspring of two different sklerotomes, nor can the basidorsal fuse with its own offspring, namely, with the interventral, because both became, and remain, separated by the chorda and its sheath; they are connected only by the indifferent connective tissue of the membrana reuniens, but not by cartilage-forming cells.

The presence of interbasalia, besides the basalia, is of fundamental importance in the whole genesis, both phylogenetic and individual, of the axial skeleton.

Their occurrence is not a freak or peculiarity of the Elasmobranchs and cartilaginous Ganoids. They are present from Cyclostomes onwards in every Fish, and in every other Vertebrate, although by no means always as independent typical interbasalia, but frequently modified into seemingly quite heterogeneous parts.

The Division of the Chordal Sheath into Centra or Bodies of Vertebræ.

The proper conception of the different modes of the formation of vertebral centra has suffered many vicissitudes.

In 1860 KÖLLIKER already distinguished between the following kinds of centra:—

A. Centra produced entirely by the chordal sheath. These he called "Chordale Wirbelkörper," *e.g.*, *Hexanchus*.

B. Centra formed by the chordal sheath and by the outer skeletogenous layer, the biconcave central cones being strengthened by the external addition of bone, *e.g.*, most Elasmobranchs.

C. Centra formed entirely by the outer skeletogenous layer, namely, by the cartilaginous arches, *e.g.*, certain vertebræ of Skates, Amphibia, and Amniota.

KÖLLIKER's discovery contains really the two fundamental differences, because he distinguished between chordal centra, centra which are not chordal, and centra which

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are chordal besides something else, he being conscious of the existence of intermediate forms.

GEGENBAUR in 1867 ("*Lepidosteus*," p. 393) enumerated four forms of centra, which, however, cannot be defined with our present knowledge of the modifications of the chordal sheath.

HASSE ("Stammesgeschichte," p. 17) expresses the differences as follows :—

Elasmobranchs are animals with originally independently formed vertebral bodies (selbstaendige Wirbelkoerperanlagen), while the Tectobranchi do not possess such independently formed centra. This statement does not meet the point, because Holocephali and Dipnoi are Tectobranchi as well as the Ganoids, and certainly possess exactly the same "ursprünglich durch Ausbildung einer Elastica [externa] ausgezeichnete selbstaendige Wirbelkoerperanlage" as the Elasmobranchs.

The salient differences could not be stated clearly until KLAATSCH had shown how the chordal sheath received its cartilage from the skeletogenous layer. The share of the skeletogenous layer in the formation of the centra is therefore not the only criterion. He promptly distinguished between—

1. Chordale Wirbelkoerper, adopting KÖLLIKER'S term ; such centra as are formed to the inside of the elastica externa, practically by the chordal sheath.

2. Perichordale Wirbelkoerper, such as are formed to the outside of the elastica externa, without help from the chordal sheath. This term "perichordal" is most unhappily chosen, because it is so misleading. The chordal centra, being formed out of the chordal sheath, are literally perichordal, and remain so, a great part of the chorda showing persistent growth; on the other hand, the perichordal centra of most higher Vertebrata actually destroy and take the very place of the chorda; they are consequently more properly chordal in position and extent than the chordal centres themselves. I therefore propose to distinguish between chorda-centra and arch-centra.

I. *Chorda-centra.*—Centra which are cut out of the full of the chordal sheath, which itself has been strengthened by invasion of cartilaginous cells from the skeletogenous layer. Such chorda-centra might be called auto-centra, *i.e.*, centra in their own right, independent of the arches, as will be shown further on. Chorda-centra are possessed by *all* Elasmobranchs. Potentially chordo-centrous are also the Holocephali and the Dipnoi, because their thick chordal sheath is partly chondrified, but it remains unsegmented.

II. *Arch-centra.*—Centra formed from the skeletogenous mass which remains entirely on the outside of the chordal sheath, which takes no share in their formation.

Such arch-centra are possessed by the osseous Ganoids, Teleostei, Amphibia, and Amniota. These centra are absolutely and directly dependent upon the existence of arcualia, and the cartilage of these arcualia themselves is produced by and in the skeletogenous layer.

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There remain those fishes the vertebræ of which are destitute of centra or bodies, a want which is *not* due to degeneration. These fishes are :—

(1.) All the Cyclostomata.

(2.) The recent cartilaginous Ganoids, namely, *Acipenser*, *Polyodon*, and *Scaphirhynchus*.

(3.) The Holocephali and Dipnoi mentioned above as potentially chordo-centrous, because they would have true chorda-centra if they possessed centra at all. On the other hand, the Cyclostomata are essentially arco-centrous, because their thick chordal sheath is surrounded by a rather thick elastica externa which remains unbroken and is never invaded by skeletogenous cells, although there may be dorsal and ventral cartilaginous arcualia in the same region of the body.

Much speculation has been rife as to the phylogenetic value of these various stages.

The proper view is that expressed in the following schematic form.

Chordal sheath.

Remains entirely chordagenous.
Cyclostomata
Cartilaginous Ganoids.

Strengthened by invasion of skeletogenous cells, therefore possibility of chorda-centra.
Dipnoi . . . *Holocephali.*

Centra are now formed . . . *Osseous Ganoids.* . . . . *Elasmobranchs.*

Teleostei. *Amphibia.* *Amniota.*

ARCH-CENTRA. CHORDA-CENTRA.

We have to bear in mind the following considerations :—

No centra are formed either in the chordal sheath, or outside it, in the skeletogenous layer, without the previous existence of cartilage. The latter makes its appearance in the shape of arcualia, whence in some fishes it invades the chordal sheath, and thus makes it possible to cut this sheath up into successive blocks which can serve as centra. Dipnoi, Holocephali, and Elasmobranchs, are not necessarily nearer related to each other than are the Dipnoi with either Holocephali or with cartilaginous Ganoids. In some respects the Elasmobranchs are higher, have attained a higher level of general development than the Dipnoi, for instance, in respect of vertebral centra, heart, paired fin skeleton, heterocercous tail ; the reverse is the case with dentition, scales, air-bladder, &c. But the possession or want of centra does not indicate nearer relationship, only the height or stage of development which has been reached by various groups independently of each other.

The immigration of cartilage into the chordal sheath was a side-departure hit upon independently by the Elasmobranchs and also by the Dipnous and Holocephalous

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members of the Proto-Gano-Dipnoi. This means that the primitive axial rod (chorda with its chordogenous sheath) is gradually superseded by predominance of skeletogenous, mesoblastic tissue. This same end, however, could also be, and has been, produced in a different way, namely, *by the gradual suppression, not by conversion, of the chordal sheath.*

It was certain that sooner or later the skeletogenous mesoblastic tissue would gain the upper hand and take the lead wherever there was a question about supporting tissues. The struggle for supremacy showed itself first in the conversion, not of the chorda itself, but of its produce, its sheath. With the introduction of skleromerism (itself an innate result of the conversion of the bulk of the skeletogenous layer into cartilage) the partly converted chordal sheath had necessarily to partake of this metamerism, and its existence was thenceforth guaranteed in the shape of chorda-centra.

Another form of the struggle exhibits the *suppression of the chordal sheath.* When this first began we do not know. The few recent cartilaginous Ganoids and Cyclostomes do not show any reduction of the sheath, but in the osseus Ganoids and Teleosteans it was the consequence of the fact that the same skleral metamerism had asserted itself. It is obvious that gradual suppression of a more primitive rival is a more complete victory than its conversion.

It is wrong to assume that the so-called membranous stage of the vertebral column is followed by a likewise non-segmented continuous cartilaginous stage.

Such a notion was based upon the observation, subsequently shown to be erroneous, that in the five days' chick embryo the chorda becomes surrounded by an unsegmented tube of continuous cartilage before it shows any indication of metamerism. Had the observation been true, the structure in question must undoubtedly have been considered as a cœnogenetic feature. For we now know that in fishes even the uniformly unsegmented layer of cartilage in the chordal sheath is a secondary feature. The occurrence of this layer in Elasmobranchs is analogous to what was supposed to exist in the five days' chick. The sklerotomic clusters are metamerically arranged from their first appearance, but, strictly speaking, there is no metamerism of skleromeres so long as there are several successive cartilaginous pieces to each skleromere. It is only when some of these pieces have become very small and others of preponderating size that a predilection for the mechanical bending or yielding between certain pieces asserts itself and forms the beginning of transverse joints. It is obvious that the chondrified chordal sheath is affected by the "centra of motion," which establish themselves according to the way in which the fish "wriggles."

The number of myomeres need not correspond with that of the primitive joints.

According to the establishment of a break or "centre of motion" between every two or three or four successive arcualia, there will be shorter or longer chorda centra. This establishment of discontinuity is purely mechanical, but how it is

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determined, and what it depends on in detail, we do not know. Suffice it for the abstract notion to refer to a simile.

Supposing a hose filled with freshly made plaster of Paris (chondrified chordal sheath) be put into vibration; the plaster will set, and breaks will be established at the nodes (the internodes being the chordal centra). Supposing, further, that hose contains a solid india-rubber axis (chorda) and a mantle of loosely packed blocks (arcualia), then the axis will not be affected by the vibrations, but the outside blocks will, according to their size and position, modify and determine the position and number of nodes in the setting plaster. The firmer and more solid the material, the greater is the necessity for elaborate joints in the skeleton.

The formation of arch centra being the superior mode, we need not be surprised that in a roundabout way the auto-centrous or chordo-centrous type may sometimes come to resemble the second or arco-centrous type. KLAATSCH has lucidly shown that there is now the tendency—as illustrated by the Rajidæ in comparison with the Squalidæ—to transfer the immigration of cartilaginous cells into the chordal sheath into such early ontogenetic stages that the recapitulation of a cell-less sheath becomes more and more obscured,* implicating at the same time the reduction of the elastica externa.

KLAATSCH most properly uses this as an instance of the necessity of first making sure of the systematic position of the type we happen to study, without which knowledge our conclusions do more harm than good, even if they are based upon careful observations. Indeed, mischief enough has been done by the selection of Rajidæ for the elucidation of fundamental morphological questions.

Other instances which look much more seriously like arco-centrous formations are afforded by numerous Selachians in this way, that the dorsalia and the ventralia grow towards each other, and ultimately meet, or even fuse together, succeeding in enveloping the true chorda centrum with a ring of truly arcual substance.

It is conceivable that, if this process of enveloping the chorda centra with rings formed by the arches were gradually shortened and referred to earlier ontogenetic stages, this might lead to the suppression of the chordal sheath, and henceforth result in the formation of arch centra. But instances of this kind of centrum formation are unknown, unless, indeed, the Amphibia and Amniota possess such arch centra, which are then, of course, structures only analogous to those of the osseous Ganoids and Teleosteans. Analogous only, not homologous, although both are formed from exactly the same material, namely, the skeletogenous layer, and by the same instrumentality, namely, the arcualia; still, genetically they are not quite the same.

* This cœnogenetic case explains why KÖLLIKER erroneously classed "certain vertebræ of skates" with those of Amphibia, &c., under Group C, *cf.* p. 189.

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Some consequences of the Chorda Centra being independent of the Arcualia.

It has long been known that the number of arcualia carried by one centre is not always the same in various Elasmobranchs, nor even in different regions of the vertebral column of the same individual.

J. MÜLLER ("Myxinoiden," p. 156) remarked, "bei Zygaena fand ich noch das merkwürdige dass an einigen Wirbeln des mittleren Theiles der Wirbelsäule sogar 3 Bogenstücke hinter einander auf einen Wirbel jederseits kommen, während die meisten Wirbel nur 2 Bogenpaare haben. Hier sind also ausnahmsweise 2 ossa intercalaria auf jeder Seite, die an Groesse den eigentlichen Bogenschenkeln gleich kommen."

He gave the right explanation in so far as he explained the occurrence of three pairs of dorsalia by the occurrence of two pairs of "intercalaries," these being, of course, a pair of interdorsals and a pair of supradorsals, the latter having wedged themselves in instead of remaining on the top.

KÖLLIKER ('Würzburg,' 1860) in referring to *Heptanchus*, remarked that "bei Heptanchus im hinteren und vorderen Theil der Wirbelsäule die Zahl der Wirbel um das Doppelte grösser ist als in der Mitte." This is a most unfortunate mode of description, and has caused many misunderstandings. It would have been better to say that the number of vertebral centra (not "Wirbel") in the middle of the trunk is only half that of those in the ends of the trunk. But the simple fact is this: in the middle of the trunk of *Heptanchus* the length of each vertebral centrum is double that of the centra in the anterior and posterior portion of the trunk; the arcualia all being of the same size, it follows that the long centra carry more arcualia than the short centra.

It is the variable length of the chorda centra which causes the discrepancies. Thus, in *Heptanchus*, there correspond with each centrum of the middle of the trunk, about four pairs of dorsalia (and these happen to be two pairs of basidorsalia and two pairs of interdorsalia, as proved by the number of nerve exits) so that each long centrum actually belongs to two true segments; in MÜLLER's Zygæna there happen to be three pairs of dorsalia, in other specimens strictly speaking two and a half or three, and these happen to be the dorsalia of *one* segment, namely, basidorsal and interdorsal and supradorsal intercalated.

Frequently each centrum corresponds with or "carries" one basidorsal and one interdorsal, but even in these cases the greatest variation exists in the different regions of the body, as to the extent to which the interdorsals actually rest upon the centrum, the interdorsals either being as broad as the basidorsals or just touching the centrum or not touching it at all, being wedged into the dorsal gaps between the successive basidorsals.

These apparent irregularities reach their climax in the tail of many Elasmobranchs, where exactly the reverse takes place to what occurs in the trunk, in this way, that

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the chorda centra are so numerous, or so short, that two of them fall to the share of one true segment. The number of the dorsal cartilaginous pieces varies extremely, as many as five or six pairs (namely, two superimposed sets of basi- and interdorsals, supradorsals and dorsospinals) belonging to each segment as limited by the nerve exits, while the number of the ventralia remains small and regular.

The intercalation or wedging in of these various cartilages can be followed from the simplest to the most complicated conditions in the Rajidæ. A simple selection of figures from HASSE's monograph, Plates 19, 23, would, however, not be sufficient for this purpose, because the terms intercalaria, neuralia, accessoria, spinalia, have been applied promiscuously.

This discrepancy between chorda centra and "arches," or the difference between the metamerism of the centra and that of the arches, has caused considerable confusion.

JHERING (Lit., No. 20, p. 229), bent upon the search for proofs of inter- and excalation of vertebræ, came (p. 221) to the conclusion that "in the primary condition two segments fall to one segment of the body; in all higher Vertebrata the complete body segment is composed of one skleromere, one myomere, and one neuromere. Such segments, which contain only one vertebra, I call *monospondylous* segments, and I oppose to them as *dispondylous* segments, those which contain two vertebræ, *i.e.*, those in which two vertebræ fall to each myomere or neuromere."

On p. 235 he gives some examples :—

Acipenser : all the segments are monospondylous.

Amia : exquisitely dispondylous in the tail.

Elasmobranchs : mostly dispondylous in the tail.

(Scymnus is monospondylous.)

Higher vertebrates.—Monospondylous [because they are arco-centrous].

While KÖLLIKER, in speaking of *Heptanchus*, obviously meant by "Wirbel" only their centra or bodies (because he said, "die Zahl der Wirbel ist um das doppelte grösser als in der Mitte") JHERING meant by Wirbel the centra + arches. Not much fault can be found with such a conception of a "vertebra."

However, the very notion of a vertebra, Wirbel, or spondylus, has been founded upon the higher Vertebrata, not upon Fishes, many of which have no vertebral centra; the term vertebra should therefore be restricted to a complete skleromere, ten skleromeres or vertebræ belonging to as many myomeres or neuromeres. In fact *a vertebra is a skleral segment.*

HASSE ("Monograph," p. 21) applied JHERING's terms only to the centra, supplanting a somewhat different meaning for these well-meant terms, and thus causing confusion, especially since he introduced the unfortunate notion of "Polyspondylie." He mixed up two totally different processes, namely, the increased number of arcualia in a given segment with the increased number of chorda centra,

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else he would not have alluded to the numerous calcareous rings in the chordal sheath of *Chimæra*.

Moreover, by introducing the term "aspondylous" for those fishes which, like Cyclostomata, have no vertebral centra, he used the term "spondylous" in a different sense from what is implied by diplo- and monospondylous. Lastly, the very same portions of the axial skeleton of *Amia*, which induced JHERING to take *Amia* as an illustration of "exquisitely diplospondylous" conditions, have very appropriately been called "Halbwirbel," for instance, by P. MAYER ('Lit.,' No. 27). Consequently, "Halbwirbel" are the same as Doppelwirbel. The term "half-vertebræ" might be kept to advantage. "Aspondylous" signifies a centreless vertebra, but poly- and diplospondylous are terms without any reasonable meaning.

CYCLOSTOMATA.

The chordal sheath is thick, slightly fibrillar, almost hyaline in appearance, it closely adheres to the chordal epithelium. Externally it passes into the elastica externa, which always appears as an unbroken, highly refractive membrane of appreciable thickness; frequently owing to shrinkage of the whole chordal sheath, the elastica externa assumes in sections a wavy appearance. (See fig. 30 on p. 176).

The skeletogenous layer remains outside the elastica.

SCOTT (Lit., No. 38, p. 162) has correctly traced the origin of the skeletogenous cells. They grow from the inner, lower corner of the protovertebræ as clusters of cells, which spread towards the ventral side of the chorda; by the time that the muscle-cells are differentiated, the skeletogenous cells have formed a complete bridge below the chorda. The first budding clusters have the same segmentation as the myomeres, or the protovertebræ, but later on they fuse together into one continuous tube, which surrounds the chorda, and ultimately forms the membrana reuniens, continuous with the intermuscular septa.

Cartilage is developed in the skeletogenous layer in the shape of arcualia. The distribution of these arcualia is so irregular and variable that, in all probability, the Cyclostomes, although representing the lowest stage of a "vertebral column" no longer show a complete, unaltered record of the original conditions. The only correct and complete description of these cartilages is that given by SCHNEIDER (Lit., No. 37).

The principal features are the following:—

In *Ammocœtes* and *Myxine* cartilaginous elements are restricted to the tail in the shape of dorsalia, but cartilaginous fin-supporting rays are also present in the trunk.

Petromyzon fluviatilis.—In the region of the gillbasket, each neuromere possesses, on each side, one large and one small dorsal piece; the motor nerves pass through the large piece of cartilage. Behind this latter follows the exit of the sensory nerve,

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then the smaller cartilage of the second or posterior dorsale. These smaller pieces are variable; they disappear in the trunk, but there each of the larger pieces can be traced to split or to have split into two, so that in the trunk, one dorsale, one motor root, the next dorsale, and then the sensory root follow upon each other.

Consequently, both in the cervical and in the trunk region, are twice as many pairs of dorsalia as of neuromeres, one neuromere being equal to one motor and one sensory nerve.

In the trunk region each neuromere possesses, moreover, four, namely, two right and two left cartilaginous rods, which support the unpaired dorsal fin, and are not connected with the arcualia.

In the tail, the dorsalia of the right and left side form two continuous ridges of cartilage, which are dorsally continuous with the fin-supporting rays; there are moreover, ventralia, likewise continuous with ventral fin rays, and likewise fused into continuous bands of cartilage. Metamerism is indicated by the nerve exits only.

Holocephali.

Chimæra monstrosa. (Adult.) The chorda shows persistent uniform growth, except in the cervical region, and in the whip-like continuation of the tail. The chordal sheath is very thick. The elastica externa is broken through at the bases of the arcualia by the skeletogenous cells, which are easily seen to have pervaded the whole thickness of the chordal sheath. In about the middle lies a well-marked zone of calcification, dividing the whole sheath into an inner zone, which consists of numerous concentric fibres, thickly interspersed with prochondral tissue of spindle-shaped cells, and an outer zone, in which hyaline cartilage predominates.

The arcualia themselves consist chiefly of hyaline cartilage, and form two longitudinal dorsal and ventral rows, which do not meet round the chordal sheath. The number of dorsalia to each neuromere is five or six, namely, two right and two left, and one or two pieces enclosing the top. Of the dorsalia proper, one basidorsal is pyramidal, rests with its basis upon the elastica externa, and is generally pierced by the ventral root of the spinal nerve; the other piece (interdosal) is larger, with its apex directed downwards and wedged in between the others. The dorsal gaps are filled by the paired, or unpaired intradorsals. The sensory nerve-roots pass through between two successive interdorsals. On the ventral side each neuromere corresponds with one pair of arcualia only. There is no indication of a metameric breaking up of the chordal sheath into centra, although this sheath contains, as in Elasmobranchs, all the elements necessary for the completion of centra. The calcareous rings, mentioned above, alternate with ringless portions; the number of successive rings to one neuromere varies in different parts of the trunk, mostly four or five. Although, in their mode of deposition, and in their position exactly analogous with the concentric calcification within the centra of the "Cyclospondylous" Elasmobranchs, they do not

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cause any constriction of the chorda itself, nor of the inner zone of its sheath, and can only, in a general way, be compared with the "polyspondylous" condition which prevails in the trunk of Notidanidæ, and a few other fishes. Although it stands to reason that the chordal sheath will be more flexible between these rings, they are absolutely independent of the arcualia, and these alone are the ultimate cause of the jointing of the central portion of the axial skeleton.

Conclusion.—The axial trunk skeleton of *Chimæra* agrees fundamentally with that of Elasmobranchs and Dipnoi, in so far as the invasion of the chordal sheath by skeletogenous cells has rendered the sheath potentially fit for the production of *chorda-centra*, *i.e.*, centra formed by the entire chordal sheath. In other words, Holocephali remain throughout life at a stage which corresponds with that of embryonic Elasmobranchs. The numerous calcareous rings in the chordal sheath of *Chimæra* are absent in *Callorhynchus*.

There remain to be mentioned the modifications in the cervical and in the caudal regions.

In the cervical region the dorsal and ventral arcualia fuse with each other and enclose the chorda in a continuous mantle of cartilage, the original metamerism being indicated by the nerve holes only. The elastica externa persists and makes it possible for us to trace the share of the fused arcualia in the envelopment of the chordal sheath.

In the tail the calcified rings gradually disappear, and the arrangement of the arcualia becomes very irregular, there being not only more to each neuromere, but they fuse with each other, and split again, as the case may be, in the most variable manner.

Lastly, in the whipcord-like end of the tail, the dorsal and ventral arcualia fuse into a uniform mass of cartilage. The elastica externa has disappeared, and not only the tissue of the chordal sheath, but also that of the chorda itself is gradually transformed into cartilage, as can be demonstrated in series of sections proceeding towards the end of the tail. The spinal cord does not reach far into this undoubtedly much-modified and retrograded tail; the absence of spinal nerves makes the determination of metameres impossible.

Dipnoi.

The chorda shows persistent, uniform growth. The chordal sheath is pervaded by skeletogenous, later on cartilaginous, cells, but forms no metameric centra whatever. The dorsal and ventral arcualia do not meet laterally. Besides the dorsal and ventral basalia, interbasalia (so-called intercalaries) are present. In *Ceratodus* they occur regularly in the tail, irregular, however, as interdorsalia in the trunk; in the trunk of *Protopterus* they are rudimentary.

Protopterus annectens, young, 8 centims. length. See fig. 13 on p. 212.

The chordal sheath is of considerable thickness, about one-third of that of the

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chorda; the prevailing direction of the fibrillæ is concentric, but frequently these fibrillæ show a wavy distribution, the wavy parts being arranged in more or less radiating lines through the inner, or through the middle third of the thickness of the chordal sheath. There is, however, no evidence that these radial systems of wavy disturbances pass into, or are directly connected with the really radiating stands of the meshwork of the chorda itself, as WIEDERSHEIM thought and figured (Lit., No. 40, Plate 3, fig. 12).

Although there is no chordal epithelium visible, the limit between chorda and sheath is distinctly marked.

The elastica externa persists as a complete ring, which is however broken in four places, which correspond with the bases of the dorsal and ventral arcualia. Skeletogenous cells have passed through the gaps so formed, and cartilaginous cells are pervading the whole thickness of the sheath, being (in the 8 centim. specimen) arranged in about half a dozen concentric, but broken, rows. There is no evidence of the chordal sheath being differentiated into metameric blocks comparable to vertebral centra.

Concerning the arcualia, each neuromere corresponds with a pair of dorsal and ventral cartilages. The dorsals are large, surround the spinal cord, fuse above it, and carry the unpaired dorsal spines. The basidorsals alternate with swellings of connective tissue, through or above which pass the spinal nerves.

The ventral arches are rib-like cartilages; they likewise alternate with swellings of connective tissue.

These dorsal and ventral swellings are composed of closely packed cells, while the rest of the membrana reuniens is much thinner and is densely fibrous. The position of these swellings agrees with that of intercalaries, which indeed they represent in a rudimentary or prochondral condition, the only difference being that they are not cartilaginous, at least not in the trunk. In the tail, however, they are converted into cartilage, explaining thereby the following conditions which prevail in the tail of the adult :—

The chorda stops short some distance from the end. The chorda-less portion contains a rod of hyaline cartilage, rather regularly segmented, but the number of arcualia corresponding with each neuromere is increased to about double of those of the trunk.

Ceratodus Forsteri.—Adult.

The basidorsals form a semi-ring, which bridges over the chordal sheath and encloses the spinal cord; each arch carries a separate gable-piece (in the shape of ⅄), which with its legs encloses the ligamentum longitudinale, and carries on its top the unpaired dorsospinal.

A pair of small cartilages is frequently intercalated in the dorsolateral corner, between the otherwise juxtaposed basidorsals; the intercalated interdorsals do not reach down to the chordal sheath.

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The ventral arches or basiventrals follow closely upon each other without intercalaries, carry long ribs, and meet below the chorda to form semi-rings. The dorsal and ventral semi-rings do not meet each other, leaving along the side of the chorda a broad thin belt of non-cartilaginous membrana reuniens. But there are two exceptions :

(1.) In the first two or three cervical segments, the dorsal and ventral semi-rings are confluent, forming complete rings around the chorda.

(2.) In the latter half of the tail, the chorda stops suddenly ; just before the chorda ends, within the extent of a few segments, the dorsal and ventral cartilaginous rings meet around the chorda. Then follows the chordaless portion, forming an entirely cartilaginous axis, which is transversely broken up into about ten or more blocks of variable length, each block carrying a variable number of gable-pieces and dorsal and ventral unpaired fin-supporting rays of cartilage.

The Dipnoi strongly resemble the Holocephali in so far as in this portion of the tail the whole chordal sheath is converted into cartilage and is fused with the arcualia, the tail of the adult *Ceratodus* showing greater coalescence of its cartilaginous elements than *Protopterus*.

Cartilaginous Ganoids.

The chorda shows uniform and persistent growth throughout life. The chordal sheath is thick ; its elastica externa remains entirely unbroken. The skeletogenous layer remains restricted to the outside of the elastica, and produces dorsal and ventral arcualia which remain laterally asunder, being there connected by the membrana reuniens only.

Acipenser sturio.—Embryos of 7 millims. in length. The chordal sheath is still extremely thin, although the elastica externa can already be distinguished, owing to its strong refractive peculiarity.

In embryos of 14 millims. the chordal sheath shows the usual characters, being concentrically fibrillar, and being thicker than the elastica externa. The skeletogenous cells arrange themselves in two dorsal and two ventral longitudinal rows, preparatory to the formation of the arcualia and the membrana reuniens, but no cells enter the chordal sheath.

In the *adult* each complete segment possesses two pairs of ventral acualia, and at least two pairs of dorsal arcualia.

The larger pair of the ventrals, the basiventrals, carry the ribs, and alternate with smaller " intercalaries" ; towards the tail the latter withdraw from contact with the chordal sheath, and appear wedged in ventrally between the then juxtaposed basiventrals. The ribs are often broken up into several bits of cartilage. The basiventrals often form semi-rings by fusion.

The dorsalia all rest upon the chordal sheath. They consist (1) of a pair of large cartilages, generally and reasonably called the dorsal arches, which close above the chordal sheath (mostly without fusing into a semi-ring) and carry a forked piece, the

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legs of which enclose the ligamentum longitudinale, and then either appear as the dorsal spines, or they carry another system of unpaired cartilages which ultimately carry the fin; (2) two, rarely one, pairs of small cartilages, generally called intercalaries, wedged in between the bases of two successive arches; the anterior one of these intercalated pieces is sometimes pierced by the motor root of the spinal nerve; towards the tail these pieces are reduced to one pair. Both the sensory and motor nerves, as a rule, pass through the large dorsal arch, near its hinder margin.

Each pair of basiventrals can form a semi-ring by fusion below the chorda; the basidorsals or dorsal arches rarely fuse across, but oftener at some distance above, the spinal cord.

Polyodon folium.—Adult. Essentially the same as *Acipenser*.

The large basidorsalia coalesce, right and left, above the spinal cord, and carry a forked gable-piece, which spans over the longitudinal ligament and then carries a similar top-piece of the shape of an ⅄. In the hinder portion of the trunk each of these top-pieces or neural spines is double, consisting of a right and a left half. Small interbasals, one dorsal and one ventral pair to each segment, are wedged in between the basal corners of the chief ventralia. The motor and the sensory roots pass between two juxtaposed chief basidorsalia, the motor root mostly through or above the apex of the small intercalated piece

Osseous Ganoids.

Amia Calva (figs. 1–14).

The Vertebral Column of the Adult Fish (see fig. 14, on p. 205) shows several most important peculiarities. Vertebræ 1–38 consist each of (1) one centrum which carries; (2) on its posterior dorsal corner a pair of long dorsal "arches," which ultimately fuse into one neural spine; (3) from about the middle of the central disc springs a lateral stump, the basiventral, which carries a free typical rib. This basiventral stump varies in the different regions of the trunk; it sometimes arises nearer the anterior, in other vertebræ nearer the posterior end of the disc. The last rib, very short and slender, is carried by vertebra 38.

From vertebra 39 tailwards, each vertebra carries on its ventral side a pair of strong bony pieces which enclose the caudal canal, and below it are fused together, carrying, moreover, an unpaired ventrispinal piece. This latter piece, at first movably jointed to the Y-shaped combined basali ventralia fuses with them from about the 17th caudal vertebra onwards (*cf.* Gegenbaur, 'Jenaische Zeitschrift,' 1867, Plate 9, fig. 22), who homologized these ventralia with ribs.

The most remarkable feature of the central discs of most of the caudal vertebræ is that they are double.

Whilst the first 42 vertebræ (in Gegenbaur's specimen apparently 41 only) each

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possess one centre disc only, the following skleromeres, or skeletal segments (as proved by the spinal nerves) each possess two centre discs. One of these discs carries both the dorsal and the ventral arches (ribs), while the other disc carries nothing. The question arises whether the archless disc lies in front of or behind the other arch-bearing disc, together with which it makes up one complete skleromere. The position of the dorsal arches does not decide anything because of their extremely variable position. The same applies to the attachment of the costal arches. Accidentally, in the 17th caudal skleromere (the 55th of the whole column), both discs are completely fused together, and show the archless portion to form the posterior half of the whole. This is not much to go by, but the assumption that the archless disc is the posterior half, gives satisfactory results.

I, therefore, call the arch-bearing disc the precentrum, the archless disc the post-centrum.

Amia. *Young.* Total length about 57 millims. (figs. 1–13, pp. 204, 205).

The central part of the *chorda* consists of a network of radiating strands, while the greater part of the protoplasm, and the nuclei, are arranged near the periphery, forming there the chordal epithelium. The *chordal sheath* is, compared with that of Elasmobranchs, Dipnoi, and Cartilaginous Ganoids, a decidedly thin ring of closely-packed concentric fibres, with no cells between them.

The *elastica externa* is present as a thin refractive membrane. Outside this elastica follows a thick zone of loose connective tissue which forms a layer of bone on its inner surface, and in this zone of connective tissue cartilage cells, from the basal portions of the arcualia, grow round the chordal sheath preparatory to the formation of the central discs. The ossificatory process partly destroys the elastica externa, and converts a thin outermost portion of the chordal sheath itself into bone.

Arcualia.—There are in opposition to the adult two dorsal and two ventral pairs of cartilages to each segment, namely, dorsal and ventral basalia and "intercalaries." Their arrangement differs in the tail from that in the trunk.

Tail.—All the arcualia rest upon the thin layer of bone which lies immediately outside the elastica externa, and are themselves surrounded for the most part by bone (perichondral ossification). The *basidorsals* have a broad base and extend upwards at the sides of the spinal cord; they do not fuse into one spine, except in their upper fourth or third, high above the spinal cord and the longitudinal elastic ligament. The *interdorsals* have as broad a base, but only extend a little way up the sides of the spinal cord. The roof of the neural canal is formed by membrane only, except between the legs of the basidorsals, against the inner side of which rests a pair of small cartilages; these meet each other just above the spinal cord and below the longitudinal ligament. Although we have traced them through an uninterrupted series of sections, they were nowhere seen in direct connection either with the cartilage of the basidorsals or with the interdorsals; they were always separated from the basidorsals by a thin ossified layer. There can scarcely be a doubt that they are examples of J. MÜLLER's

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Intercalaria spinalia, but this statement does not throw light upon their morphological value.

The *basiventrals* meet below the caudal vessels, and carry an unpaired spine.

The *interventrals* do not meet below.

It is important to note that the homotype pieces do not lie in the same transverse plane, each basiventral lying below an interdorsal, and the interventrals corresponding in position with the basidorsals.

Arcualia in the Trunk.—Only the dorsal and ventral intercalaries rest upon the thin layer of bone round the elastica externa. The *basidorsals*, which are by far the largest of the arcualia, rest with their broad bases above the interdorsals. The *basiventrals* have shifted upwards and tailwards so as to lie in the same transverse plane as the intercalaries. Owing to this shifting and the broad extent of the bases of the basidorsals, it has come to pass that all the four arcualia overlap each other, with the exception of the anterior half of the basidorsals. The basiventrals extend laterally in the shape of basal stumps and carry well-developed movable ribs. The interventrals are small, meet ventrally, and lie below and slightly in front of the basiventrals.

Formation of Centra in the Tail.—The anterior half of each ventral arcuale* and the posterior half of each dorsal arcuale send out a mass of skeletogenous cells, which not only connects the right and left pieces with each other, but grows towards and past the middle of the chorda; the outgrowth of the dorsalia points with its apex downwards, the pyramidal growth from the ventralia points upwards.

Consequently each pair of arcualia produces a semi-ring, thickest above (or below) the chorda, with its ends pointing downwards (or upwards). These opposite outgrowths meet in such a way that the ventral mass or semi-ring extends upwards *in front* of the down-growing dorsal semi-ring.

These masses fuse with each other into a complete ring of cartilage, hyaline, and perichondrally ossifying in the arcualia, more fibro-cartilaginous in the newly-formed belt. These belts do not constrict the growth of the chorda and its sheath. Owing to the number of basalia and interbasalia which all rest upon the chordal sheath, and owing to their alternate position, two belts are formed within each complete segment.

The anterior belt is formed by the outgrowth of the basiventral joining that of the interdorsal above, the posterior belt by the interventral with the basidorsal above.

However, not all the skeletogenous cells sent out from the arcualia are converted into cartilaginous cells; about one half of each outgrowth consists of indifferent, later on fibrous connective tissue, and is directly converted into bone, and henceforth hinders, or constricts, the chorda in its further growth.

* This expression is not accurate, but it may pass in the text for the sake of shortness. In our 56 millim. *Amia*, the arcualia consist already of hyaline cartilage with a definite boundary line against the pyramidal or crescent-shaped cell masses. In reality both the arcualia and these masses are the offspring of the same matrix, namely, of the dorsal and ventral ends of the sklerotomes. Probably the arcualia turn first into cartilage, while the centrum-forming masses grow out later, and still later turn into cartilage, repeating the course of phylogenesis.

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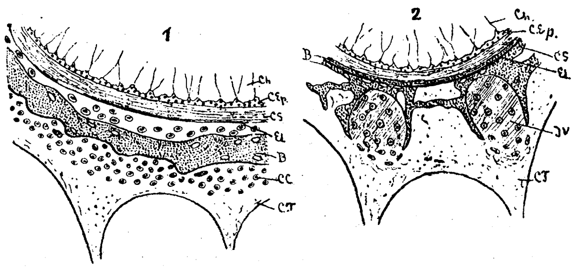
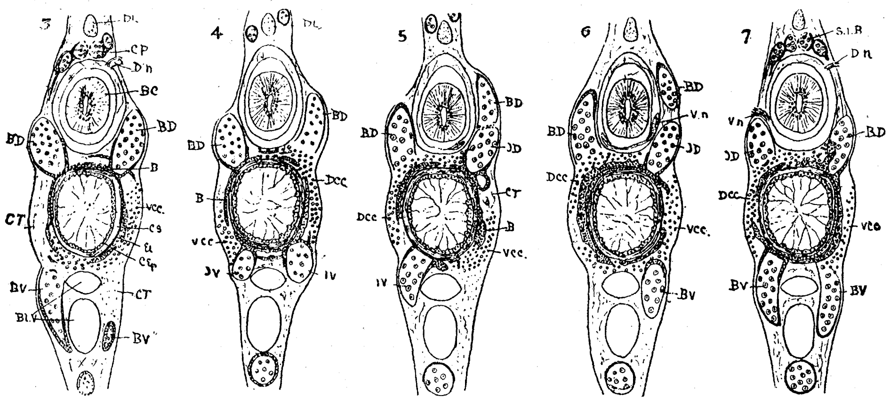
Thus each segment contains two cartilaginous and two osseous belts, which alternate. Owing to the rapidly proceeding ossification which also affects the perichondrium of the arcualia, the two bone belts firmly connect the dorsal and ventral pieces with each other.



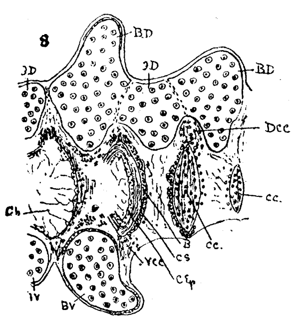
Figs. 1 and 2. Transverse sections through portion of a trunk segment.

Fig. 1. Plane passing through the basiventral cartilages. Bone indicated by dotted area.

Fig. 2. Plane passing through the intervertebral cartilage.



Figs. 3 to 7. Series of transverse sections through *one* caudal vertebra, traced backwards. (One vertebra of both trunk and tail represents about 100 sections.) Showing the dorsal and ventral masses of cartilaginous cells which arise from the masses of the arcualia, and grow upwards and downwards around the outside of the chordal sheath.



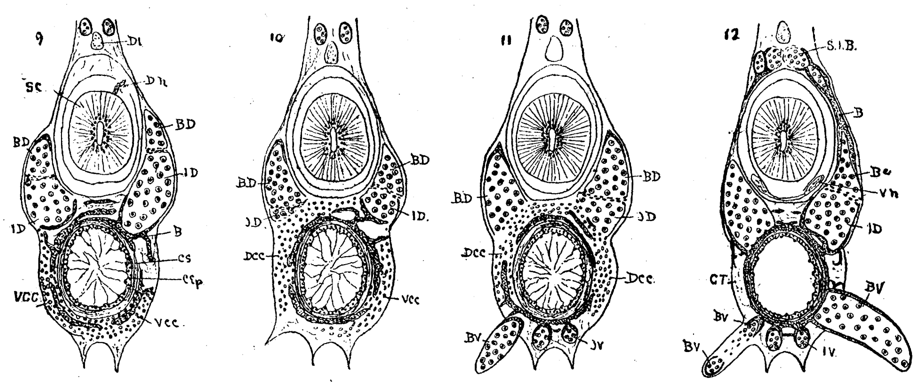


Fig. 8. Sagittal section through the tail, showing the relative position of the arcualia, also that the chorda is constricted by both basalia and interbasalia, and that a belt of cartilage occurs between these constrictions. The right side (posterior) of the section is more lateral than the left end.

Figs. 9 to 12. Series of transverse sections through one vertebra of the trunk, showing the shifted position of the basiventrals, which are in the same transverse plane with the interbasals, both interdorsals and interventrals.

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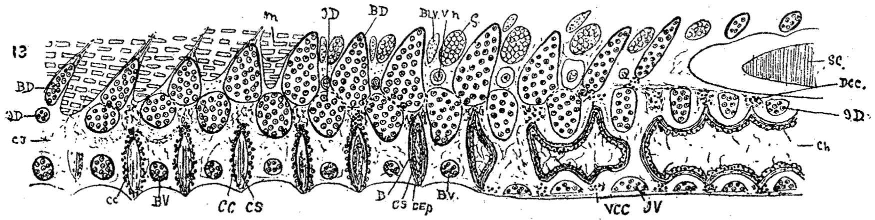

Fig. 13. Combined sagittal sections through the trunk, the anterior (left) end being cut more laterally, the posterior (right) end more centrally. The chorda is constricted by the interbasals only; see left end of drawing.

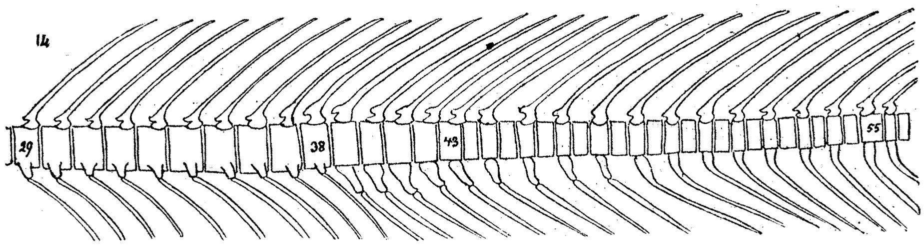

Fig. 14. *Amia calva*, adult; left-sided view of the vertebral column from the 29th to 56th vertebra. Mus. Zool., Cambridge.

Explanation of the Lettering of the figs. 1 *to* 14, *illustrative of* Amia calva.

B. = Bone.
B.D. = Basidorsal } Basalia.
B.V. = Basiventral } Basalia.
Bl.V. = Blood vessel.
C.C. = Cartilaginous cells which surround the chorda.
C.Ep. = Chordal epithelium.
Ch. = Chorda.
C.S. = Chordal sheath.
C.T. = Connective tissue.
D.C.C. = Dorsal cartilaginous cells.
D.L. = Dorsal longitudinal ligament.
D.N. = Dorsal nerve-root.
El. = Elastica externa.
G. = Ganglion of dorsal nerve-root.
I.D. = Interdorsal.
I.V. = Interventral.
S.C. = Spinal cord.
S.I.B. = Supra-interdorsals.
V.C.C. = Ventral cartilaginous cells.
V.N. = Ventral nerve-root.

Every anterior bone belt combines the basalia, while every posterior bone belt connects the interbasals or intercalaries. Ultimately a severance takes place between the bone and the cartilage belts, the split occurring in a transverse plane behind each bone belt (or in front of each cartilage belt).

In the adult, the cartilaginous parts also are ossified and each complete caudal skleromere consists of two jointed successive halves :—

1. One anterior disc, which carries on its dorsal posterior end the pair of large "dorsal arches," and on its ventral side the "ventral arches" (basiventrals inclusive of ribs).

2. One posterior disc, or *postcentrum*, carrying no "arches" but containing the

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interbasals, which have become merged into its formation. The chordal sheath does not contribute any material to the formation of the centra, these being formed entirely by and from the arcualia.

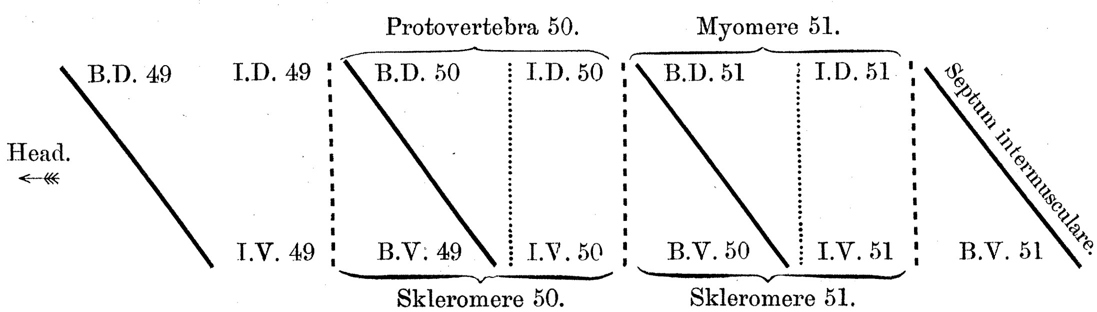
This is the first instance of truly *ectochordal ecto-* or *arco-centra* in a well jointed bony vertebral column.

As it happens, this first "attempt" is still imperfect, because it implies a contradiction to the principles or tendencies hitherto followed by (or observed in) the phylogenesis of the axial skeleton.

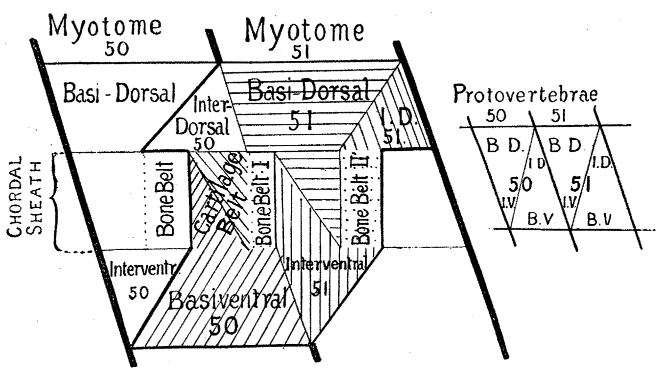
To understand this properly, we have to resort to numerical analysis of the vertebral constituent parts.

The Arabic numbers refer to the serial numbers of the protovertebræ or sklerotomes. BD. and ID., BV. and IV., signify basidorsals, interdorsals, basiventrals and interventrals.

We had concluded (p. 188, Elasmobranchs) that in the early stages the interdorsals follow behind the basidorsals of the same protovertebra, but that the interventrals precede the basiventrals. Owing to the slant of the whole protovertebræ, it comes to pass that unequally numbered homotypes stand in the same transverse vertical plane, thus:



The oblique black lines indicate the intermuscular septa.
The vertical strong dotted lines indicate the separation between successive adult skleromeres.
The vertical thin dotted lines mark the separation between precentrum and postcentrum.



Analysis of a caudal vertebra of *Amia*.

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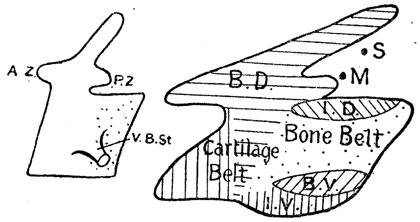
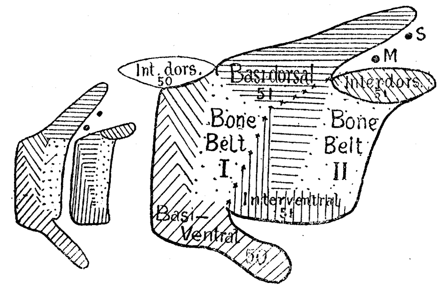


A vertebra of the trunk of *Amia*. V.B. St. = Ventral basal stump, to which the rib is attached.



A complete caudal skleromere (precentrum and postcentrum) of *Amia*. The line of asterisks indicates the separation of the pre- and postcentrum.

M. and S. = Motor and sensory portion of spinal nerve.

In the more advanced stage (the 56 millims. specimen, for instance), in the half-grown skleromeres the interbasals follow behind their basals or "arches," not only on the dorsal side, where the original condition is retained, but also on the ventral side, where unequal numbers are combined, B.V. 50 being followed by I.V. 51. The anterior cartilaginous belt of skleromere 50 (taking the skleromere formed by portions of sklerotomes 50 and 51) is formed by B.V. 50 and I.D. 50: the first bone belt is formed by the anterior portion of B.D. 51, and the posterior portion of B.V. 50; consequently the arch-bearing precentrum is moved by (or gives surfaces of attachment to) myomeres 50 and 51, as it should be. The posterior belt is formed by outgrowths from I.V. 51 and B.D. 51; the posterior bone belt from I.V. 51 and I.D. 51, consequently the archless postcentrum coincides in position with one skleromere only, namely, 51.

Certainly we know nothing about the conjoint play of the tail muscles of *Amia* (or, for the matter of that, of any fish), and there is no doubt that the zigzag course of the septa, with the far overlapping dorsal and ventral spines, makes the tail an effective motory organ, but in spite of all this morphologically the caudal skleromeres seem to be constructed upon faulty and imperfect lines.

This deficiency has been overcome in the trunk.

Formation of Centra in the Trunk.

Owing to the different position of the arcualia (the basidorsals appearing pushed upwards, the basiventrals back and upwards) each complete skleromere or segment shows only one constriction of the chorda, namely, the one corresponding with the cartilage massed together in the shape of the interbasals and basiventrals. The spaces between these three pieces are filled with indifferent connective tissue and ossify early. In front of this osseous and cartilaginous constricting piece lies the belt of cartilage produced by the downgrowth from the anterior portion of the basidorsal, and an upgrowth of cells which start chiefly from the space between the successive interventrals. We suppose that this ventral pyramidal outgrowth belongs

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to the same sklerotome, which also gave rise to the basiventral, but how the latter has been shifted backwards we do not know.

At any rate, both in the tail and in the trunk, the posterior half of the basidorsals seems to send out the belt-forming cells in the shape of downgrowing pyramids or half rings. Ultimately ossification extends through the whole of the central mass, welding together (into *one* single centrum) the anterior cartilaginous belt, and the posterior somewhat larger portion, the transverse truly intervertebral division taking place in front of the cartilaginous belt, just as in the tail. We have here, for the first time, a typical vertebra, which consists of one centrum or body, carrying a pair of dorsal and a pair of ventral arches. The centre itself is a compound structure, produced entirely by the arcualia on the outside of the chordal sheath, the latter not contributing anything to the formation of the body (the narrow zone of ossification to the inside of the elastica externa can practically be neglected), although chorda and sheath persist throughout life in portions, namely, in the trunk intervertebrally (the vertebræ being biconcave), and in the tail, both *inter*vertebrally as well as *intra*-vertebrally (both pre- and postcentra being biconcave).

Comparison of Amia *with Jurassic Ganoids.*

Zittel (" Palæozoologie, Vertebrata," pp. 137–139, 228–231, 234) gives figures of trunk and tail vertebræ of several Jurassic Ganoids. Some of these figures are much restored and should therefore be accepted only with caution. They show rather well what they are intended to prove, but it is questionable if the explanation of the composition and formation of these vertebræ is correct. With certainty only the following homologies and synonymous elements can be recognized.*

Zittel assumed in his text-book that the posterior disc (our post-centrum) is formed by the gradual downward extension of the dorsal semi-ring, and a judicious selection of upper Jurassic Ganoids (*e.g.*, *Caturus*, *Callopterus*, *Eurycormus*, trunk and tail) make such a view very plausible—but in reality we saw that both pre- and postcentra of *Amia* are much more complicated structures than down- and up-growth of simple semi-rings.

The fossil Ganoids show, however, several points clearly. *First*, the extraordinary amount of apparent shifting of the dorsal arch or spine, either on to the top of an interdorsal following behind, or upon the " up-grown apex of the hypocentrum." The same amount of change in the position of the dorsal arch with reference to the whole vertebra prevails in the various regions of the trunk and tail of *Amia*, and of many Teleosteans.

* Basidorsals = Neural or dorsal arches.

Interdorsals = " Pleurocentra," *i.e.*, the dorsal semi-ring which in the trunk of *Eurycormus* and *Caturus* carries nothing, but which in *Callopterus* carries the dorsal arches.

Basiventrals and Interventrals = " Hypocentra," *i.e.*, the ventral semi-ring, which in *Eurycormus* carries the ribs as well as the dorsal arches and forms the precentrum in the trunk and tail.

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Secondly, there can be no doubt that the dorsal and ventral inverted pyramidal cartilages in the fossil Ganoids indicate an up- and down-growing tendency, and that this same feature is repeated in the growing pyramidal masses of skeletogenous cells produced by the embryonic sklerotomes as described in embryonic Elasmobranchs and in the young of *Amia*. The principle concerning the formation of vertebral centrum-forming belts is the same in the recent and in the fossil Ganoids. *Caturus* has remained at, or reached, a stage which in *Amia* occurs in the embryonic and early life only. Another illustration of the repetition of early phylogenetic conditions by embryonic phases of recent descendants, is the fact that the "Hypocentral semi-ring" is frequently double, *i.e.*, it retains the original right and left ventralia without their fusing across below the chorda.

Lepidosteus Osseus.

The following description could be kept short because, through the kindness of Professor W. N. Parker, we were enabled to study the same sections which served for Balfour and Parker's Memoir, in 1881.

Concerning the adult and postlarval fish, Gegenbaur's work has well nigh exhausted the subject. Suffice it to remember that the vertebral column of *Lepidosteus*, both in the trunk and in the tail, shows externally typical Teleostean features; there are no arch-bearing discs or centra alternating with archless discs or postcentra.

Larva of 2·5 *centims.* in length. Figs. 1 to 3, p. 210.

The bulk of the axial column is formed by the chorda itself; the chordal sheath is thin, only about one-tenth, or even less, the thickness of the chorda. The elastica externa is a complete ring; no skeletogenous cells migrate into the chorda sheath. The membrana reuniens is thin on the sides. Of arcualia only basidorsals and basiventrals are present as cartilaginous masses; they lie in the same transverse plane. The basidorsals reach round about three-quarters of the spinal cord, but they do not meet either above or below it. The basiventrals are small, and do not meet each other in the trunk, but in the tail they are larger, meeting and fusing below the caudal canal into an unpaired process.

Larva of 5·5 *centims.* Figs. 4 to 6.

A complete cartilaginous ring or tube has been formed round the chordal sheath outside the elastica externa, which is still present. The greater portion of this cartilaginous tube is situated between successive basalia, taking up that space which, in the 2·5 centims. larva, is still membrana reuniens only, resembling, in this respect, the young *Protopterus*. The cells of this "intervertebral" ring are more closely packed than those of the basalia, with which the ring, at least in this stage, is continuous. The intervertebral ring constricts the further growth of the chorda considerably; a much slighter constriction is caused by the cartilage of the basalia. A line of incipient division into opisthocœlous centra has appeared within the middle of the intervertebral ring.

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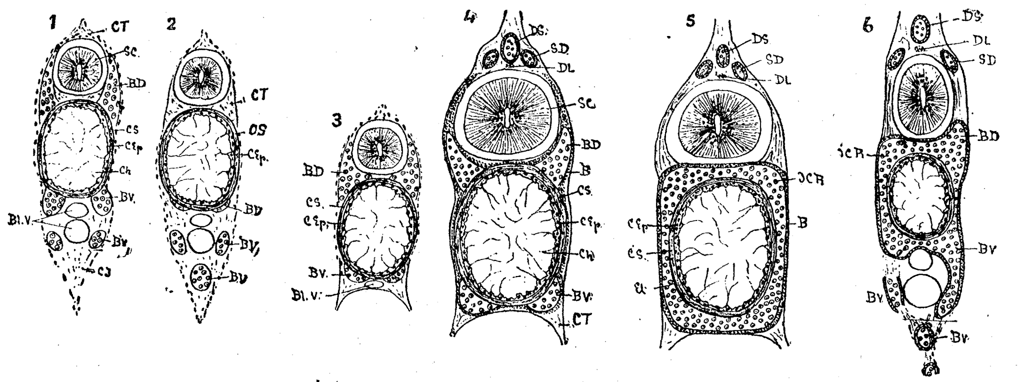

Figs. 1 to 3. Transverse sections of the vertebral column of a larva of about 2·5 centims. in length.

1. Through the vertebral region in the tail, showing the cartilaginous basalia. The basidorsals extend almost to the top of the spinal cord, and the basiventrals coming down to meet below the blood vessels. Two successive basiventrals are cut in this section, namely, B.V. and $B.V_1$.

2. Section through an intervertebral region in the tail, showing the connective tissue which replaces the basalia.

3. Section through a vertebral region of the trunk, showing the basidorsals extending up almost to the dorsal part of the spinal cord, while the basiventrals are very small.

Figs. 4 to 6. Transverse sections of a larva of 5·5 centims. in length.

4. Section through the vertebral region of the trunk showing the cartilaginous basalia not connected with each other, and surrounded by a layer of bone, which also extends round the chorda. The paired supradorsals are cut through just above the spinal cord, and the unpaired spine lies between them.

5. Section through the intervertebral region of the trunk, showing the intervertebral ring of cartilage surrounding the chorda. This ring of cartilage is thicker at the four corners, and surrounded by bone.

6. Section through the tail of the same embryo, but cut obliquely, so that the section passes through the vertebral region on the right side, and the intervertebral on the left, and so shows that the cartilage of the intervertebral ring is continuous with that of the basalia.

Several other structures have made their appearance in the vicinity of the basidorsals, namely, the longitudinal dorsal ligament and a pair of supradorsals. These supradorsals (*na′* in fig. 70 of Balfour and Parker) (*α″* "Fortsatz der Bögen" of Gegenbaur) are placed in a very slanting position on the right and left side of the longitudinal ligament. They nearly touch, but are not continuous with the top ends of the basidorsals, being connected with them by part of the membrana reuniens only. They do not meet above the ligament. Between their tops above the ligament arises the unpaired dorsospinal cartilage.

Perichondral ossification begins to spread in this stage.

Larva of 11·5 *centims.* Figs. 7 to 11.

The intervertebral ring has become very thick, and is gradually being converted into bone by centripetal ossification. The transverse split or the formation of the opisthocœlous joints is scarcely further advanced than in the last stage.

Considerable changes have taken place in the region which carries the basalia or

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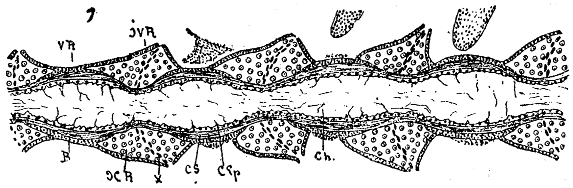
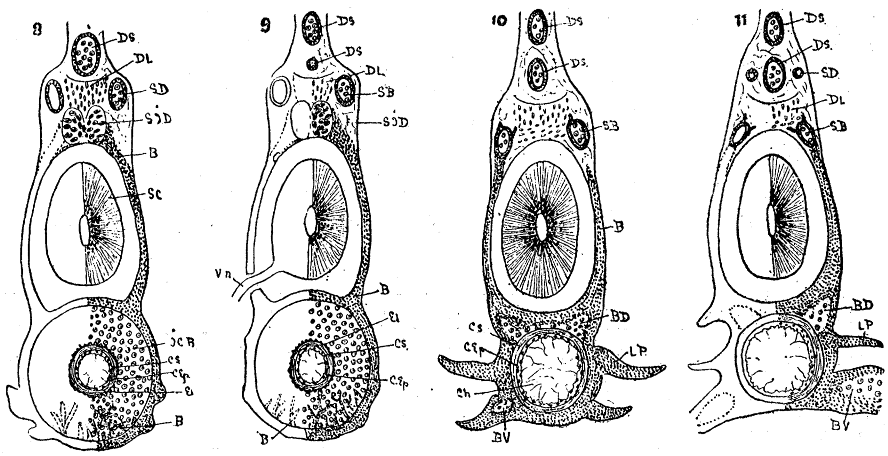


Fig. 7. Longitudinal horizontal section of a larva of 11·5 centims. in length. Showing the intervertebral constriction of the chorda by means of the cartilaginous ring, as well as the previously existing slight vertebral constriction due to a thickening of the chordal sheath. It also shows the line of division between the vertebræ in the middle of the cartilaginous ring. The line is curved, the posterior part being concave, so that the vertebræ will be opisthocœlous.



Figs. 8–11. Series of transverse sections through one vertebra of a larva of 11·5 centims. in the trunk.

8. Section through an intervertebral region, showing the very thick cartilaginous ring surrounding the chorda, and of equal thickness all round. It is surrounded by bone, which is advancing inwards and destroying the cartilage. The chorda is very much constricted by this ring, and the elastica is thrown into folds. The spinal cord is roofed in by cartilaginous pieces, the supra-interdorsals, which lie just below the dorsal ligament. A layer of bone surrounds the intervertebral ring, runs up laterally to the spinal cord, and extends as far as the supra-interdorsals.

9. Section through the intervertebral region showing the nerve exit, which occurs about the middle of the intervertebral ring, where the line of separation between the vertebræ arises. The extreme end of the dorsal spine is cut, showing that it has no connection with the paired supradorsals.

10. Section through the beginning of a vertebral region, showing the cartilaginous basalia just appearing, and the thick layer of bone which separates the cartilage of the basalia from that of the intervertebral ring. The supra-interdorsals are not cut in sections of the vertebral region.

11. Section through the vertebral region showing the cartilaginous basalia, but the basiventrals do not rest on the chordal sheath in this section. Two successive supradorsals are cut as they overlap slightly in the vertebral regions.

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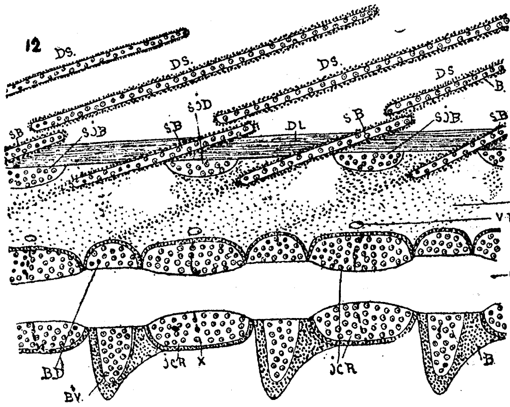

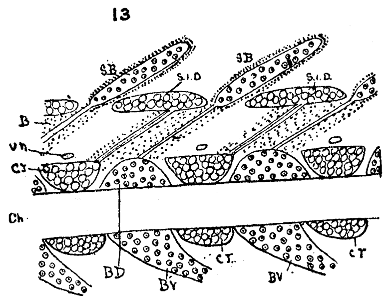

Fig. 12. Diagram to illustrate the relative arrangement of parts in *Lepidosteus*, reconstructed from a series of transverse sections. The basalia are opposite each other. The intervertebral regions are longer than the vertebral and constrict the chorda. The nerve exit is in the middle of the intervertebral ring, and the line of separation between successive vertebræ runs through the cartilaginous ring. Paired supradorsals run obliquely from near the dorsal surface of the spinal cord to the top of the dorsal ligament. The cartilage of these pieces is not continuous with that of the basidorsals, but they are connected by bone, and form a continuous arch in the adult. Supra-interdorsals are paired pieces which alternate with the supradorsals, but are more median in position. They are connected by bone with the supradorsal behind. The dorsal spines are unpaired, and lie parallel to the supradorsals but above them; they are so long that they extend over two complete vertebræ.

Fig. 13. Diagram to illustrate the arrangement of parts in the vertebral column of *Protopterus* of about 8 centims., reconstructed from transverse sections. The basalia are opposite each other and are cartilaginous. Between successive basalia are masses of connective tissue in the same position as the cartilaginous ring of *Lepidosteus*. The supradorsals are large and join each other above the spinal cord, but in *Protopterus* they are connected with the basidorsals by a slender rod of cartilage. Another mass of connective tissue lies above the spinal cord in a similar position to the supra-interdorsals of *Lepidosteus*, and this receives connective tissue strands from the connective tissue mass between the arches. The nerve exits are just above the connective tissue masses, and in the middle of them in a similar position to those of *Lepidosteus*.

Explanation of the Lettering of figs. 1–12, *illustrative of* Lepidosteus, *and fig.* 13 *of* Protopterus.

B. = Bone.
B.D. = Basidorsals.
B.V. = Basiventral.
Bl.V. = Blood vessel.
C.Ep. = Chordal epithelium.
Ch. = Chorda.
C.S. = Chordal sheath.
C.T. = Connective tissue.
D.L. = Dorsal longitudinal ligament.
D.S. = Dorsal spine.
El. = Elastica externa.
I.C.R. = Intervertebral cartilaginous ring.
I.V.R. = Intervertebral region.
L.P. = Lateral process.
S.C. = Spinal cord.
S.B.D. = Supra-basidorsal.
S.I.B. = Supra-interdorsal.
V.N. = Ventral nerve root.
V.R. in fig. 7 = Vertebral region.
X. in fig. 7 and 12 = Line of separation between successive vertebræ.

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arches. There, except in the arches themselves, the cartilage has been entirely supplanted by bone, which now rests directly upon the chordal sheath. This bony belt is now longer than the intervertebral cartilaginous belt, while originally the reverse was the case. Moreover, the intervertebral cartilage is now completely separated from that of the arches themselves. Of course, all this indicates that the vertebral column grows faster in length in the intravertebral or arch-bearing region than intervertebrally. The nerve-exits occur in level of the middle of the intervertebral ring, where the joint is forming, so that in the adult the exit of the spinal nerve comes to lie between two vertebræ.

The longitudinal dorsal ligament has been formed, and the roof of the spinal canal is now completed by two cartilaginous pieces, which occur between successive pairs of interdorsals, but are connected by tissue with the top ends of the basidorsals next following. Those connecting pieces are mentioned by GEGENBAUR as Schluss-stücke, marked a' in his figures. BALFOUR marked them *i.c.*, and perhaps also *d.c.*; described them as "intercalated cartilaginous elements of the neural arches"; and considered them, erroneously, as "directly differentiated from the ligamentum longitudinale." There is, however, scarcely any doubt that these supra-interdorsals, as I propose to call them, stand in the same relation to the interdorsals as the supradorsals to the basidorsals; they are both the distal ends of the still paired, or not yet united, dorsalia.

The basiventrals grow out laterally in the trunk, but in the tail they bend down and meet below the caudal canal.

Adult. Figs. 12–13.

The intervertebral constriction is completed. The whole centrum is ossified. The dorsal arches broaden out at their basal portions, so that two successive arches almost touch each other, leaving only a small space between them for the passage of the spinal nerve. The paired supradorsals are now fused, co-ossified with the dorsal arches, and help to form a sort of posterior zygapophysial projection, which receives a corresponding anterior outgrowth from the broadened-out shaft of the basidorsal proper. The supradorsals are fused into an unpaired mass of cartilage, which remains in this condition, placed intervertebrally immediately below the dorsal ligament; the successive pairs are connected with each other by the remnant of the membrana reuniens.

Summary.

It is easy after the examination of *Amia* to make an analysis of such a vertebral segment of *Lepidosteus*.

We have the following data :—

1. A first cartilaginous ring is formed by a pair of basidorsals and basiventrals . . . . Belt I.

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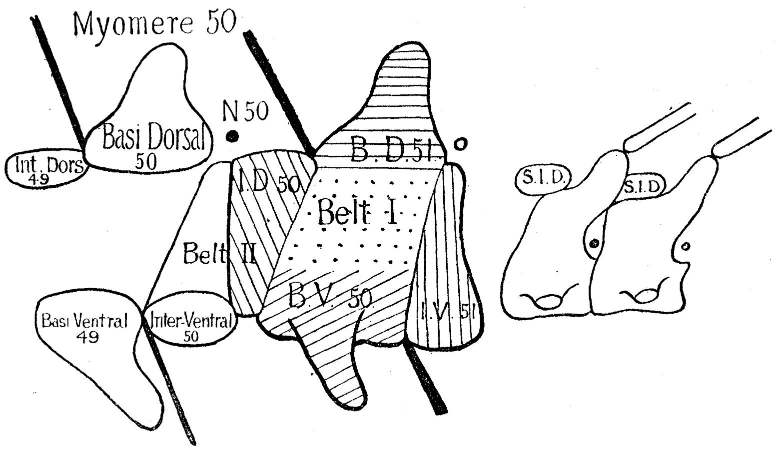
2. A second cartilaginous ring is formed by masses corresponding with interdorsals and interventrals . . . . Belt II.

3. Belt I. is transformed into bone, and assumes a greater length than Belt II.

4. The intervertebral joint is formed across the middle of Belt II., giving half of its mass to the hinder end of the preceding, the other half to the anterior end of the next following vertebra.

5. The spinal nerve lies in the transverse plane of this joint.



Diagrammatic sketch of two trunk vertebræ of *Lepidosteus*. N = position of spinal nerve-exit. The two thick black lines indicate the septa which divide myomere 50 from its neighbours.

Consequently, in the number of belts (one bony, one cartilaginous), *Lepidosteus* agrees with the trunk of *Amia*, but, in the mutual position of the arcualia, it resembles more the tail of *Amia*.

The resemblance with the tail of *Amia* becomes greater after the intervertebral belt has been split into two halves, there being henceforth two (secondary) adjoining cartilaginous belts, and one bone-belt to each complete segment. But there is this difference, that in *Amia* the posterior halves of the interbasalia have produced a second bone-belt, which separates the otherwise adjoining cartilaginous belts. Reference to the diagrams will make this clearer than long descriptions.

The position of the joint and nerve in *Lepidosteus* is different from that in *Amia* in the trunk, as well as in the tail.

This arrangement, or the combination of parts into one vertebral complex, is superior to that of *Amia*, because each vertebra now belongs, with its entire anterior half (interdorsal, 50 + basiventral, 50), to myomere, 50, and, with its entire posterior half (basidorsal, 51 + interventral, 51), to myomere, 51; in other words, the vertebral mass is equally divided between two successive myomeres, or, the myomeres have an equal share in the skleromeres. The vertebræ are now truly bi-protovertebral. Referring back to p. 189, the new skleromere is composed of $a + b$.

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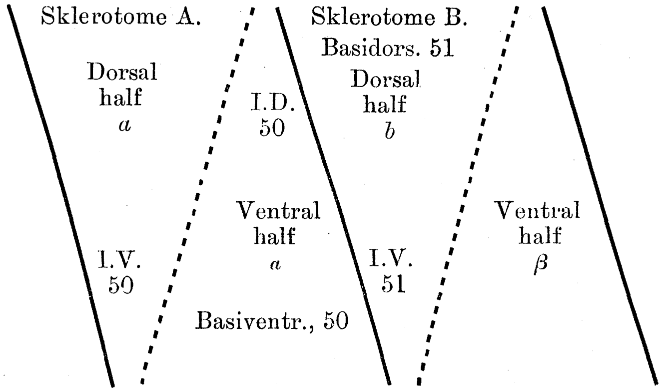

Black lines = intermuscular, protovertebral septa.
Dotted lines mark the boundary of the vertebra.

TELEOSTEI.

Teleostei have been frequently examined, notably by GEGENBAUR, SCHEEL, and, above all, by GRASSI, of whose extensive and amply-illustrated memoir a meagre extract has been published in 'Morph. Jahrbuch.' However, the Teleosteans examined belong, without exception, to one of the most specialized and undoubtedly recent group of periarctic fresh-water forms, namely, *Salmo*, *Fario*, *Esox*, *Leuciscus*, *Rhodeus*.

We ought to bear in mind that the extremely few surviving osseous Ganoids are not the direct ancestors of any recent Teleostean families, and that the *Teleostei* are probably polyphyletic, evolved from various Ganoids, which in the Jurassic period already exhibited an extraordinary variety of types.

It is rash to set up one European family as the type, and explain all other forms in the usual way as due to "secondary" and "unimportant" modifications. In most European fresh-water fishes, for instance, the dorsal and the ventral arches are carried by the anterior portion of the vertebral body, as in the 55th tail vertebra of *Amia*, and in *Thrissopater salmoneus* from the Gault; in the oligocene *Meletta* (*cf.* ZITTEL, fig. 285) the dorsal arch is fused with the posterior end, the ventral arch with the middle of the vertebral body. In the trunk of *Thrissops salmoneus*, AG. ('Lithogr. Solenhofen.') the dorsal arch is carried by the middle, the basal stump, with the rib, by the anterior half of the centrum, resembling in this respect *Lepidosteus*. In *Serranus gigas*, *Xiphias gladius*, and in the tail of the peculiar Pipe-fish, *Aulostoma coloratum*, the dorsal arch is carried by the posterior, the ventral arch by the anterior end of the centrum, as in the trunk of young *Lepidosteus*. The arrangement, dorsal arch carried by the anterior, ventral arch by the posterior end of the body of the vertebra, seems to be peculiar to the trunk of *Amia*. The chief features concerning the vertebral column of the Teleostei are consequently essentially those of osseous Ganoids.

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The chordal sheath is thin, remaining a true elastica interna, surrounded by an extremely thin elastica externa (see fig. 31, on page 176). The centrum is formed entirely by the skeletogenous layer remaining outside the elastica, its cartilage is derived from the dorsal and ventral arcualia. These arcualia themselves make their appearance as separate elements (Trout), or they, namely, the basidorsals and the basiventrals, are fused from the beginning (Rhodeus).

The amount of cartilage sent out from the basalia to form the centre varies much; the cartilage surrounds the chordal sheath with a complete mantle (Rhodeus), and is ossified later on, or very little cartilage grows round the chordal sheath, and most of the material necessary for the formation of the centrum is indifferent membrana reuniens and ossifies directly (Trout).

The chorda seems invariably to be constricted vertebrally while it grows, and extends throughout life in the intervertebral region, differing in this respect absolutely from *Lepidosteus*. Except in the posterior half of the tail, where in many fishes a great amount of stunting, fusion, and shortening takes place, the number of vertebral centra agrees with that of the complete segments, neuro-myomeres.

In the ordinary Cyprinoid type, the anterior arch, bearing half of the centrum, is formed by the basalia, which seem, as a rule, to lie in the same transverse plane, and these basalia do not interfere at first with the growth of the chorda, the great constriction being caused by the appearance of bone in the connective tissue behind the basalia, and in front of the interbasalia, if such are present, in a cartilaginous stage. It is obvious that the distribution of cartilage, within the region of the future centre, will depend upon the mutual position of the basalia and interbasalia on the dorsal and ventral side. For instance, the vertebræ of *Xiphias*, *Serranus*, and *Aulostoma* may be referable to the type represented by *Lepidosteus*, but for the massing together of intervertebral cartilage, while the vertebræ of *Barbus*, *Leuciscus*, *Salmo*, seem, but for the shifting of the basiventrals, to conform more with the type of those of *Amia's* trunk.

SUMMARY OF RESULTS.

Concerning the segmental mesodermal products the following sub-division is adhered to:—

The term *myotome* is to be restricted to the whole remainder of the protovertebra after the skeletogenous cells have been given off for the production of the *sklerotomes*.

The sum total of skelerotomes makes up the skeletogenous layer.

The ending *tome* to indicate the primary, or earlier, less differentiated; the ending *mere* to signify the final condition or product.

Consequently, the protovertebræ divide into—I., Myotomes, each of which produces (1) one myomere or segment of the general mass of trunk-muscles, (2) cutis; II., Sklerotomes which produce skleromeres or skeletal trunk segments.

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Each protovertebra produces a dorsal and a ventral sklerotome; strictly speaking, one sklerotome, which consists of a separate dorsal and ventral half.

The protovertebral segments are not transverse "plates," but are curved into S-shape, the top end curving tail- and inwards, the middle and ventral thirds bulging headwards, the amount of curvature being (in 7 millims. embryos of *Acanthias*) so great that a transverse plane will cut through the dorsal and ventral third of one, and through the middle portion of the next following segment.

This S-shaped curving and consequent overlapping of the protovertebral "plates" SS is of fundamental importance for our understanding of the formation of the vertebral column, because it explains (1) the so-called new segmentation of the axial column, (2) the almost universal occurrence of more than one dorsal and one ventral pair of arcualia (namely, arches and intercalary pieces) in each of the later vertebral segments or skleromeres.

The explanation is as follows—

1. The dorsal half of sklerotome 2 grows downwards and comes to lie behind the ventral half of sklerotome 1.

2. The ventral half of sklerotome 2 grows upwards and comes to lie in front of and below the dorsal half of sklerotome 3.

3. The formation of a physiological unit is effected by the combination or fusion of the unequally numbered sklerotomic halves, in such way that the dorsal half lies behind and above the ventral half.

The new skleromere I. (= dorsal sklerotome 2 + ventral sklerotome 1) stands now in the following relation to the myomeres; the dorsal end of the skleromere I. coincides with myomere I.; the septum between this myomere and the next previous one passes between dorsal sklerotome 2 and ventral sklerotome 1, that is to say, right across the new skleromere I. This skleromere lies within the influence or range of action of two successive myomeres. Taken as a whole, the skleromere is "interprotovertebral," more correctly biprotovertebral, because it is composed of two successive sklerotomes, namely, the ventral half of one and the dorsal half of a second.

Consequently, the "resegmentation," or "neugliederung," is brought about in a manner fundamentally different to that hitherto supposed to have taken place. If A and B mean two successive sklerotomes, a and b their dorsal, α and β their respective ventral halves, then the new skleromere is composed of $b + \alpha$ and not of $\frac{A + B}{2}$, because $b + \alpha$ is the same as $\frac{\text{B dorsal}}{2} + \frac{\text{A ventral}}{2}$.

The formation of a skleromere by the combination of alternating dorsal and ventral halves of sklerotomes explains also the presence of eight (four pairs) cartilaginous pieces, namely, basalia (so-called dorsal and ventral arches) and interbasalia (so-called intercalary pieces) for each complete segment.

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The dorsal and ventral halves of the sklerotomes are pyramidal in shape, with their apices pointing respectively downwards and upwards. Each ventral pyramid extends with its apex above the chorda, and founds there (separated from the ventral mass by the subsequent rapid growth of the chorda and its sheath) a cluster of cells which remains henceforth behind (tailwards from) the basal mass of the dorsal pyramid. The latter founds, with its down-growing apex, a colony of cells below the chorda, and in front of the basal ventral mass. Thus are produced the basalia and interbasalia, each colony or cluster of cells developing into a separate piece of cartilage. The basidorsal does not fuse with its interdorsal because both are the offspring of two different sklerotomes, nor can the basidorsal fuse with its own offspring, namely, with the interventral, because both became, and remain, separated by the chorda and its sheath; they are connected only by the indifferent connective tissue of the membrana reuniens, but not by cartilage-forming cells.

Concerning the formation of centra or bodies of the vertebræ, we distinguish:—

I. *Chorda-centra, i.e.*, centra formed by the entire chordal sheath, which itself has been strengthened by invasion of cartilaginous cells from the skeletogenous layer. This migration of cartilage into the chordal sheath had already been hinted at by KŒLLIKER more than thirty years ago; it has recently been proved by KLAATSCH, and has been corroborated by us. Chorda-centra are possessed by all Elasmobranchs, potentially by Dipnoi and Holocephali.

II. *Arch-centra, i.e.*, centra formed by the skeletogenous mass which remains entirely on the outside of the chordal sheath, which latter takes no share in their formation: osseous Ganoids and Teleostei.

Chorda-centra and arch-centra represent two different modes of development, each starting from an acentrous condition. This can be expressed as follows:—

Chordal sheath remaining entirely chordagenous.	Chordal sheath strengthened by invasion of skeletogenous cells, therefore with possibility of chorda-centra.
Cyclostomata, Cartilaginous Ganoids.	Dipnoi and Holocephali.

Formation of Centra.

Osseous Ganoids, Teleostei.	Elasmobranchs.
ARCH-CENTRA.	CHORDA-CENTRA.

The formation of chorda-centra being independent of the arcualia explains how and why the number of "centra" does not necessarily agree either with that of the arcualia or with that of the trunk-segments, *e.g.*, *Hexanchus*, and tail of most other Elasmobranchs.

These leading differences and their modifications have been traced in *Petromyzon*,

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Acipenser, *Amia*, *Lepidosteus*, *Protopterus*, *Chimæra*, and in numerous Elasmobranchs.

In *Amia calva*, the *postcentrum*, *i.e.*, the posterior, archless disc of a complete tail-vertebra, was found to be formed by the interdorsalia and interventralia of the same sklerotome, while the *precentrum*, *i.e.*, the arch-bearing disc or anterior half is formed by the basidorsals of the same sklerotome and the basiventrals of the next previous sklerotome. Thus skleromere 51 is composed of a postcentrum which carries interdorsal 51 + interventral 51, and of a precentrum which carries basidorsal 51 + basiventral 50. The intermuscular septum runs obliquely across the precentrum, or in other words, the precentra are bi-protovertebral or bi-myomeric, but not the postcentra. The postcentra of the tail of *Amia* are possibly homologous with the "pleurocentra" in the tail of the Jurassic *Eurycormus*, while *Amia's* precentra are the same as the "hypocentra" of *Eurycormus*.

In *Lepidosteus osseus* the combination of parts into one vertebral complex is superior to that of *Amia*, because each vertebra belongs, with its entire anterior half (interdorsal 50 + basiventral 50), to myomere 50, and with its posterior half (basidorsal 51 + interventral 51), to myomere 51. In other words, the vertebral mass is equally divided between two successive myomeres, or the myomeres have an equal share of the skleromeres. The vertebræ are now truly bi-protovertebral or bi-myomeric, each vertebra being composed of $a + b$.

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