VI. *On the Evolution of the Vertebral Column in Birds, illustrated by its Development in* Larus *and* Struthio.

By JOHANNES PIIPER, *Professor of Zoology and Comparative Anatomy in the University of Tartu* (*Dorpat*), *Estonia.*

(*Communicated by* PROF. E. W. MACBRIDE, *F.R.S.*)

(Received March 23, 1927,—Read January 19, 1928.)

(PLATE 18.)

INTRODUCTION.

The justification of the following research work is found in the fact that notwithstanding the investigations of REMAK (1851), GEGENBAUR (1862), JÄGER (1858), SCHWARK (1873), BRAUN (1881), FRORIEP (1883), MÄNNICH (1902), SCHAUINSLAND (1905), and SONIES (1907), which deal with the development of the vertebral column in birds, there still remains a great deal of uncertainty in some essential questions regarding the development of the membranous and cartilaginous components of the vertebræ from the mesenchymatous sclerotomes, as well as the morphological value of these components. The most important of these undecided questions, to the solution of which the present study tries to contribute, may be briefly summarised as follows: (*a*) what is the exact genetic relation of the mesenchymatous sclerotomes and their derivatives to the membranous and cartilaginous components of a developing vertebra with its intervertebral parts, (*b*) what is the real nature of these components as regards their number, quality and topographical relations to the neighbouring parts within the

[Published April 17, 1928.

limits of a cartilaginous vertebra, (*c*) what are the differences shown by the various regions of the developing vertebral column with reference to points (*a*) and (*b*) ?

The investigation was carried out in 1923–1925 at the Huxley Research Laboratory of the Imperial College of Science and Technology under the supervision of Prof. E. W. MacBride, F.R.S. It is my pleasant duty to express my best thanks to Prof. E. W. MacBride for his suggestion that I should undertake this work, as well as for much advice and useful criticism, and for valuable suggestions made during the progress of the research. My thanks are also due to Prof. H. Graham Cannon (University of Sheffield) for much technical help and advice. I also wish to express my deep indebtedness to Prof. D. M. Watson, F.R.S. (University College, London), for benevolent criticism and valuable suggestions, and to Mr. J. R. Norman (British Museum, Natural History) for useful hints and advice.

Material.

The material used in this research consists of a series of embryos of *Larus canus* L. representing the Carinatæ and of *Struthio australis* Gurn., as representative of the Ratitæ. The *Larus canus* L. material was collected from the Vaika islets near Filsand, a small island off the west coast of Oesel (Saaremaa) in Estonia. I obtained about 48 specimens representing an almost continuous series of developmental stages, from the 2nd to the 10th day (inclusive) of incubation. The age of the embryos was determined approximatively by marking the newly made nest containing the first-laid egg with a label, and noting the day of the laying of the last (third) egg as the beginning of the period of hatching. My best thanks are due to the keeper of the Filsand Lighthouse, Mr. A. Thom, through whose kind assistance the above collection became possible. The *Struthio australis* Gurn. embryos, including five different stages of development, were obtained by the help of Prof. MacBride from the Laboratory of Prof. I. E. Duerden, in Rhodes University College, University of South Africa, Grahamstown, to both of whom I express my best thanks.

Method.

Nitric acid, sublimate and acetic acid, sublimate-formol, were used for the fixation of earlier stages of the gull. The later stages were fixed by 10 per cent. formol. All these fixatives gave good results. Although the method used for the fixation of the ostrich embryos could not be ascertained, the structures investigated displayed an excellent fixation. The material was preserved in 2 per cent. formol and in 70 per cent. alcohol. The specimens were stained in bulk by borax-carmine and cleared in cedar-wood oil. Paraffin wax sections were prepared. Most of the specimens were cut at a thickness of 10 μ ; a few only at a thickness of 7 μ. The sections were stained on slides by Mallory's triple stain, which gave a very reliable differentiation for the various developmental stages of prechondral tissue and cartilage.

Continuous series of sagittal, frontal and transversal sections through cervical, thoracic, lumbo-sacral and caudal regions of all above-mentioned developmental stages were prepared. Some graphic reconstructions were made in order to elucidate the reciprocal relations between the parts of a developing vertebra. The figures (except 30, 31, 32) are camera lucida drawings at a magnification × 80. The diagrammatic figures 30, 31 and 32 are drawn on the basis of comparative study of series of sections. The Plate 18 figure is drawn by microprojection apparatus at a magnification × 330.

Mainly *Larus* is described. *Struthio* is considered only so far as it differs from *Larus* or offers, because of its slower development and larger size, better opportunity to follow the development of some important parts, as, for example, of the perichordal tube, interdorsals and interventrals. In order to give a picture as continuous as possible of the evolution of birds' vertebra, the more important stages of *Struthio* were inserted in chronological order between the corresponding stages of *Larus*.

EMBRYO OF *Larus Canus*, AGED ABOUT 2 DAYS.

The notochord does not exhibit any regular constrictions or expansions.

The chordal sheath is a very thin homogeneous structure of uniform thickness throughout (fig. 3 *c.s.*). Only in the caudal portion does it become gradually thinner and it disappears with the notochord in this region.

A varying degree of vacuolisation is exhibited in the different regions of the chorda. In the cervical region the vacuolised cells are predominant, and, as is usually the case, the vacuolisation is uniformly distributed in the central as well as in the peripheral regions (fig. 2 *n.v.*). In the trunk region only isolated cells exhibit vacuolisation, and the vacuoles are smaller than those occurring in the cervical region (fig. 3 *n.v.*). In the hinder part of the trunk region (fig. 3 *nch.*), as well as in the tail region, the vacuolisation is absent.

The vacuolisation of the intracranial (= occipital) region is similar to that of the thoracic region, being less advanced than that of the cervical region. From this it appears that the vacuolisation of the chordal cells commences in the cervical region and subsequently spreads towards the cranial and caudal region.

The mesodermal masses flanking both sides of the neural cord and chorda are already differentiated into metamerically arranged somites except in the hindermost region of the trunk (fig. 2, *sm.*, and fig. 3, *sm.*). The right and left somite belonging to the same metamere have an exactly opposite position.

The cervical somites are each differentiated into a dorso-lateral dermato-myotome and ventro-mesially located sclerotome, separated by a narrow fissure (fig. 1*a*, *sm.*, *dt.*, *mt.*, *st.*, *f.*). The sclerotomes consist of a very loose mesenchymatous tissue, whereas the dermato-myotomes are denser structures composed of epithelioid cells.

The sclerotomic mesenchyme fills up nearly the whole space between the dermato-myotome and the main organs of the median sagittal plane—the neural cord, the notochord and the dorsal aorta (fig. 1*a*, *dt.*, *mt.*, *n.c.*, *nch.*, *ao.*). Strands of sclerotomic mesenchyme are wedged in the longitudinal grooves between chorda and aorta and single mesenchymatous cells penetrate into the narrow space between these two organs (fig. 1*a*, *pch.m.*). On the contrary, the wedge-shaped spaces between the neural cord and notochord are devoid of sclerotomic elements, and none of the mesenchymatous cells have grown in between these two organs, which, in fact, are in close apposition (fig. 1*a*, *nc.*, *nch.*).

The cleft separating two successive somites, and consequently their respective sclerotomes, the intersomitic or intersclerotomic fissure, is very distinctly developed in the cervical (fig. 2, *ir.f.*) and anterior half of the thoracic region (fig. 3, *ir.f.*). In the hinder portion of the trunk region, where the somites are in process of formation, the intersclerotomic fissure is hardly noticeable (fig. 3, *c.ir.f.*). In the region of the intersclerotomic fissures one can trace the incipient intermetameric blood vessels—the interprotovertebral or intersclerotomic blood vessels (fig. 2, *is.bl.v.*).

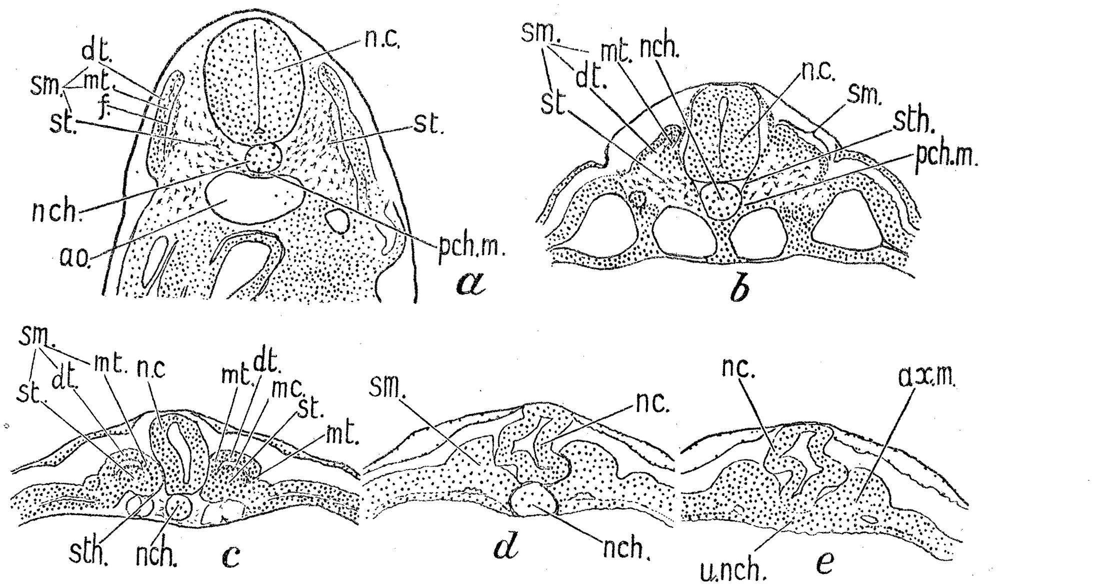


Fig. 1.—Transverse section of a 2-day Gull embryo. *a*, heart region. *b*, thoracic region. *c*, pelvic region. *d*, anterior portion of the caudal region. *e*, posterior portion of the caudal region. *ao.*, aorta; *ax.m.*, undifferentiated axial mesoderm; *dt.*, dermatome; *f.*, fissure separating the dermato-myotome from the sclerotome; *m.c.*, myocœle; *mt.*, myotome; *n.c.*, neural cord; *nch.*, notochord; *pch.m.*, perichordal mesenchyme; *sm.*, somite; *st.*, sclerotome; *sth.*, sclerotheca; *u.nch.*, undifferentiated portion of the notochord.

The newly formed somites and those which show the very first beginnings of the differentiation into dermato-myotomes and sclerotomes are surrounded by a very thin homogeneous membrane which may be termed *somotheca* or *sclerotheca* (fig. 3, *sth.*, and fig. 1*c*, *sth.*). In the posterior portion of the cervical region and in the anterior part of the trunk region, where the somites are already finally differentiated into sclerotomes and dermato-myotomes, this membrane is only partially preserved (fig. 2, *sth.* and fig. 1*b*, *sth.*). In the anterior cervical sclerotomes this membrane is no longer traceable, having broken down completely (fig. 1*a*, *st.*, and fig. 2, *st.*). The rupture and dissolution of this membrane (sclerotheca) starts partly in the angle between the notochord and the aorta, partly on the anterior and posterior faces of the sclerotomes.

Each sclerotome is divided by a narrow cleft, the *intrasclerotomic fissure,** passing almost through the whole extent of the sclerotome into a cranial and caudral half (fig. 2, *ia.f.*, *cr.scl.*, *cd.scl.*, *st.*). The intrasclerotomic fissure, or sclerocœle, appears in sclerotomes whilst they are still surrounded by membrane (sclerotheca) (fig. 2, *sth.*).

Both sclerotomal halves are of nearly equal size. The caudal half of the sclerotome as compared with the cranial shows a somewhat denser composition of tissue. The sclerotomes as well as their cranial and caudal halves are not absolutely isolated from each other by the corresponding fissures. There are narrow cell bridges passing through the intersclerotomic fissures and thus connecting successive sclerotomes. The halves of each sclerotome are likewise joined by tiny cell threads traversing the intrasclerotomic fissure. The cranial and the caudal halves of a sclerotome may for the sake of brevity be termed respectively the *cranial* and the *caudal sclerotomites.*

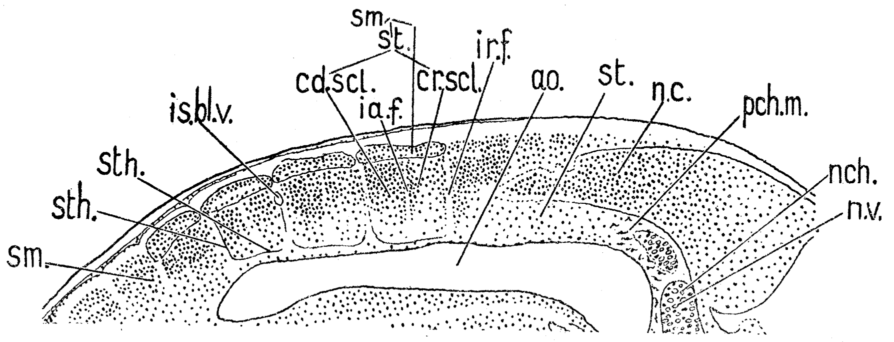


Fig. 2.—Parasagittal section through the cervical and thoracic region of a 2-day Gull embryo. Anterior end of section to the right. Abbreviations as in fig. 1, except *cd.scl.*, caudal sclerotomite; *cr. scl.*, cranial sclerotomite; *ia.f.*, intrasclerotomic (= intervertebral) fissure; *ir.f.*, intersclerotomic fissure; *is.bl.v.*, intersclerotomic blood vessel; *n.v.*, notochordal vacuoles; *pch.m.*, perichordal mesenchyme.

In the cervical region the notochord is surrounded at least on its ventral and lateral aspects by loose mesenchymatous cells (fig. 1*a*, *pch.m.*, and fig. 2, *pch.m.*). These cells, as has already been mentioned, are of sclerotomic origin, and have migrated from the ventromesial aspect of the sclerotomes through the points of rupture of the sclerotomic membrane (sclerotheca).

In the trunk region the somites appear in transverse section in trapezoidal shape (fig. 1*b* and *c*, *sm.*) with the longest side facing ventrally. The mesio-dorsal and the dorsolateral walls of the thoracic somites consist of 3–4 rows of closely connected epithelioid cells and represent the incipient dermato-myotomes (fig. 1*c*, *mt.*, *dt.*). The inner core of the somite consists of a mass of condensed tissue, the ventral portion of which forms the base of the somite (fig. 1*c*, *st.*). This is the sclerotome in its earliest stage of development.

---

* The " Intervertebralspalte " of v. Ebner.

Between the dorsal face of the sclerotome and the ventral aspect of the dermato-myotome there is a crescentic space (in transverse section) (fig. 1*c*, *mc.*), the myocœle. There is no noticeable communication between the myocœle and the sclerocœle (= intrasclerotomic fissure). The intersomitic fissure contains loose cells (fig. 3, *ms.*), probably derived from the sclerotomic region of the somite.

The longitudinal space between the notochord and the somites is, in the hinder division of the trunk region, completely devoid of cells, or, in other words, the perichordal mesenchyme is not yet developed in that region (fig. 3, *nch.*, *sm.*). The intrasclerotomic fissure has not yet made its appearance in the trunk region.

The elongated area of unsegmented axial mesoderm in the hinder portion of the trunk region (fig. 3, *ax.m.*, and fig. 1*d*, *sm.*) does not show any differentiation into sclerotomes and dermato-myotomes. The ventro-mesial aspect of it is closely applied to the dorso-lateral face of the notochord.

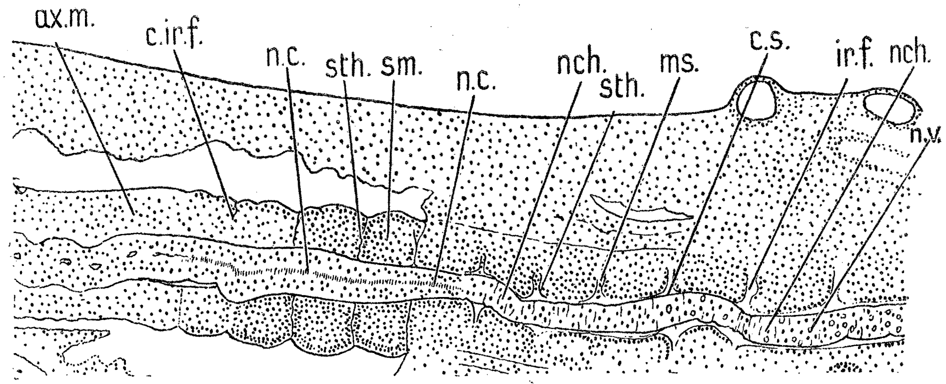


Fig. 3.—Frontal sections through the posterior trunk and caudal regions of a 2-day Gull embryo. Anterior end of section to the right. The anterior end of the sections is at a lower plane than the posterior end. Abbreviations as in figs. 1 and 2, except *c.ir.f.*, incipient intersclerotomic fissure; *c.s.*, chordal sheath; *ms.*, loose mesenchymatous cells.

Posterior to the end of the developing notochord and just in front of the remains of the neurenteric canal, the right and left masses of the unsegmented axial mesoderm are connected by a bridge of tissue passing underneath the neural chord (fig. 1*e*, *nc.*, *u.nch.*). This connecting bridge represents the primordium from which will be formed the caudal end of the fully developed notochord.

Embryo of *Larus Canus*, Aged about 3 Days.—Cervical Region.

In contrast to the previous stage in which the notochord is of uniform diameter throughout, the present stage exhibits a notochord of slightly moniliform structure (figs. 4 and 6, *dil.*, *con.*). The faint dilatations are confined to the middle portions of the sclerotomes while the constrictions occur in the intersclerotomic regions (fig. 4, *st.*, *ir.f.*). Closer examination of the sagittal sections shows that the ventral dilatations of the notochord are very often shifted somewhat cranialwards with respect to the corresponding dorsal dilatations (fig. 6, *dil.*).

The chordal sheath (fig. 6, *c.s.*) is thin and homogeneous and does not reveal any difference in thickness in the dilated and constricted regions.

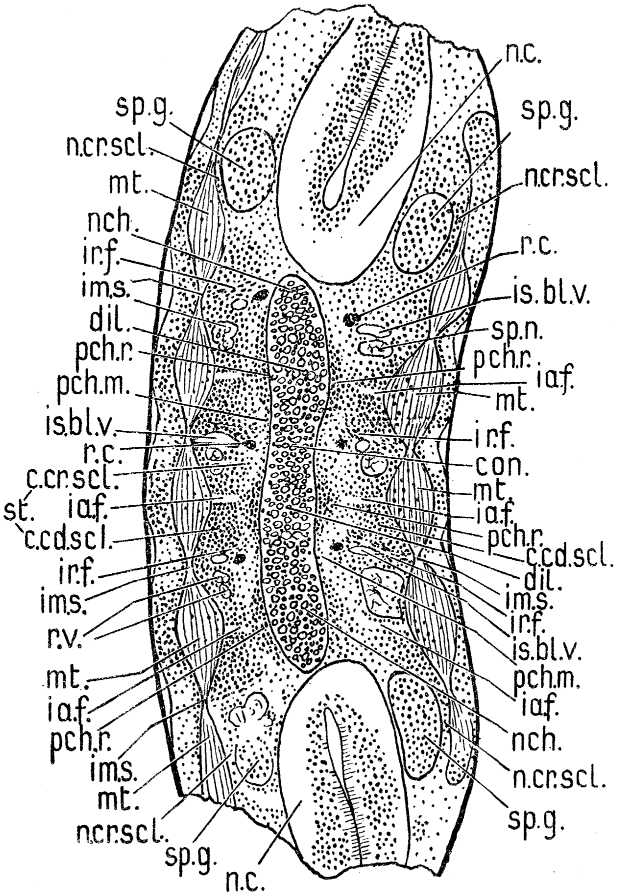


Fig. 4.—Frontal section through the notochord and the sclerotomes of a 3-day Gull embryo. Cervical region. Owing to the curvature of the embryo, the section in the middle of the preparation has passed through a lower level than at both ends. Anterior end of section above. *c.cd.scl.*, chordal portion of the caudal sclerotomite; *c.cr.scl.*, chordal portion of the cranial sclerotomite; *con.*, constricted portion of the notochord; *dil.*, dilated portion of the notochord; *ia.f.*, intrasclerotomic fissure; *im.s.*, intermyotomic septum; *ir.f.*, intersclerotomic fissure; *is.bl.v.*, intersclerotomic blood vessel; *mt.*, myotome; *n.c.*, neural cord; *nch.* notochord; *n.cd.scl.*, neural portion of the caudal sclerotomite; *n.cr.scl.*, neural portion of the cranial sclerotomite; *pch.m.*, perichordal mesenchyme; *pch.r.*, perichordal ring; *r.c.*, ramus communicans connecting spinal and sympathetic ganglia; *r.v.*, ramus ventralis of spinal nerve; *sp.g.*, spinal ganglion.

The degree of vacuolisation of the chordal cells has increased. In contrast to the 2-days' embryo, in which stage the vacuoles are of uniform size and distribution, the more central ones are large and slightly polygonal, while the more peripheral ones are comparatively smaller and of round or oval shape (fig. 9, *nch.*). In the latter case they are disposed radially. It thus appears probable that the increase in size of the vacuoles commences in the more central zones and spreads towards the periphery.

The nuclei of the chordal tissue, which were uniformly distributed in the previous stage, are here more numerous in the peripheral layers of the notochord.

Examined in a frontal (horizontal) section, the intersclerotomic fissures exhibit a slight deviation from the transverse body axis, their mesial portions being directed cranialwards (figs. 4 and 5, *ir.f.*).

It must be noticed that the lumina of the intersclerotomic fissures in this stage are not so clearly developed as in the previous one (2 days) because of the presence of a very loose mesenchymatous tissue, the oval nucleated cells of which mostly run parallel to the direction of the fissures (fig. 4, *ir.f.*). In a dorso-ventral direction the intersclerotomic fissures extend from the base of the sclerotomes up to the dorsal level of the spinal ganglia, and can be traced in a less distinct form up to the dorsal border of the intermyotomic septum (fig. 7, *ir.f.*, *sp.g.*, *im.s.*). In a frontal (horizontal) direction the intersclerotomic fissures stretch from the intermyotomic septum to the neural cord and notochord, being separated from the latter by a thin layer of mesenchymatous cells (fig. 4, *ir.f.*, *im.s.*, *n.c.*, *nch.*, *pch.m.*), the perichordal mesenchyme.

In close relation to the intersclerotomic fissures, embedded in the mesenchyme of the anterior border of the cranial half of the sclerotomes, are the intersclerotomic (= inter-protovertebral) blood vessels and the rami communicantes connecting the sympathetic ganglia with the spinal ganglia. The rami communicantes are situated internally to the blood vessels (fig. 4, *is.bl.v.*, *r.c.*, *sp.g.*).

The subchordal latero-ventral portions of the intrasclerotomic fissures have undergone obliteration (text-fig. 7, *br.*). Obliteration of the fissures has also taken place in the level of the upper half of the spinal ganglia and in the region disposed above the latter (text-fig. 7, *sp.g.*). As a result of this the dorso-ventral extension of the intrasclerotomic fissures has become shorter.

But in the more mesially disposed subchordal zone lying immediately below the perichordal rings (*vide infra*) the right and the left intrasclerotomic fissures still meet (fig. 5, *c.ia.f.*). The lumen of this subchordal common intrasclerotomic fissure is somewhat masked by groups of mesenchymatous cells.

The dorsal or *neural* portion of the cranial sclerotomite is mainly occupied by the spinal ganglion, the dorsal and ventral roots of the spinal nerve and the ramus dorsalis of the latter (figs. 4, 7, *sp.g.*, *n.cr.scl.*, and 9, *n.cr.scl.*, *sp.g.*, *eg.d.r.*, *hg.d.r.*, *v.ro.*, *r.d.*). Compared with the 2-days' stage, the spinal ganglia have increased considerably in size, having pushed the tissue of the sclerotome aside. As a result of the latter process the dorsal portion of the cranial half of the sclerotome is reduced to narrow strips of tissue surrounding the spinal ganglion, the most conspicuous of which is included in the space between the spinal ganglion and the cranial half of the corresponding myotome (figs. 4 and 9, *n.cr.scl.*, *sp.g.*, *mt.*).

The lower or *chordal* portion of the cranial sclerotomite (figs. 7 and 9, *c.cr.scl.*) contains the ramus ventralis of the spinal nerve (figs. 4 and 9, *r.v.*).

In transverse section it is to be seen that the caudal sclerotomite consists of a dorsal curved portion disposed above the median horizontal prominence of the myotome and a ventral straight portion (fig. 8, *n.cd.scl.*, *m.p.mt.*, *c.cd.scl.*). The curved or *neural* portion extends round the latero-ventral portion of the neural cord (fig. 8, *n.cd.scl.*, *n.c.*). The lower straight or *chordal* portion stretches ventrally between the perichordal mesenchymatous ring (*vide infra*) and the ventral half of the corresponding myotome (fig. 8, *c.cd.scl.*, *pch.r.*, *mt.*).

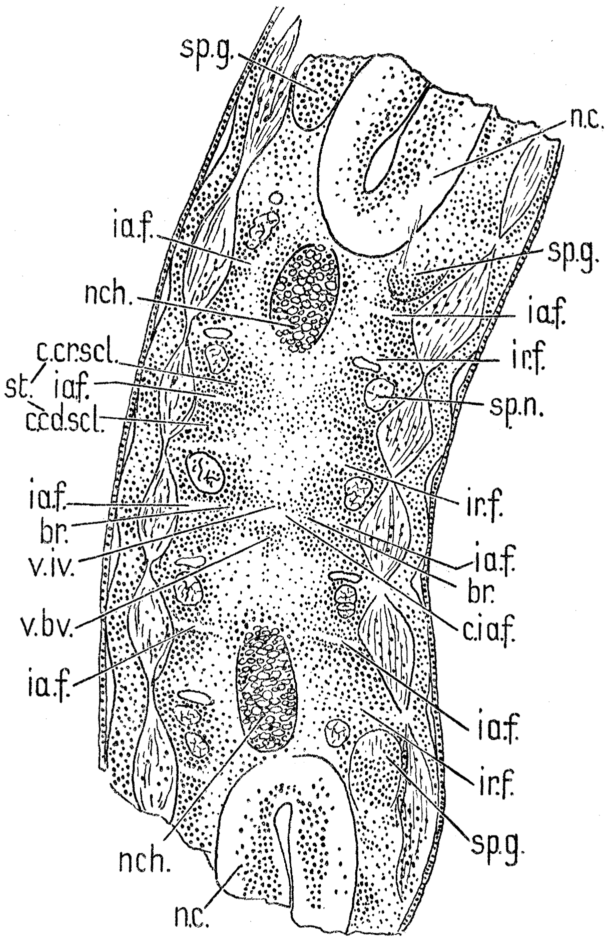


Fig. 5.—Frontal section, including the same sclerotomes as fig. 4, at a lower level through the subchordal region. Anterior end of section above. Abbreviations as in fig. 4, except *br.*, bridge of cells connecting in subchordal region the cranial and caudal sclerotomites of a sclerotome; *c.ia.f.*, common subchordal intrasclerotomic fissure; *sp.n.*, spinal nerve; *st.*, sclerotome; *v.bv.*, ventral unpaired portion of the subchordal portion of the caudal sclerotomites; *v.iv.*, ventral unpaired portion of the subchordal portion of the cranial sclerotomites.

The boundary between the curved neural and the straight chordal portions of the caudal sclerotomite is marked by the difference in the disposition of the cells in both portions. The oval nuclei of the neural portion are radially arranged with respect to the notochord, whereas the tissue of the lower chordal portion do not display any definite orientation of their cell-elements.

The mesenchymatous cells, which in the previous (2-day) stage were given off from the sclerotomes and covered the lateral and ventral faces of the notochord, have in the present stage considerably increased in number, and have penetrated in the space between the neural cord and the notochord (figs. 8 and 9, *pch.r.*). The production of the mesenchymatous cells is most intense in the middle portion of the sclerotome divided by the intrasclerotomic fissure. As a result of this process the dilated divisions of the notochord confined to the sclerotomes become inclosed by ring-like formations consisting of mesenchyme (figs. 4 and 6, *pch.r.*, *ia.f.*, *dil.*, *st.*). These rings may be called *perichordal rings.*

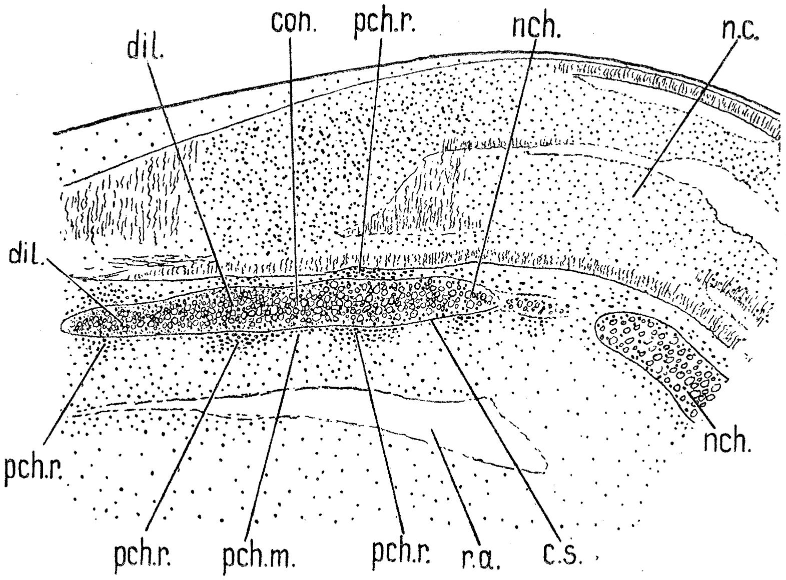


Fig. 6.—Section partly sagittal, partly parasagittal, of the cervical region of a 3-day Gull embryo. Anterior end of section to the right. Abbreviations as in figs. 4 and 5, excepting *con.*, constricted portion of notochord ; *c.s.*, chordal sheath ; *dil.*, dilated portion of the notochord ; *r.a.*, radix aortæ.

From the above it is evident that the anterior half of each perichordal ring is flanked on both sides by the cranial sclerotomites, whereas its caudal half is contained between the caudal sclerotomites (figs. 4, 8 and 9, *pch. r.*, *c.cr.scl.*, *c.cd.scl.*).

The sclerotomes (and sclerotomites) of the preceding (2-days') stage which have not yet produced the mesenchymatous rings may be termed the *primary sclerotomes* and *prim. sclerotomites* respectively. After the formation of the perichordal rings the sclerotomes (and sclerotomites) will be called the *secondary sclerotomes* (and sclerotomites)* respectively.

---

* For the sake of brevity, henceforth the terms sclerotome and sclerotomite, respectively, will be used instead of the terms secondary sclerotome and secondary sclerotomite.

Although there is an intimate genetical connection between the mesenchymatous perichordal rings and the corresponding sclerotomes (the former being derivatives of the latter), they are separate formations because of their different histological structure.

The perichordal mesenchymatous rings consist of spindle-shaped, more or less flattened cells, arranged in concentric layers round the notochord (fig. 8, *pch.r.*, *nch.*). The flattest cells occur in the innermost layers, whereas in passing outwards the cells gradually assume the isodiametrical shape of the ordinary sclerotome cells. The nuclei of the innermost cells are spindle-like, and those of the middle and outer layers of a more or less oval shape, their long axes being disposed tangentially to the notochord. Between the cells there is an intercellular substance, partly homogeneous, partly fibrillar, staining intensely with aniline blue.

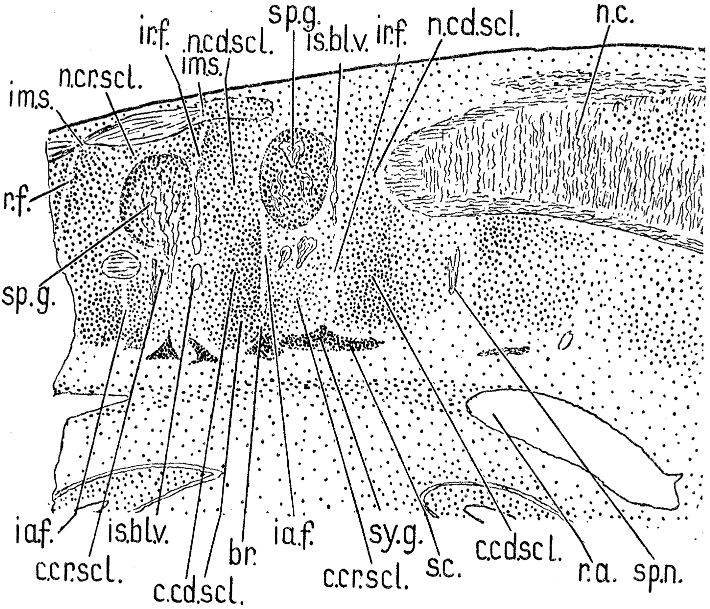


Fig. 7.—Specimen and region as in fig. 6. Section has passed more laterally than in fig. 6. The section has passed more mesially at the cranial end than at the caudal. Anterior end of section to the right. Abbreviations as in figs. 4, 5 and 6, except *s.c.*, sympathetic cord ; *sy.g.*, sympathetic ganglion.

The sclerotomites, in contrast to their mesenchymatous composition in the previous (2-day) stage, now consist of closely set isodiametric polygonal cells with but a small amount of homogeneous bluish intercellular substance. The caudal sclerotomites still display a denser texture than the cranial ones (figs. 4 and 7, *c.cr.scl.*, *n.cr.scl.*, *c.cd.scl.*, *n.cd.scl.*). It is of interest to note that the densest portions of the caudal as well as of the cranial sclerotomites are confined to the areas associated with the myotomes and with the intrasclerotomic fissures (fig. 4, *mt.*, *ia.f.*). The density of the connective tissue of these areas is greater than that of the perichordal rings (fig. 4, *pchr.r.*).

The craniomesial and the caudomesial parts of the sclerotomes bordering on the intersclerotomic regions are of a looser consistency.

The cranial as well as the caudal components of the right and left sclerotomes have grown under the perichordal ring until they have met in the ventro-median plane of the notochord and fused. The ventral median fused portion of the caudal sclerotomites exceeds in bulk the corresponding portion of the cranial sclerotomites and is separated from it by the above-mentioned common intrasclerotomic fissure (fig. 5, *v.bv.*, *v.iv.*, *c.ia.f.*).

The structures represented in the area of the future atlas and axis vertebræ do not exhibit any noticeable difference from those of the remaining portion of the cervical region. The single reliable criterion in distinguishing between the atlas (first) and axis (second) sclerotomes (resp. sclerotomites) from other cervicals is the rudimentary condition or the absence of their spinal ganglia.

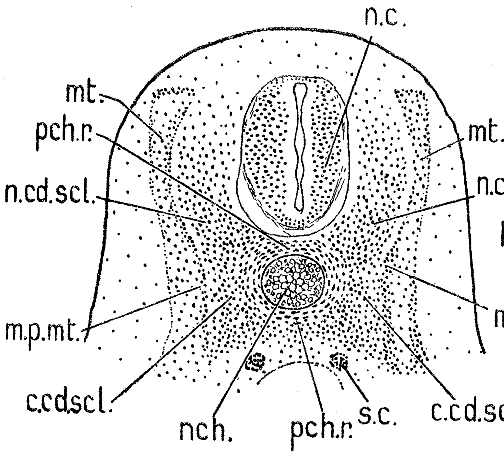


Fig. 8.—Transversal section of the cervical region of a 3-day Gull embryo. Section has passed through the region of the caudal sclerotomite.

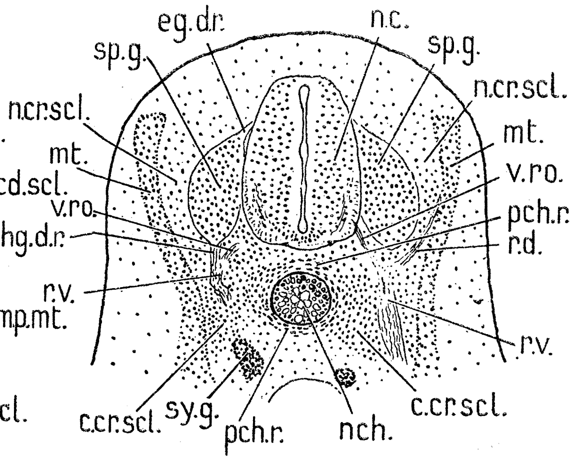


Fig. 9. Specimen and region as in fig. 8. Section has passed through the region of the cranial sclerotomite. Abbreviations as in fig. 8.

Abbreviations as in figs. 4, 5, 6, 7, except *eg.d.r.*, epiganglionic portion of the dorsal root of the spinal nerve ; *hg.d.r.*, hypoganglionic portion of the dorsal root of the spinal nerve ; *m.p.mt.*, median prominence of myotome ; *r.d.*, ramus dorsalis of spinal nerve ; *r.v.*, ramus ventralis of spinal nerve ; *v.ro.*, ventral (motor) root of spinal nerve.

Extracervical Region.

The lateral portions of the perichordal ring in the thoracic region show considerably greater thickness than the dorsal and the ventral ones. The hinder portion of the caudal region retains the somites in their primitive sac-like condition. The somites of the anterior part of the tail already show a differentiation into the dermato-myotome and sclerotome. The sclerotomes are not yet divided by the intrasclerotomic fissure. In the level passing through the lower aspect of the notochord the formation of the perichordal mesenchyme from the sclerotomes has already begun. This proves that in the caudal region the perichordal skeletogenous tissue is formed in contrast to the cervical region before the development of the intrasclerotomic fissure, and that the ventral and ventro-lateral portions of this tissue are formed first of all.

EMBRYO OF *Larus Canus*, AGED ABOUT 4 DAYS.—CERVICAL REGION.

The moniliform differentiation of the notochord is more accentuated than in the previous (3-day) stage, especially as concerns the ventral and lateral aspects of this organ, the intrasclerotomic dilatations being in these regions more pronounced and the intersclerotomic constrictions deeper (figs. 12 and 13, *nch.*, *dil.*, *con.*).

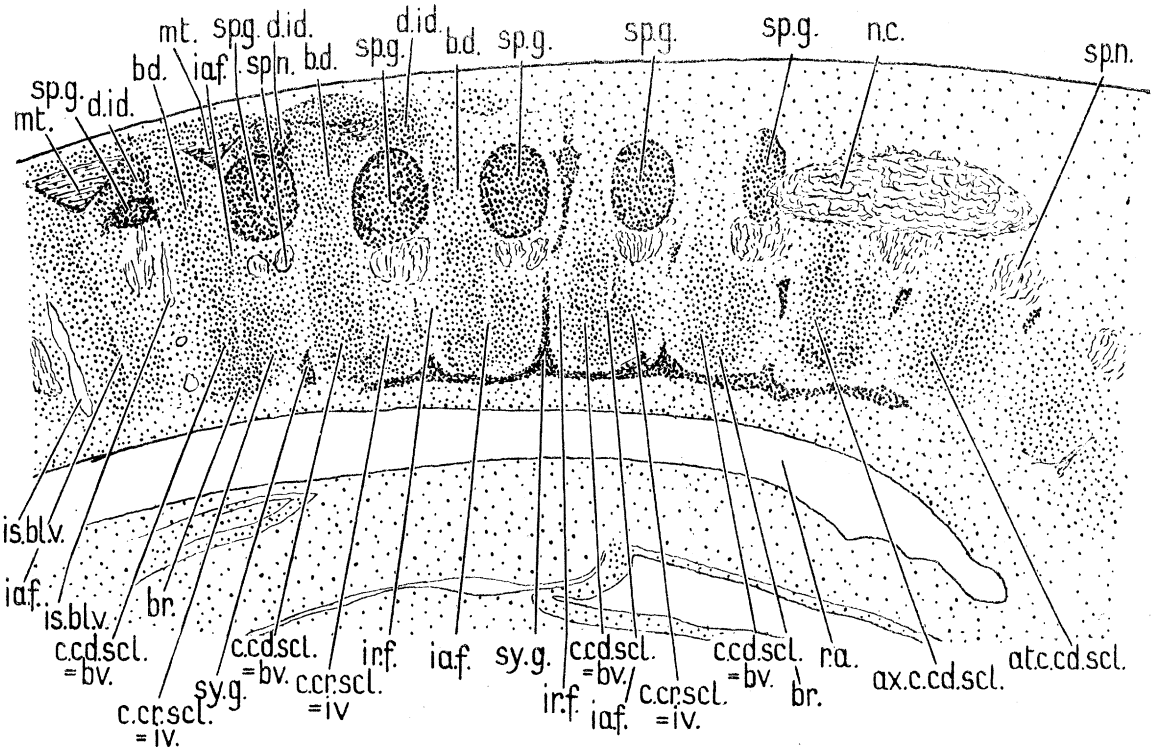


Fig. 10.—Lateral sagittal section through the cervical region of a 4-day Gull embryo. The section has in the cranial portion passed more mesially than in the caudal, and this is also the case in figs. 11, 12 and 13, representing the same specimen and region. Anterior end of section to the right. This is also the case in figs. 11, 12 and 13. *at.c.cd.scl.*, chordal portion of the caudal sclerotomite of atlas; *ax.c.cd.scl.*, chordal portion of the caudal sclerotomite of axis; *br.*, bridge of cells connecting in subchordal region the cranial and caudal sclerotomites of a sclerotome; *bd.*, basidorsal; *c.cd.scl.*, chordal portion of the caudal sclerotomite; *c.cr.scl.*, chordal portion of the cranial sclerotomite; *d.id.*, dorsal portion of the interdorsal (= dorsal-interdorsal); *ia.f.*, intrasclerotomic fissure; *ir.f.*, intersclerotomic fissure; *is.bl.v.*, intersclerotomic blood vessel; *mt.*, myotome; *n.c.*, neural cord; *r.a.*, radix aortæ; *sp.g.*, spinal ganglion; *sp.n.*, spinal nerve; *sy.g.*, sympathetic ganglion.

The distinction in size and shape between the central and peripheral vacuoles of the notochord has considerably diminished, most of the peripheral vacuoles having increased in size and assumed a polygonal shape. The number of the protoplasmatic cells in the peripheral portion of the notochord exceeds that of the central part.

Although the obliteration of the intersclerotomic fissures is nearly complete (fig. 11, *ir.f.*), it is none the less easy to distinguish them as areas of feebly stained rarefied tissue from the interposed sclerotomes displaying a denser composition and deeper colour (fig. 11, *n.cr.scl.*, *c.cr.scl.*, *n.cd.scl.*, *c.cd.scl.*).

The intrasclerotomic fissures are still open (fig. 11, *ia.f.*), but they have become slightly narrow and traversed by threads of mesenchymatous cells, a sign of their incipient obliteration. In comparing the lumina of the intrasclerotomic fissures in their successive parasagittal sections, it becomes evident that the obliteration sets in at the mesial and lateral portions and proceeds towards their middle part (fig. 11, *m.ia.f.*, *l.ia.f.*).

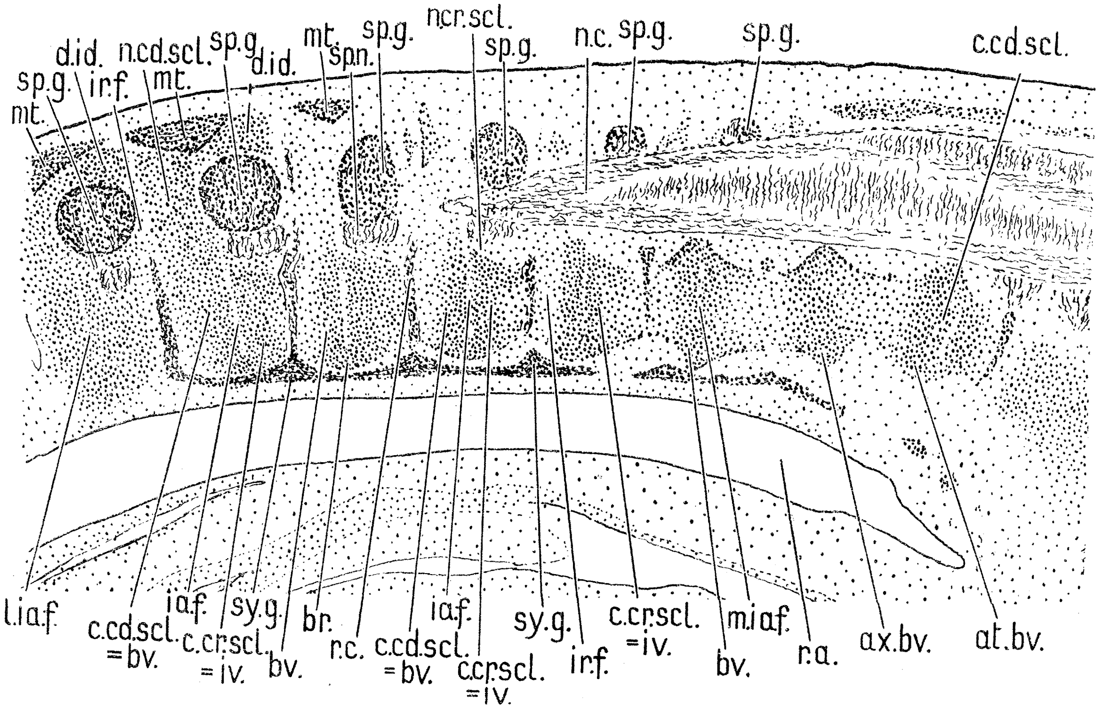


Fig. 11.—Specimen and region as in fig. 10. Section has passed more mesially than in fig. 10. Abbreviations as in fig. 10, except *at.bv.*, atlas-basiventral; *ax.br.*, axis-basiventral; *bv.*, basiventral; *l.ia.f.*, lateral portion of the intrasclerotomic fissure; *m.ia.f.*, mesial portion of the intrasclerotomic fissure; *n.cd.scl.*, neural portion of the caudal sclerotomite; *n.cr.scl.*, neural portion of the cranial sclerotomite; *r.c.*, ramus communicans connecting spinal and sympathetic ganglia.

The successive perichordal rings, which were nearly independent of each other in the previous (3-day) stage, have fused into a moniliform tube enclosing the notochord—the *perichordal tube* (fig. 13, *pch.t.*). This loss of individuality of the perichordal rings is especially pronounced in their dorsal portion, and is due to the intense growth of the perichordal mesenchyme in the region corresponding with the obliterated intersclerotomic fissures indicated by the intersclerotomic blood vessels (fig. 13, *is.bl.v.*).

Although the walls of the fused perichordal rings have grown thicker and have become denser in consistency, their intimate structure, consisting of concentrically disposed flattened cells and of a limited quantity of intercellular substance, has remained mainly the same as in the previous stage. The relation between the dilated and constricted areas of the notochord and the fused perichordal rings resembles that of a 3-day *Larus*. Laterally and ventrally, the perichordal tube has become intimately concrescent with the chordal and subchordal portions of the sclerotomes.

The sclerotomites, as compared with the preceding stages, consist of a more advanced form of connective tissue, composed of closely set isodiametric cells and a limited amount of intercellular substance. The tissue of the caudal sclerotomites is, on the whole, more advanced than that of the cranial sclerotomites. It contains more of the intercellular substance, and upon the colour of the latter depends the bluish tint of the caudal halves of the sclerotomes as compared with the reddish and violet hue of the cranial ones.

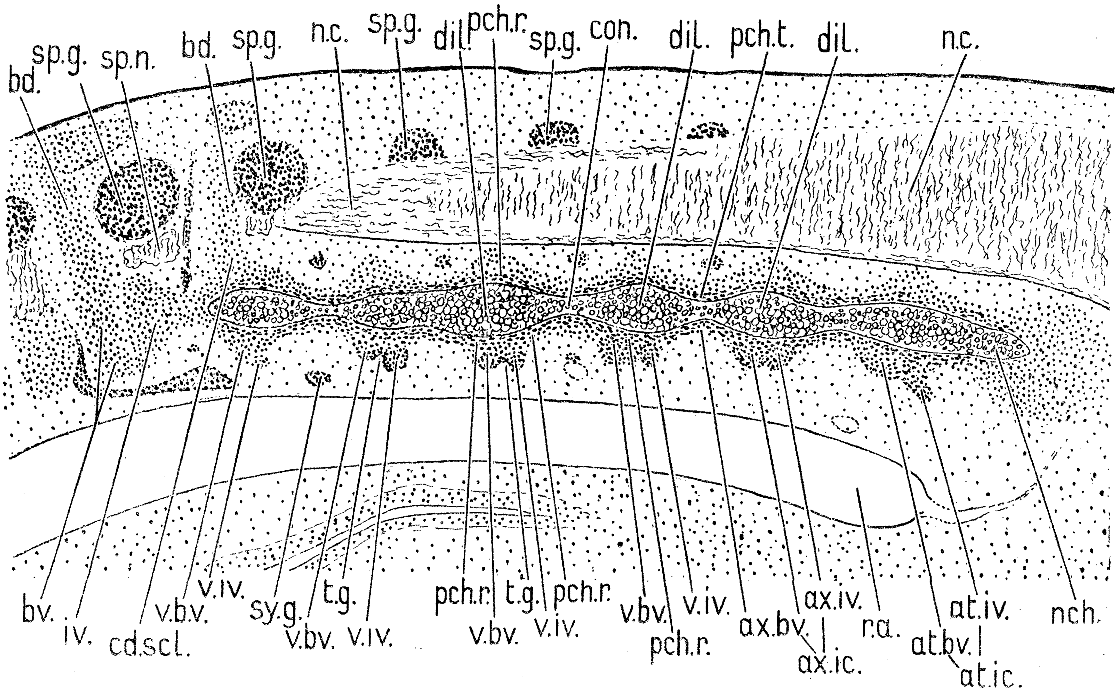


Fig. 12.—Specimen and region as in fig. 10. Section has passed more mesially than in fig. 11. Abbreviations as in fig. 11, except *at.ic.*, atlas-intercentrum; *at.iv.*, ventral-most unpaired portion of the atlas-interventral; *ax.ic.*, axis-intercentrum; *cd.scl.*, caudal sclerotomite; *con.*, constricted portion of the notochord; *dil.*, dilated portion of the notochord; *iv.*, interventral; *nch.*, notochord; *pch.r.*, perichordal ring; *pch.t.*, perichordal tube; *t.g.*, transverse groove separating the subchordal portion of the basiventrals from the corresponding portion of the interventrals; *v.bv.*, ventral-most portion of the basiventrals; *v.iv.*, ventral-most portion of the interventrals.

The ventral and ventro-lateral portions of the subchordally fused right and left caudal sclerotomites have increased in size, and consist of prechondral tissue composed of polygonal isodiametric cells and moderate quantity of palish blue intercellular substance. Such structure renders it possible to distinguish these portions of the caudal sclerotomites from the adjacent perichordal tube, the latter being composed of concentrically disposed flattened spindle-shaped cells with elongated nuclei and deeply blue-stained intercellular substance (figs. 12 and 13, *pch.t.*, *pch.r.*). These portions of the caudal sclerotomites are chronologically the first formations in the developing vertebral column, which consist of prechondral tissue. Being placed immediately in front of the intersclerotomic blood vessels and the roots of the spinal nerves, these ventral and ventro-lateral portions of the subchordally fused right and left caudal sclerotomites must be regarded as the fused anterior pairs of incipient ventral arcualia, and may be termed *basiventrals* (Gadow) (figs. 10 and 11, *bv.* or *c.cd.scl.*).

In front of the basiventrals, and separated from them subchordally by shallow transverse grooves (figs. 12 and 13, *t.g.*), are placed the subchordally fused chordal portions of the cranial sclerotomites (figs. 10 and 11, *iv.* or *c.cr.scl.*). These portions of the cranial sclerotomites are less conspicuous than the basiventrals, although they extend to a somewhat more ventral level than the latter. In contrast to the basiventrals, they contain but very little intercellular substance between their isodiametric cells, and show, instead of the blue colour of the basiventrals, a more or less violet hue. The chordal and subchordal portions of the cranial sclerotomites being placed behind the intersclerotomic (= intersegmental) blood vessels, and the corresponding roots of the spinal nerves being homologous with the posterior pairs of fused ventral arcualia. Gadow's term, *interventrals*, may be used for the denomination of the latter.

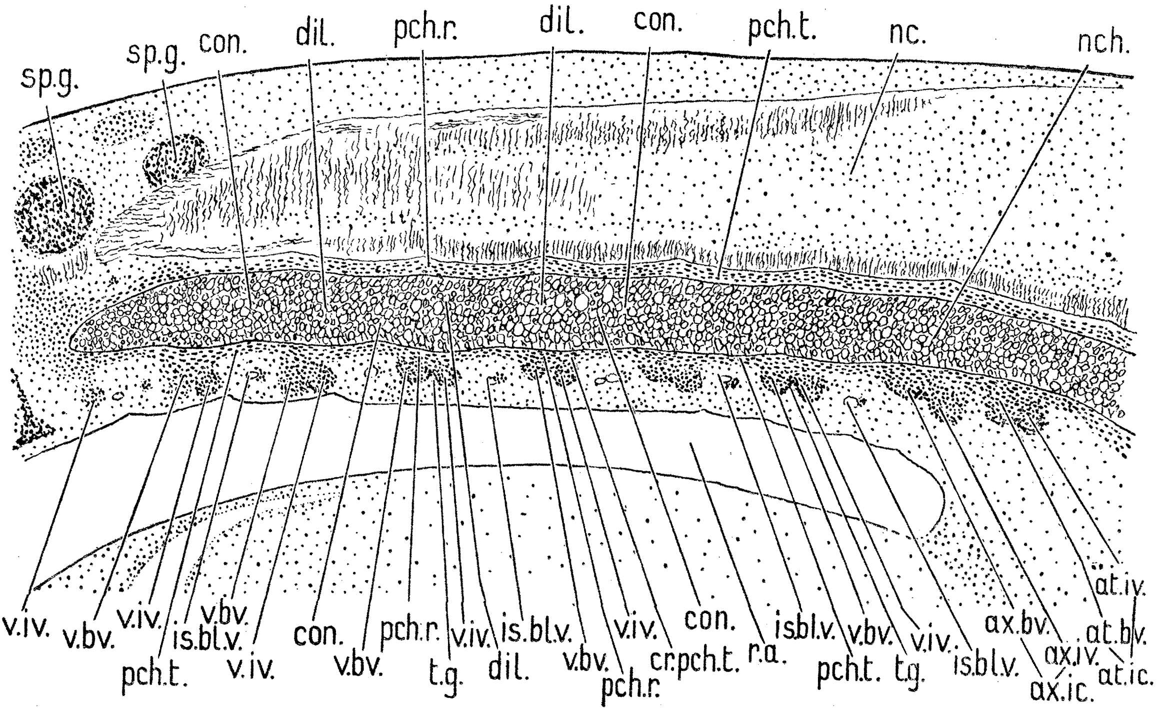


Fig. 13.—Specimen and region as in fig. 10. Median sagittal section. Abbreviations as in fig. 12.

Despite the superficial groove separating the ventral-most portion of the basiventrals from the corresponding portion of the interventrals, both these portions are very intimately coalesced (figs. 12 and 13, *v.bv.*, *v.iv.*). The intrasclerotomic or intervertebral position of the structure resulting from the fusion of the subchordal portions of the inter- and basi-ventrals justifies us in calling it an *intercentrum*. But it must be emphasised that the main bulk of a cervical intercentrum is formed of the ventral portion of the fused basiventrals. The corresponding portion of the interventrals forms the smaller anterior histologically less advanced division of an intercentrum.

The above-mentioned transverse grooves between successive ventral-most portions of basi- and inter-ventrals (figs. 12 and 13, *t.g.*) appear as remainders of the common intrasclerotomic fissures (fig. 5, *c.ia.f.*) open in the 3-day *Larus*, but obliterated at the the present stage.

The neural portions of the sclerotomites, disposed between successive spinal ganglia surrounding the neural cord on both sides and passing laterally into the intermyotomic septa, represent the membranous forerunners of the *basidorsals* (Gadow), *i.e.*, anterior portions of the future neural arches (figs. 10, 11 and 12, *n.cd.scl.* or *bd.*). The basal portions of the basidorsals leaning against the dorso-lateral face of the perichordal tube represent their most advanced portions, being composed of incipient prechondral tissue.

The supraganglionic portion of the cranial sclerotomites is of special interest. In this region, viz., between the dorso-lateral face of the spinal ganglion and the dorso-mesial aspect of the corresponding myotome (figs. 10 and 11, *sp.g.*, *mt.*) there can be distinguished a more condensed area in the common connective tissue matrix (figs. 10 and 11, *d.id.*). This cell-condensation is laid down *in loco*, and is genetically independent of the neural (supraganglionic) portion of the caudal sclerotomites (basidorsals) disposed immediately in front and behind of it (figs. 10 and 11, *n.cd.scl.* or *bd.*). This formation belongs to the system of the posterior pair of dorsal arcualia or *interdorsals* (Gadow). It represents the upper portion of the interdorsals, and will be called *dorsal-interdorsal*. It gives rise to the posterior zygapophysis. In the atlas-sclerotome, this formation is very much reduced. The intercentra of the atlas and axis are of slightly larger size than those of other cervicals (figs. 12 and 13, *at.ic.*, *ax.ic.*).

Extracervical Regions.

The moniliform differentiation of the notochord is fully developed in the thoracic region, but is almost absent in the more caudally disposed areas of it. The relation of the dilated and constricted segments of the notochord to the sclerotomes resembles that found in the cervical region. The thoracic and lumbar regions exhibit the same degree of vacuolisation as the cervical. The anterior portion of the tail shows very few vacuoles, whereas the posterior part of the tail is as yet entirely devoid of any vacuolisation.

The process of differentiation of the sclerotomes into the cranial and caudal sclerotomites resulting from the development of the intrasclerotomic fissures has reached nearly the middle of the tail. The hinder portion of the tail persists in the state of undivided sclerotomes, whilst its extreme posterior end persists in the condition of undifferentiated somitic sacs. The formation of the perichordal tube has extended into the base of the tail, whilst the middle portion of the latter remains in the stage of perichordal rings. The formation of the subchordal condensations of the sclerotomes (= intercentra), representing the ventral-most divisions of the united incipient basi- and inter-ventrals, has progressed to the base of the tail.

The rudiments of the thoracic intercentra, like those of the cervical, arise, *prima origine,* as unpaired formations. In the lumbar, sacral and anterior portion of the caudal region, the intercentra are, on the contrary, laid down as paired formations. Investigating frontal sections passing through the synsacral region, one can observe how the unpaired last thoracic intercentra in passing over into the anterior lumbar ones gradually lose their rounded shape and become more distended in a transverse direction. And whilst this transverse distention of successive lumbar intercentra is growing, a longitudinal groove becomes visible in the median sagittal plane of the intercentra. This groove, dividing the lumbar intercentra into right and left halves, widens gradually up to the sacral region (fig. 14, *t.ic.*, *l.ic.*). The space included between the right and left synsacral intercentra is occupied by the dorsal portion of the dorsal aorta. Behind the sacral region, both halves of the intercentra converge and meet again.

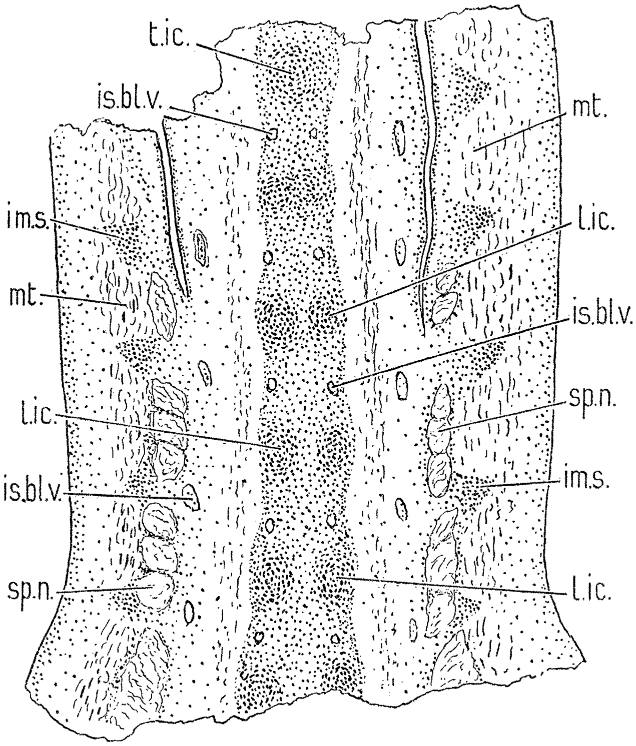


FIG. 14.—Frontal section through the anterior portion of the synsacral region a 4½-day Gull embryo. Anterior end of section above. Abbreviations as in fig. 10 except *im.s.*, intermyotomic septum; *l.ic.*, lumbar intercentrum; *t.ic.*, intercentrum of thoracic region.

In the synsacral region no median subchordal connection between the right and left sclerotomes, belonging to a metamere, is established. In addition to this the incipient synsacral intercentrum does not display any differentiation into an interventral and basiventral division. The synsacral intercentrum is laid down in the mesenchyme of the ventral-most (subchordal) portion of the fused cranial and caudal sclerotomites of a sclerotome and occupies at its first origin a strictly intrasclerotomic (= intervertebral) position. These facts explain the paired character of the synsacral intercentra and the absence of a transverse groove on the ventral surface of them in comparing them with the intercentra of the cervical and the anterior portion of the thoracic region.

EMBRYO OF *Struthio Australis*, AGED ABOUT 8 DAYS.—CERVICAL REGION.

The perichordal tube which in 4-day *Larus* and in 7-day *Struthio* exhibits a more or less uniform structure throughout, has become differentiated into two kinds of structurally different segments alternating regularly with each other. One system of these segments consists of sparse spindle-shaped cells with abundant palish blue intercellular substance. These segments of the perichordal tube surround the dilated portions of the notochord and may be called *vertebral rings* (fig. 15, *v.r.*). Comparative analysis of the following stages of development shows that these rings represent the nuclei of the vertebral centra—at least the internal and middle waist-like portion of the latter. In comparing this with the previous stage the incipient vertebral ring is seen to occupy the place of the thin-walled portion of the perichordal tube and has developed from the latter. As this portion of the perichordal tube arises by the fusion of the ends of successive perichordal rings, each vertebral ring must be looked upon at its earliest stage as compound and as an intersclerotomic formation. Its anterior half is formed by the caudal end of one perichordal ring, whilst the posterior half is developed from the cranial end of the perichordal ring immediately behind it.

The other segments formed from the perichordal tube consist of slightly denser tissue of irregularly disposed cells with comparatively smaller intercellular spaces devoid of any coloured intercellular substance (fig. 15, *is.b.*). These segments which may be called *interstitial bodies* are more massive than the vertebral rings and are confined to the constricted portions of the notochord. Exact comparison with the previous stage shows that they are developed from the middle zone of the thick-walled portions of the perichordal tube, thus occupying an intrasclerotomic position.

The atlas-intercentrum (subchordal portion of atlas-sclerotome) exhibits in sagittal section the shape of a slightly broken horn (fig. 15, *a.ic.*), the anterior limb of which is directed cranio-ventrally, the posterior caudo-dorsally. The anterior portion, homologous with the ventral portion of the interventrals, has a swollen appearance and consists of less developed prechondral tissue (fig. 15, *at.v.iv.*). The posterior portion, identical with the ventral portion of the basiventral, contains a greater amount of intercellular substance (fig. 15, *at.v.bv.*).

The subchordal portion of the axis-sclerotome, less conspicuous than that of the atlas, has become connected to the hinder aspect of the latter by strands of dense connective tissue. The whole formation reveals a slightly broken appearance, still indicating the fact that it is composed of two different portions—the ventral-most divisions of the inter- and basi-ventrals (fig. 15, *ax.v.iv.*, *ax.v.bv.*, *ax.ic.*, *ax.c.*).

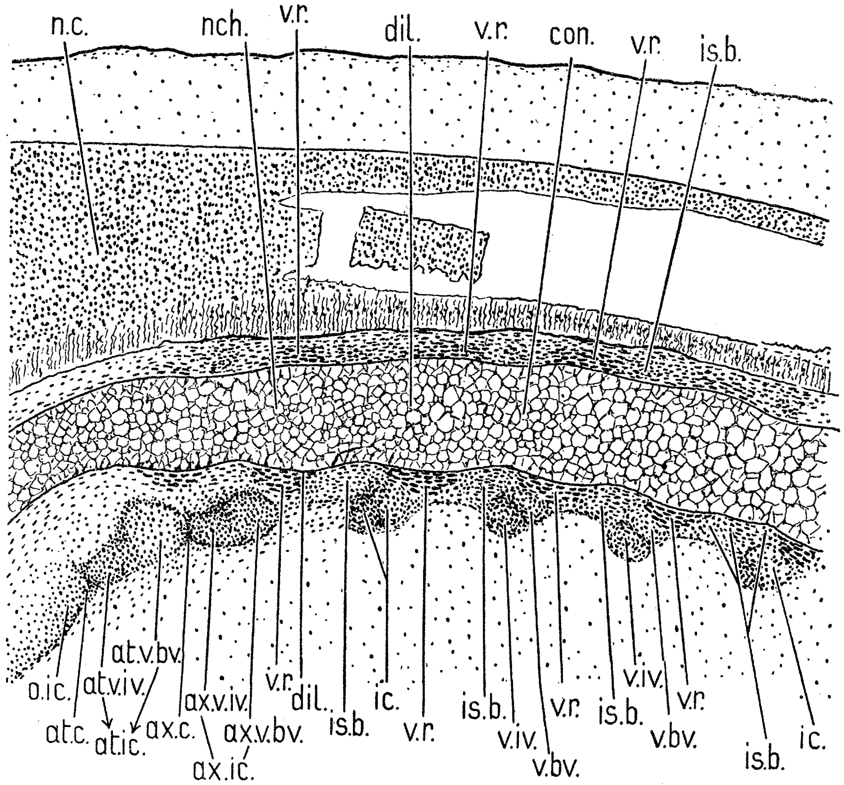
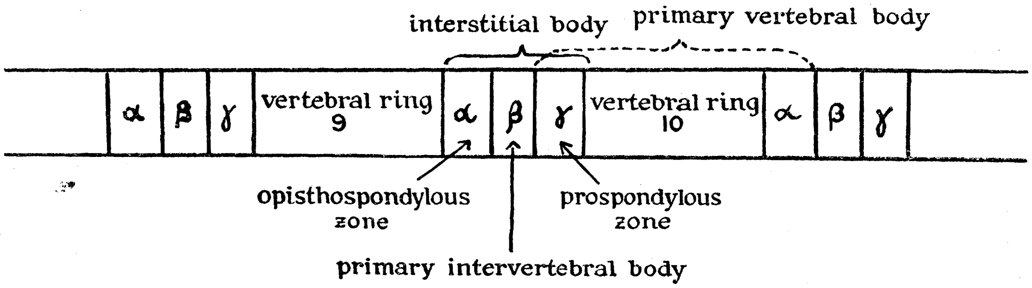


Fig. 15.—Median sagittal section through the cervical region of an 8-day ostrich embryo. Anterior end of section to the left. *At.c.*, connection between the intercentrum of atlas and the last occipital vertebra; *at.ic.*, atlas-intercentrum; *at.v.bv.*, ventral-most portion of the atlas-basiventrals; *at.v.iv.*, ventral-most portion of the atlas-interventrals; *ax.c.*, connection between the intercentra of atlas and axis; *ax.ic.*, axis intercentrum; *ax.v.bv.*, ventral-most unpaired portion of the axis-basiventrals; *ax.v.iv.*, ventral-most unpaired portion of the axis-interventrals; *con.*, constricted portion of the notochord; *dil.*, dilated portion of the notochord; *ic.*, intercentrum; *is.b.*, interstitial body; *n.c.*, neural cord; *nch.*, notochord; *o.ic.*, intercentrum of last occipital vertebra; *v.bv.*, ventral unpaired portion of basiventrals; *v.iv.*, ventral unpaired portion of interventrals; *v.r.*, vertebral ring.

EMBRYO OF *Struthio Australis*, AGED ABOUT 10 DAYS.—CERVICAL REGION.

The vertebral rings, which in the 8-day *Struthio* displayed an incipient form of development, in the present specimen show a much more advanced stage of evolution. They appear in the form of rings stained intensely blue surrounding the dilated portions of the notochord (Plate 18, *v.r.*). The thickness of the walls of the vertebral rings is greatest in their equatorial zone; from this point the walls taper gradually towards both ends of the rings. The thickness of the walls of the equatorial zone (= waist portion) of the vertebral rings is not uniform in all directions, the lateral walls on an average exhibiting a slightly greater diameter than the ventral ones, and the latter a somewhat greater thickness than the dorsal ones. Each vertebral ring consists of spindle-shaped cells mostly disposed concentrically with regard to the notochord. The innermost layers of these cells are the flattest, whilst the peripheral ones by degrees assume an isodiametrically polygonal shape. There is a copious amount of intercellular substance exhibiting a beautiful blue colour. Owing to this blue colour the areas of the vertebral rings are very easy to distinguish from the surrounding structures, which mostly display a paler blue or violet hue. The vertebral rings of the atlas and axis do not show any marked difference from those of other cervical vertebræ.

Of particular interest is the differentiation of the interstitial bodies, *i.e.*, the portions of the perichordal tube comprised between successive vertebral rings and representing the thickened portions of the perichordal tube (Plate 18, *is.b.*). Consisting in the preceding (8-day *Struthio*) stage throughout its whole extent of more or less uniform tissue of mesenchymatous cells, they exhibit in the present stage an increase in thickness and a differentiation into three topographically and structurally different portions—a cranial, a middle and a caudal one. The middle portion corresponds exactly to the middle zone of the former perichordal ring, and consists of closely set spindle-shaped cells directed transversely with but traces of intercellular substance. This portion reveals a violet hue and represents the *primary intervertebral body* (Plate 18, *p.iv.b.*). Cranially and caudally from the incipient primary intervertebral body are arranged areas of advanced prechondral tissue consisting of cells directed tangentially with regard to the notochord and abundant intercellular substance of palish blue colour. These divisions of the interstitial body are closely applied to the tapering ends of the adjacent vertebral rings and concrescent with the latter (Plate 18, *os.z.*, *ps.z.*, *v.r.*). These formations may be called the *pro-* and *opistho-spondylous zones or segments* of the primary vertebral body, because they contribute, as later developmental stages show, to the formation of the cranial and caudal ends of the future *primary vertebral bodies* (fig. 18, *ps.z.*, *v.r.*, *os.z.*, *p.v.b.*). The above-described relations may be made clearer by the following diagram:—



α, β, γ represent the three portions of the differentiating interstitial body.

γ fuses with front end of, say, vertebral ring 10, α fuses with hinder end of vertebral ring 9.

The interventrals show signs of differentiation into an anterior and a posterior portion. The cranial portion has fused with the hinder end of the primary vertebral body (posterior division of the vertebral ring and the opisthospondylous zone) contributing to the formation of the outer portion of the hinder end of the secondary vertebral body (Plate 18, *a.iv.*, *os.z.*).

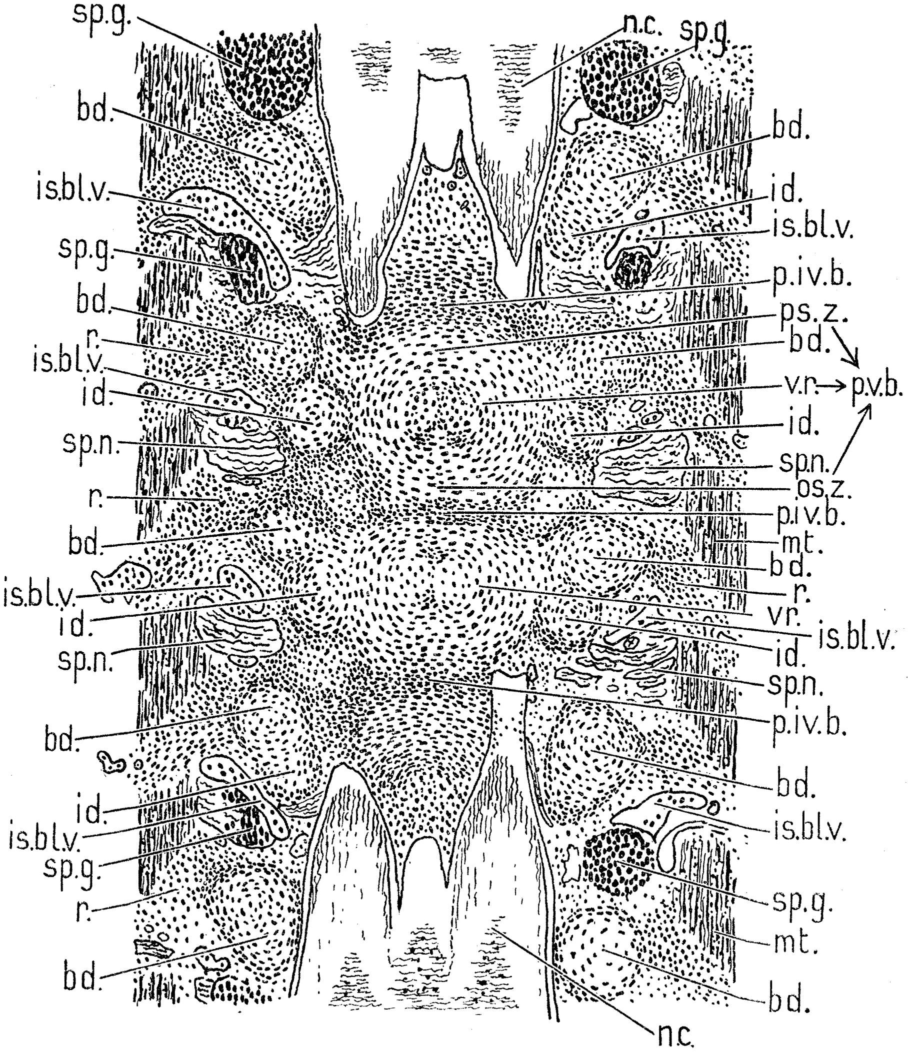


Fig. 16.—Frontal section of the middle portion of the cervical region of a 12-day *Struthio* embryo. The middle portion of the section passes through the dorsal walls of the vertebral bodies. Anterior end of section above. This is also the case in fig. 17. *bd.*, basidorsal; *id.*, interdorsal; *is.bl.v.*, intersegmental blood vessel; *mt.*, myotome; *n.c.*, neural cord; *os.z.*, opisthospondylous zone; *p.iv.b.*, primary intervertebral body; *ps.z.*, prospondylous zone; *p.v.b.*, primary vertebral body; *r.*, rib; *sp.g.*, spinal ganglion; *sp.n.*, spinal nerve; *v.r.*, vertebral ring.

The posterior portion of the interventrals is differentiated to a certain extent already in the preceding (8-day) stage into a ventral unpaired and lateral paired portion. The lateral paired portion represents the primordium from which in later stages is formed the external layer of the *secondary intervertebral body.*

The ventral unpaired portion of the posterior division of the interventrals represents the anterior portion of the intercentrum. This portion of the intercentrum in comparison with the preceding (8-day) stage shows signs of reduction (fig. 18, *a.iv.*, *p.iv.*, *v.iv.*, *iv.*).

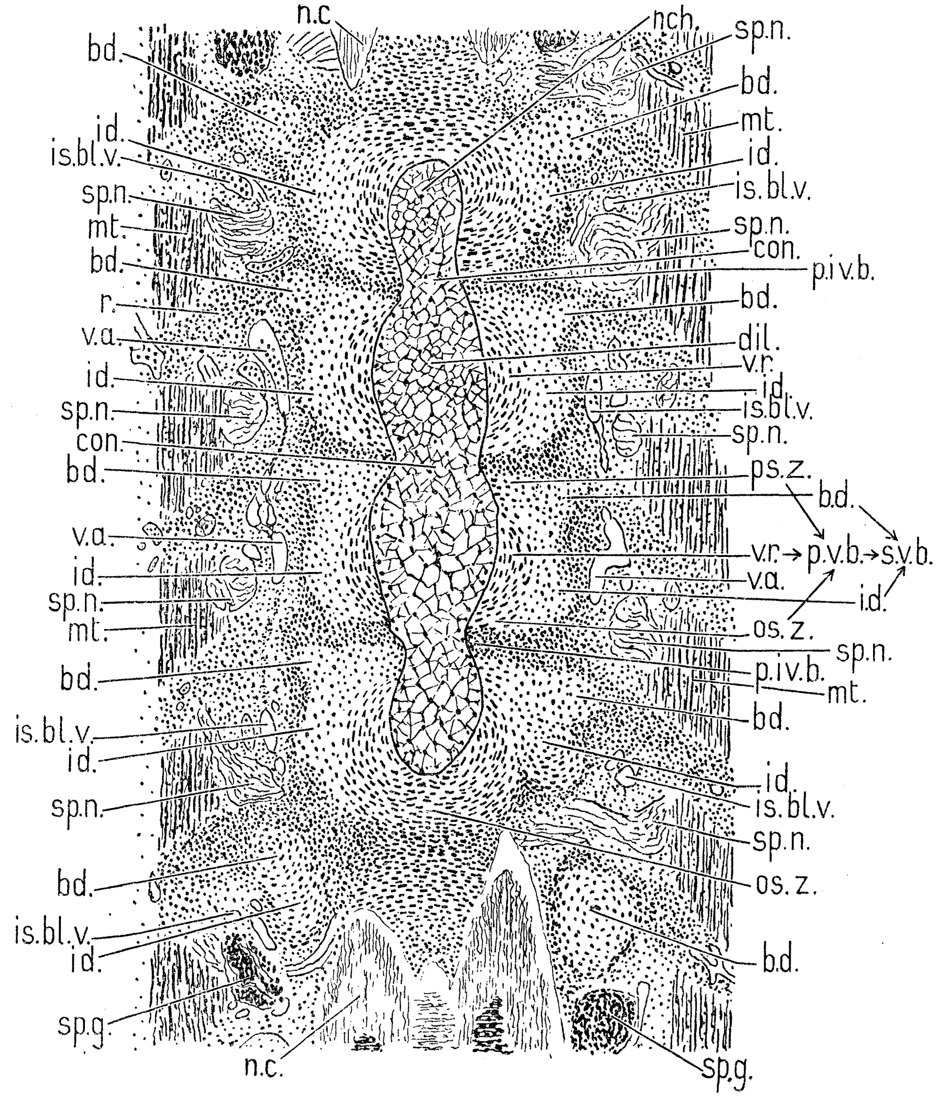


FIG. 17.—Specimen and region the same as in fig. 16. The middle portion of the section passes through the dorsal half of the notochord. Abbreviations as in fig. 16, except *con.*, constricted portion of the notochord; *dil.*, dilated portion of the notochord; *nch.*, notochord; *s.v.b.*, secondary vertebral body; *v.a.*, vertebral artery.

Examination of horizontal sections passing through the dorsal face of the notochord reveals on each side of the vertebral ring oval-shaped formations consisting of concentrically arranged cells with feebly developed intercellular substance (fig. 16, *id.*).* The dorsal end of this formation is attached to the posterior aspect of the basal portion of the basidorsal, and is separated from the vertebral ring by a space filled up with loose connective tissue (fig. 16, *bd.*, *id.*, *v.r.*). Slightly more ventrally this space disappears and the formation increasing in bulk covers the whole dorso-lateral face of the vertebral ring. But it can be easily distinguished from the blue-coloured vertebral ring by its violet stain and different structure (fig. 17, *id.*, *v.r.*). It is thus evident that the described formation extends from the base of the basidorsal slantingly backwards and downwards representing the main bulk of the dorso-lateral aspect of the secondary vertebral body (fig. 18, *id.*, *bd.*, *bv.*, *s.v.b.*). This formation is a derivative of the tissue covering in the previous (8-day *Struthio*) stage the dorso-lateral region of the vertebral ring and belongs genetically to the mesial or vertebral portion of the neural division of the cranial sclerotomite. Its position behind the corresponding

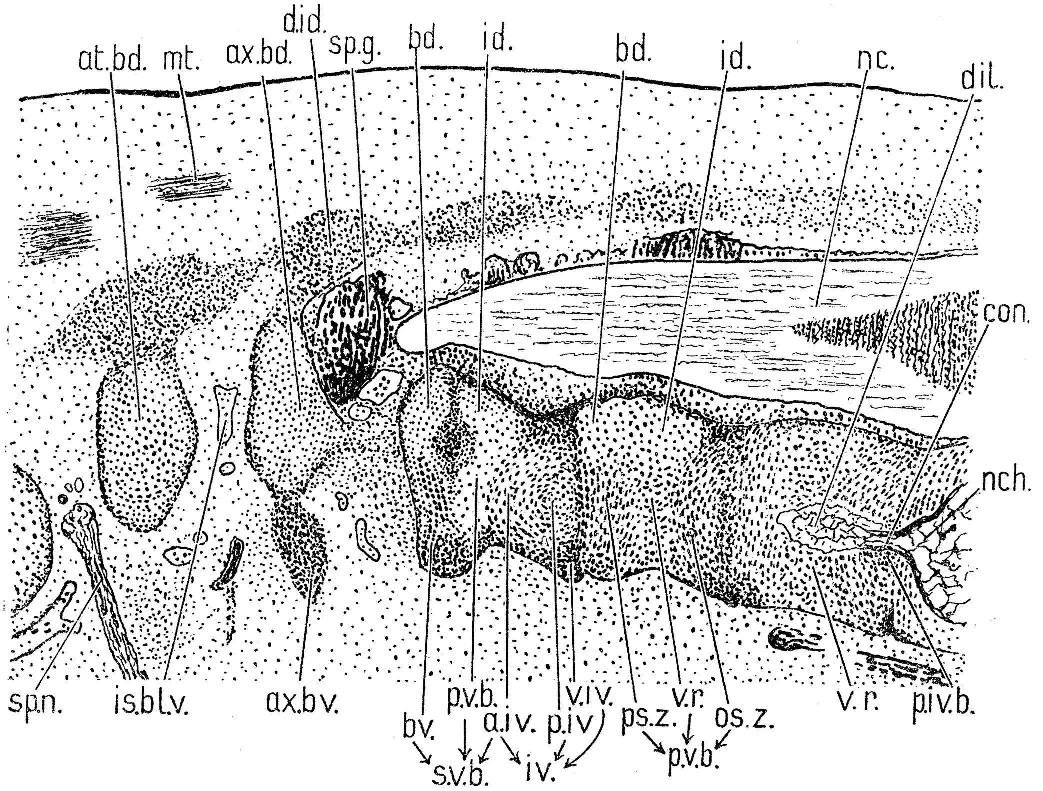


FIG. 18.—Lateral sagittal section of the cervical region of the same specimen as in fig. 16. The section has caudally passed more mesially than cranially. Anterior end of section to the left. Abbreviations as in figs. 16 and 17, except *a.iv.*, anterior portion of the interventral; *at.bd.*, atlas-basidorsal; *ax.bd.*, axis-basidorsal; *ax. bv.*, axis-basiventral; *bv.*, basiventral; *d.id.*, dorsal interdorsal; *iv.*, interventral; *p.iv.*, posterior portion of the interventral; *v.iv.*, ventral portion of the interventral.

---

* As the spatial relations of these structures in 10-day *Struthio* do not differ essentially from those in 12-day *Struthio*, the text-figures referring to the latter sufficiently illustrate the conditions in 10-day *Struthio*.

basidorsal and in the dorso-lateral region of the vertebral body allows us to identify it with the lower portion of the second pair of the rudiments of neural arches in *Hatteria* (SCHAUINSLAND) and suggests the name "*interdorsal*."

EMBRYO OF *Larus Canus*, AGED ABOUT 5 DAYS.—CERVICAL REGION.

The moniliform differentiation of the notochord in this stage as compared with that in a 4-day *Larus* shows great alterations. The difference in shape between the dorsal and ventral aspects of the notochord, which was slightly expressed in 4-day *Larus*, has considerably increased. Examination of the sagittal section shows that in the dorsal aspect of the notochord constrictions and dilatations are still less deep than in the ventral, but the dilated segments have become much longer than the constricted ones. The ventral constrictions have, on the contrary, grown deep and long, the dilatations deep but short (fig. 19, *dil.*, *con.*).

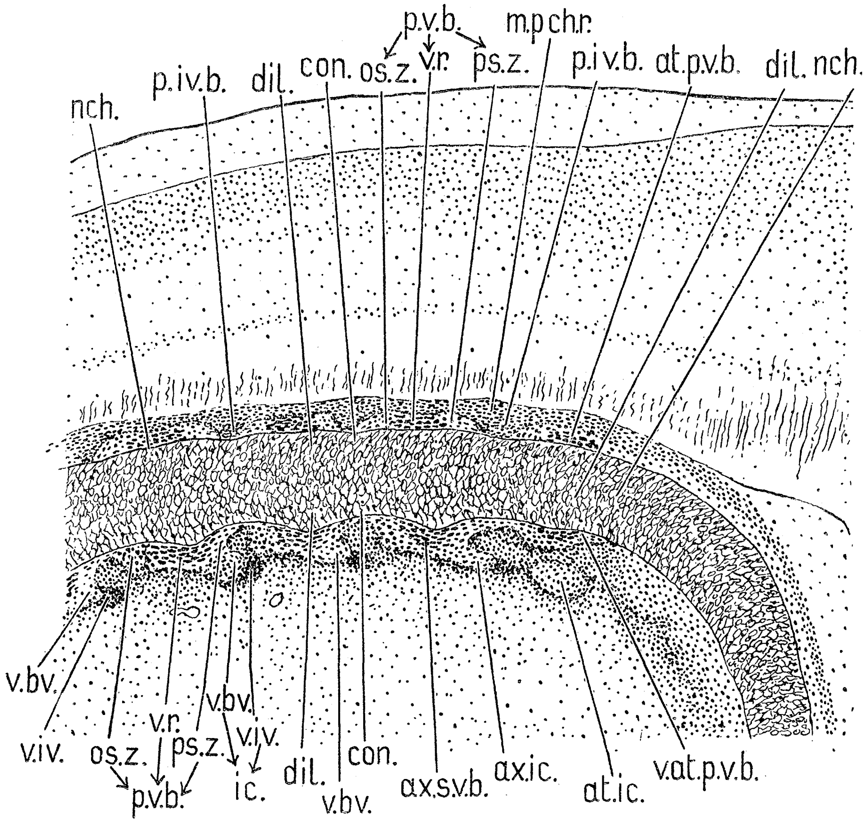


FIG. 19.—Median sagittal section of the cervical region of a 5-day Gull embryo. Anterior end of section to the right. This is also the case in figs. 20, 21 and 22. *at.ic.*, atlas-intercentrum; *at.p.v.b.*, primary vertebral body of atlas; *ax.ic.*, axis-intercentrum; *ax.s.v.b.*, secondary vertebral body of axis; *con.*, constricted portion of the notochord; *dil.*, dilated portion of the notochord; *ic.*, intercentrum; *m.pch.r.*, middle zone of the former perichordal ring; *nch.*, notochord; *os.z.*, opisthospondylous zone; *p.iv.b.*, primary intervertebral body; *ps.z.*, prospondylous zone; *p.v.b.*, primary vertebral body; *v.at.p.v.b.*, ventral portion of the primary vertebral body of atlas; *v.bv.*, ventral unpaired portion of basiventrals; *v.iv.*, ventral unpaired portion of interventrals; *v.r.*, vertebral ring.

The vacuolisation of the notochord compared with 4-day *Larus* has reached a higher degree, the protoplasmatic cells being nearly absent and the vacuoles having assumed a polygonal shape, elongated in a dorso-ventral direction (fig. 19, *nch.*). The number of the cell-nuclei has greatly diminished but is still slightly greater in the peripheral than in the central portion of the notochord.

Comparison with 3- and 4-day *Larus* shows that the regularly disposed prominences (fig. 19, *m.pch.r.*) conditioning the moniliform habitus of the perichordal tube are homologous to the equatorial zones of the former perichordal rings, thus being intrasclerotomic formations.

The differentiation of the perichordal tube consists in the appearance of regularly disposed cartilaginous rings in its violet-stained prechondral tissue (fig. 19, *p.v.b.*). These rings alternate with the intrasclerotomically disposed prominences of the perichordal tube, being therefore intersclerotomic formations. The waist portion of the rings is compressed, while both the ends are slightly swollen. The waist portion consists of young cartilaginous tissue composed of cells flattened in a radial direction with regard to the notochord, and disposed partly concentrically, partly longitudinally. The intercellular substance is copious and stained in an intense blue (fig. 19, *v.r.*).

The structure and the intersclerotomic position of the waist-portion of the new-formed cartilaginous rings of the perichordal tube allows us to homologise it with the *vertebral rings* of 8-day *Struthio.*

The inner layers of the swollen end portions of the cartilaginous rings (fig. 20, *ps.z.*, *os.z.*) consist of cells disposed tangentially with regard to the notochord with a certain amount of palish blue intercellular substance. These portions arise from segments of the perichordal tube disposed between the successive vertebral rings. Being disposed at the anterior and the posterior ends of the vertebral rings, they are respectively homologous with the *pro-* and *opistho-spondylous zones* of the primary vertebral body in *Struthio.*

From the above it is evident that the cartilaginous rings consisting in their waist portions of vertebral rings and in their end portions of pro- and opistho-spondylous zones, represent formations homologous with the primary vertebral bodies of *Struthio.*

It is of interest to notice that the ventral and ventro-lateral portions of the opisthospondylous zone are slightly stronger than the corresponding portions of the prospondylous zone. The dorsal and lateral regions of the pro- and opistho-spondylous rings show equal strength (fig. 19, *ps.z.*, *os.z.*).

The dorsal and ventral walls of the vertebral body in sagittal section show equal longitudinal extension, but their respective thickness is different, the ventral wall being slightly thicker than the dorsal. This is a consequence of the fact that the dorsal portion of a vertebral centrum persists in the condition of a primary vertebral body, while the ventral and ventro-lateral portions, being fused with portions of the caudal and cranial sclerotomites (respectively dorsal and ventral arcualia), represent those of a typical *secondary vertebral body.**

---

* The "primary" vertebral body thus consists of the bare centrum, a section of the continuous perichordal tube; the secondary vertebral body of this centrum with the fused arcualia added to it.

The portions of the perichordal tube remaining between the primary vertebral bodies after the formation of the latter represent the *primary intervertebral body* (fig. 19, *p.iv.b.*). The primary intervertebral bodies coincide with the above-mentioned prominent zones of the perichordal tube, and thus represent the middle (intrasclerotomic) portions of the former perichordal rings. The primary intervertebral bodies consist of transversely disposed cells with faint traces of palishblue intercellular substance.

It is evident from the above-described relations of the vertebral rings to the perichordal tube that each segment of the perichordal tube corresponding to the former perichordal ring gives rise to three different formations. The middle zone of the former perichordal ring is transformed into the primary intervertebral body, whereas the cranial and caudal intersclerotomically directed portions of the ring give rise to two kinds of structures. The portions of the perichordal ring proximal to the primitive intervertebral body are converted into the pro- and opistho-spondylous zones, the prospondylous zone being disposed caudally, the opisthospondylous one cranially from the primary intervertebral body.

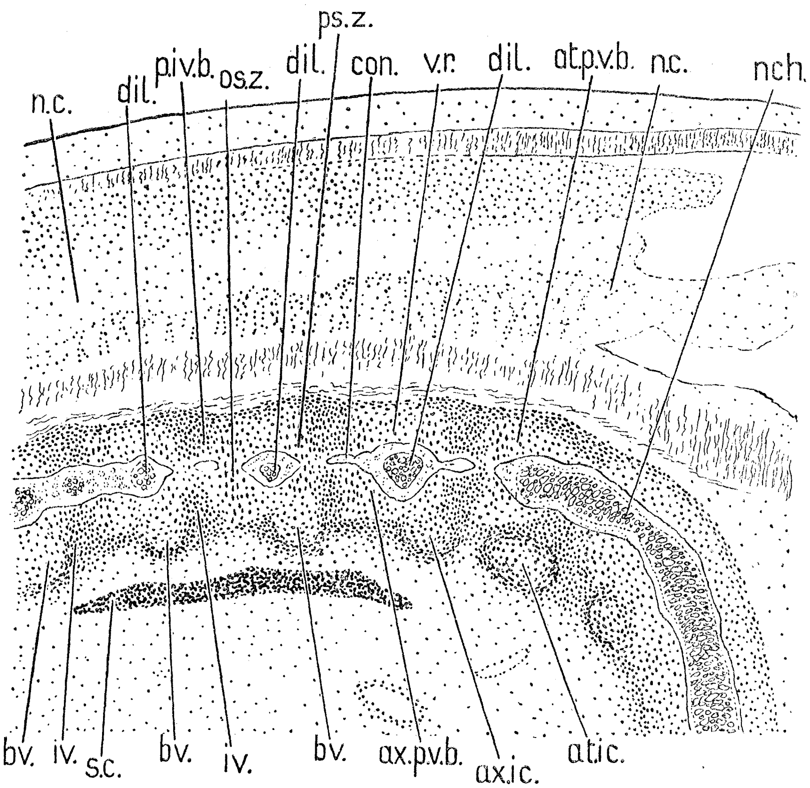


FIG. 20.—Lateral sagittal section of the cervical region of the same specimen as in fig. 19. The section passes through the lateral portion of the notochord. Abbreviations as in fig. 19 except *ax.p.v.b.*, primary vertebral body of axis; *bv.*, basiventral; *iv.*, interventral; *n.c.*, neural cord ; *s.c.*, sympathetic cord.

The portions of the former perichordal rings distal to the primary intervertebral body, which by their fusion in the intersclerotomic region gave rise to the formation of the perichordal tube, are converted into the vertebral rings. *Each vertebral ring is thus formed of two halves belonging to different metameres.*

Of special interest is the alteration in the position of the dilated and constricted areas of the notochord with regard to the inter- and intra-sclerotomic regions of the perichordal tube. The dilated regions of the notochord, which in 3- and 4-day *Larus* were confined to the intrasclerotomic portion of the perichordal tube, occupy at the present stage an intersclerotomic position, being surrounded by the vertebral rings (figs. 19 and 20, *dil.*, *v.r.*). The constricted portions of the notochord, on the contrary, which in earlier stages coincided with the intersclerotomic (or thin-walled) region of the perichordal tube, have assumed an intrasclerotomic position, being enclosed at least in their middle portion by the primary intervertebral bodies (figs. 19 and 20, *con.*, *p.iv.b.*).

The intrasclerotomic fissures have become completely obliterated. The boundaries between successive sclerotomes are indicated by the rami communicantes of the sympathetic cord (fig. 22, *r.c.*, *s.c.*), by the intersclerotomic blood vessels, and by the intermyotomic septa. The difference in staining is also a reliable criterion for the determination of the boundaries between the cranial and caudal halves of a sclerotome.

The transverse grooves, separating in 4-day *Larus* the primordia of the subchordal portions of the basiventrals from the corresponding portions of the interventrals, have completely disappeared. The basiventrals consist of very advanced prechondral tissue with copious deeply blue-stained intercellular substance (figs. 20, 21, *bv.*).

The vertebral artery and collateral sympathetic cord are formed. They are laid down on both sides of the secondary vertebral body immediately below the ventro-lateral faces of the basidorsals. They arise as horizontal branches of the intersclerotomic arteries and collateral sympathetic ganglia. By these formations the distal part of the chordal division of the caudal sclerotomite farthest from the notochord is separated off from the basiventrals.

This distal or muscular portion of the caudal sclerotomites extends from the incipient foramen transversarium lateralwards and caudalwards, ending in the intermuscular septum. It represents the incipient *rib*. The proximal portion of the rib is laid down in the form of a dorsal and a ventral limb. The dorsal limb connected with the ventro-lateral portion of the basidorsal (incipient diapophysis) represents the tubercular portion of the rib. The ventral limb continuous with the dorso-lateral portion of the basiventral (rudiment of the parapophysis) represents the capitular portion of the rib.

The rudiments of the ribs consist of prechondral tissue less advanced than that of the corresponding basiventrals and basidorsals, being composed of isodiametric cells with a moderate amount of bluish intercellular substance. There is no histological difference and no perceptible boundary line between the proximal portions of the rib and the rudiments of the paraphophyses and diapophyses.

The dorsal-interdorsals, which consisted of dense connective tissue in 4-day *Larus*, have become prechondral. They appear in parasagittal sections, passing through the middle of spinal ganglia in form of vault-like formations connecting the dorsal ends of successive basidorsals (fig. 22, *d.id.*, *sp.g.*). In more lateral sections they grow higher assuming the shape of a blunt cone. At the same time the connection between them and adjacent basidorsals appears narrower. The latter circumstance, taken in connection with the independent mode of their first appearance in 4-day *Larus*, proves that they originate independently of the dorsal portion of the basidorsals.

The interventral portions of the intercentra have undergone great reduction. They remain in the stage of dense connective-tissue strands attached to the antero-ventral border of the basiventral portions of the intercentra. Their reddish-violet colour, caused by the absence of blue-stained intercellular substance, allows us to distinguish them from the blue-stained rudiments of the basiventral intercentra (fig. 19, *v.iv.*, *v.bv.*).

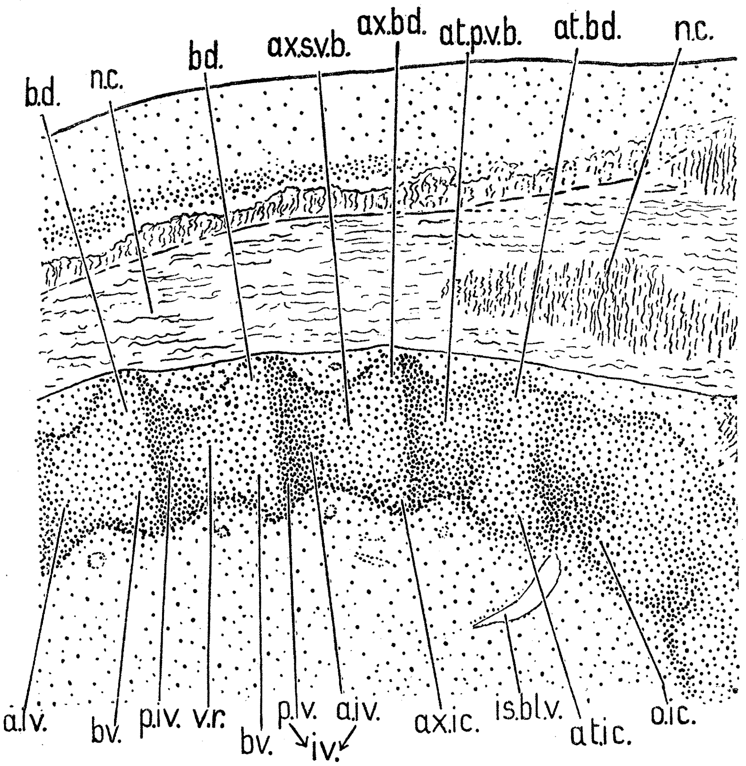


FIG. 21.—Specimen and region the same as in fig. 19. The section passes through the lateral walls of the vertebral bodies. Abbreviations as in figs. 19 and 20, except *at.b.d.* atlas-basidorsal; *ax.bd.*, axis-basidorsal; *is.bl.v.*, intersclerotomic blood vessel; *o.ic.*, intercentrum of last occipital vertebra.

Lateral portions of the interventrals have undergone the same differentiation as was described in 10-day *Struthio.*

The primary vertebral body of atlas is less developed than that of other cervicals (figs. 19, 20 and 21, *at.p.v.b.*). This refers especially to the ventral half of it, where the pro- and opistho-spondylous zones are almost absent (in sagittal section) (fig. 19, *v.at.p.v.b.*). The dilatation of the notochord enclosed by the vertebral ring of the atlas is scantily developed.

The intercentrum of the atlas is nearly twice as large as that of the axis and other cervical vertebræ. It is represented in sagittal section in the form of an elongated body, the long axis of which is almost parallel to the direction of the notochord in the occipital region of the skull. Its anterior and middle portions are separated from the vertebral body of the atlas, only the posterior dorsally directed portion being connected by a mass of prechondral tissue with the middle and hinder portion of the ventral aspect of the latter (fig. 19, *at.ic.*, *v.at.p.v.b.*). The atlas and axis intercentra consist of very advanced prechondral tissue. The atlas basidorsals are well developed, but the interdorsals and dorsal-interdorsals are absent.

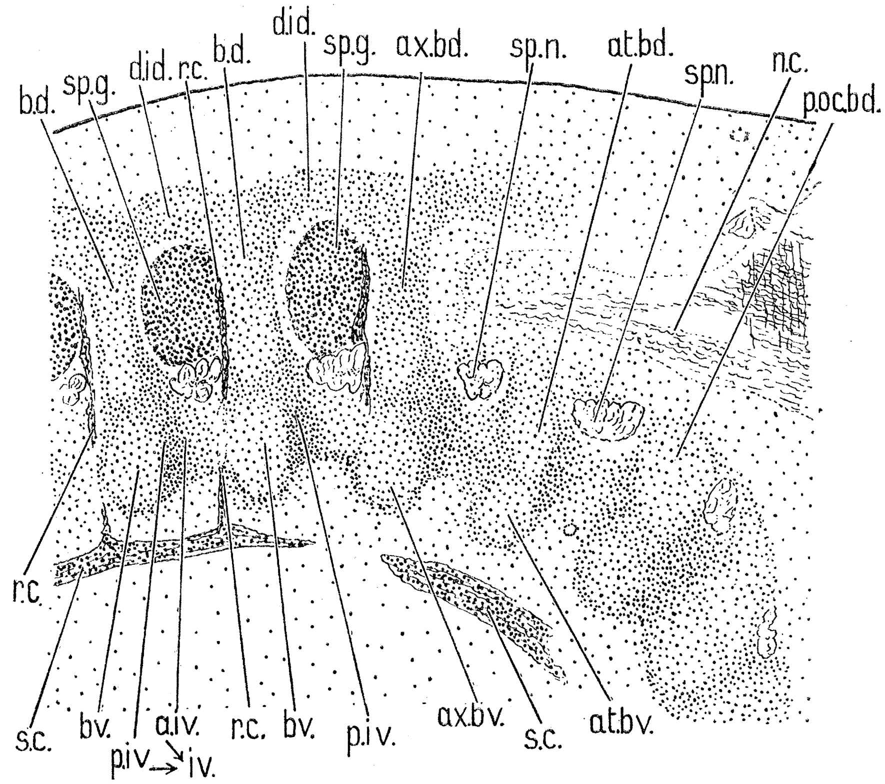


FIG. 22.—Specimen and region the same as in fig. 19. The section passes more laterally than in Fig. 21. Abbreviations as in figs. 19, 20, 21, except *a.iv.*, anterior portion of interventral; *at.bv.*, atlas basiventral; *d.id.*, dorsal-interdorsal; *p.iv.*, posterior portion of interventral; *p.oc.bd.*, posterior occipital basidorsal; *s.c.*, sympathetic cord; *sp.n.*, spinal nerve; *sp.g.*, spinal ganglion; *r.c.*, ramus communicans connecting spinal and sympathetic ganglia.

The dimension of the axis-intercentrum equals that of other cervical intercentra. The axis-intercentrum in sagittal section appears in the shape of an elongated formation attached to the antero-ventral face of its vertebral body. Its anterior end is directed ventrally and separated from the cranial end of the body of the axis by a wide gap (fig. 19, *ax.ic.*, *ax.s.v.b.*).

The basidorsals of the axis, equal in size and proportions to those of other cervicals, and its dorsal-interdorsals represent a development similar to the rest of the cervicals (fig. 22, *ax.bd.*, *d.id.*). Like the latter, the atlas and axis vertebræ bear rudiments of prechondral ribs, developed from the intermuscular portions of the caudal sclerotomites. The groove separating in 4-day *Larus* the anterior (interventral) and posterior (basiventral) divisions of the atlas and axis intercentra has disappeared. The same may be stated with regard to the histological difference expressed in 4-day *Larus* and 8-day *Struthio*. These facts suggest that both components (inter- and basi-ventral) of the atlas and axis intercentra have undergone complete fusion. The same can be stated with regard to 12-day *Struthio*.

Extracervical Regions.

The moniliform differentiation of the notochord of the thoracic region is of special interest, revealing a transitional stage in the localisation of the dilatations and constrictions with respect to the vertebral rings and sclerotomes. The conditions exhibited by the anterior portion of the thoracic region resemble those of the cervical region, the dilatations being inter- and the constrictions intra-sclerotomically disposed. The hinder portion of the thoracic and of the lumbar regions, on the contrary, show more or less distinctly expressed intrasclerotomic dilatations and intersclerotomic constrictions (as the cervical region in 3- and 4-day *Larus*). The caudal region still remains unaffected by the moniliform differentiation. The process of vacuolisation of the notochord has almost reached the caudal end of the notochord.

The inter- and intra-sclerotomic fissures are obliterated in all extracervical regions, including the tail. The differentiation of the primary sclerotomes into the secondary sclerotomes and the perichordal rings, and the fusion of these rings into the perichordal tube, has reached the end of the tail. The differentiation of the perichordal tube into the blue-stained primary vertebral and the reddish-violet coloured primary intervertebral bodies is accomplished in the thoracic, and to a less perfect degree also in the lumbar, region.

The intercentra of the thoracic region are unpaired formations fused with the anteroventral border of the primary vertebral bodies. With regard to their morphological value, they represent subchordal portions of the basiventrals only. The rudiments of the ribs formed by the intermuscular portions of the caudal sclerotomites are clearly expressed in the thoracic region.

The rudiments of the intercentra of the caudal region (middle and hinder portions) in comparison with the synsacral ones, are large formations filling up the whole space between the successive pairs of intersclerotomic arteries, and extending from the perichordal tube to the caudal artery. The incipient caudal intercentra show a transitional stage between the mesenchymatous and prechondral condition, and exhibit in sagittal section a concentric arrangement of their cells.

EMBRYO OF *Larus Canus*, AGED ABOUT 6 DAYS.—CERVICAL REGION.

The dilated portions of the notochord have increased in length and occupy the whole extension of the vertebral body. The constrictions are confined to the region of the shortened intervertebral bodies (fig. 23, *dil.*, *p.v.b.*, *s.v.b.*, *con.*, *p.iv.b.*). There are very slight secondary indentations at both ends of the vertebral body in the region of the pro- and opistho-spondylous zones (fig. 23, *s.dil.d.*, *p.s.z.*, *os.z.*).

The tissue of the notochord is reduced to a loose network of threads with sparse nuclei disposed in the knots (fig. 23, *nch.*). The thin homogeneous chordal sheath is well discernible. In the region of the intervertebral bodies, it appears slightly thickened and gathered in folds.

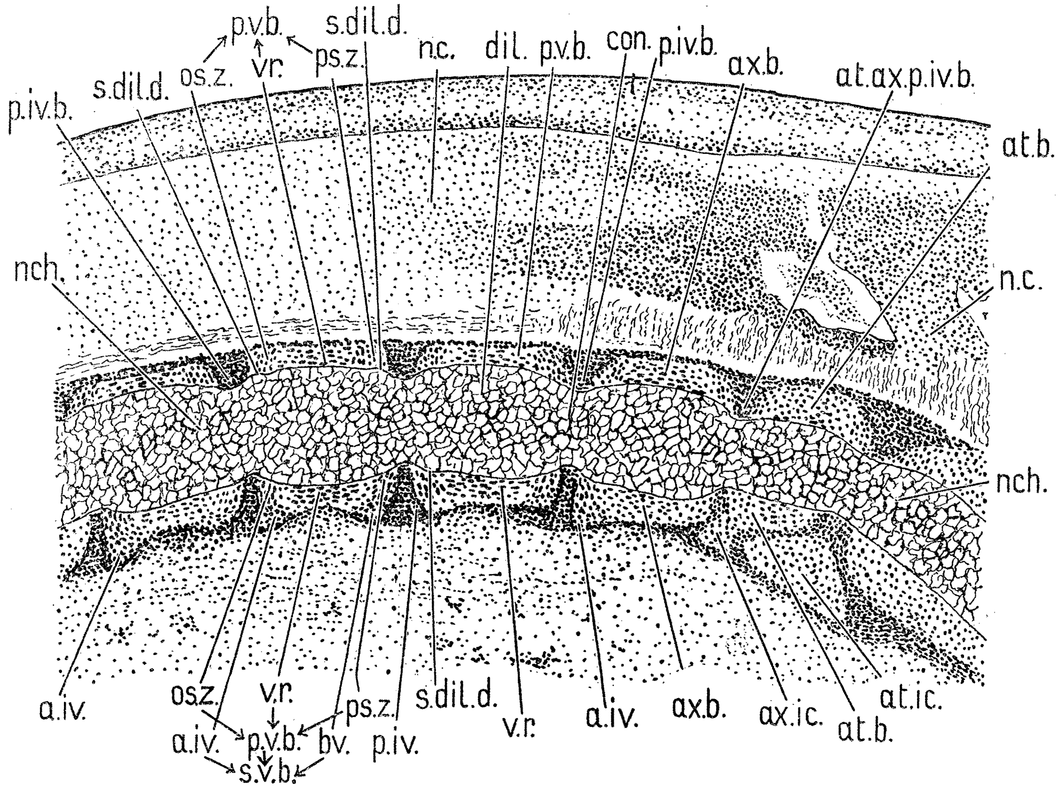


FIG. 23.—Median sagittal section of the cervical region of a 6-day Gull embryo. Anterior end of section to the right. *a.iv.*, anterior portion of the interventral; *at.ax.p.iv.b.*, primary intervertebral body between atlas and axis; *at.b.*, vertebral body of atlas; *at.ic.*, atlas-intercentrum; *ax.b.*, vertebral body of axis; *ax.ic.*, axis-intercentrum; *b.v.*, basiventral; *con.* constricted portion of the notochord; *dil.*, dilated portion of the notochord; *n.c.*, neural cord; *nch.*, notochord; *os.z.*, opisthospondylous zone; *p.iv.*, posterior portion of the interventral; *p.iv.b.*, primary intervertebral body; *ps.z.*, prospondylous zone; *p.v.b.*, primary vertebral body; *s.dil.d.*, secondary dilatation of dilated portion of notochord; *s.v.b.*, secondary vertebral body; *v.r.*, vertebral ring.

The vertebral bodies (fig. 23 and 24, *p.v.b.*, *s.v.b.*) appear in the form of hollow cartilaginous cylinders enclosing the dilated portions of the notochord. The anterior and posterior portions of the vertebral body have become swollen. This is caused by the intense growth of the pro- and opistho-spondylous zones and the bases of the dorsal and ventral arcualia.

The interdorsal is not so distinctly shaped as in 10- and 12-day *Struthio*. It is recognisable as a low bridge composed of well-chondrified tissue, extending from the hinder face of the basal portion of the basidorsal caudalwards and ventralwards (fig. 25, *id.*). The cartilaginous tissue of the interdorsals consists, as in other arcualia (basidorsal, basiventral, etc.) of isodiametrical round and oval nucleated cells and palish blue intercellular substance. As in *Struthio*, the interdorsal contributes to the formation of the dorso-lateral aspect of the vertebral body.

The basiventral divisions of the intercentra, still present in 5-day *Larus*, have undergone atrophy. The right and left latero-ventral portions of the basiventrals have grown round the ventral aspect of the prospondylous zone in replacing the atrophied intercentra. The basiventral division of the anterior end of the secondary vertebral body consists of irregularly disposed isodiametric cells, and thus can be distinguished from the underlying tissue of the prospondylous zone. The cells of the latter are still elongated and arranged tangentially with respect to the notochord.

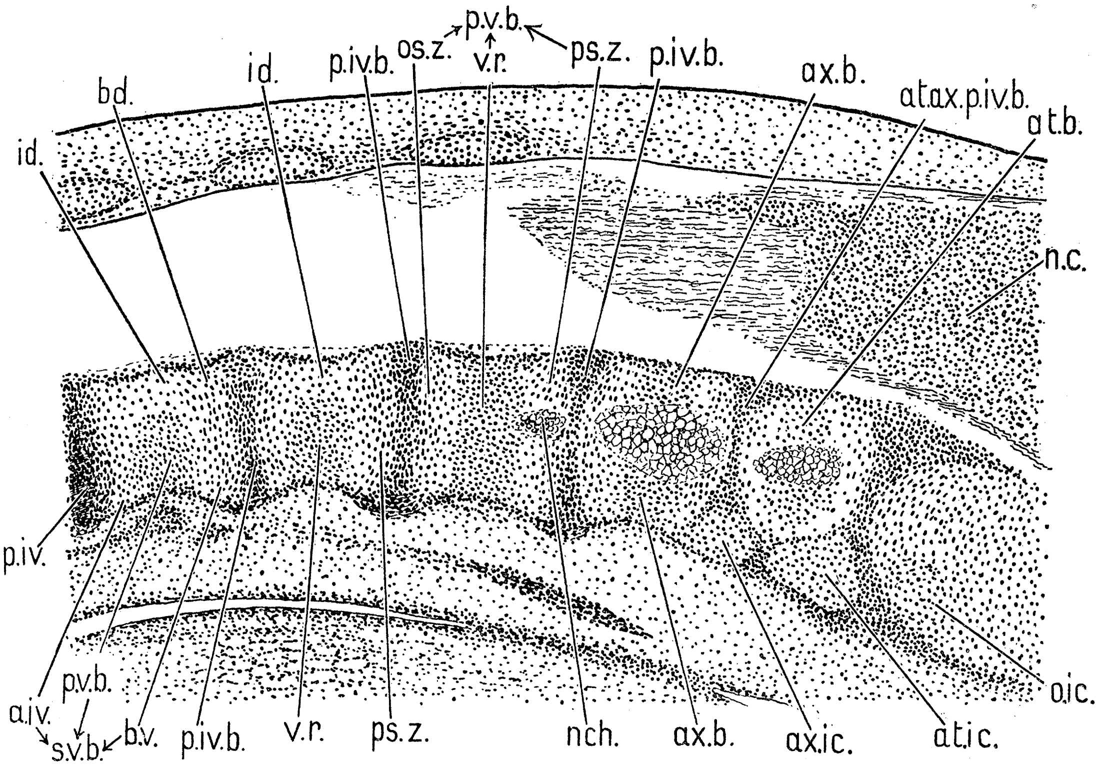


FIG. 24.—Specimen and region as in fig. 23. Lateral sagittal section through the lateral walls of the vertebral bodies. Anterior end of the section to the right. Abbreviations as in fig. 23, except *bd.*, basidorsal; *id.*, interdorsal; *o.ic.*, intercentrum of last occipital vertebra.

The lateral portions of the basiventrals are represented by the parapophyses to which the capitula of the ribs are attached. The parapophysis appears in form of a violet-stained prechondral formation connecting the antero-lateral border of the vertebral body with the partly chondrified (blue-coloured) capitulum of the rib.

The interventrals, which show a uniformly precartilaginous condition in the 5-day *Larus*, have undergone further differentiation. The thin anterior portion fused with the opisthospondylous zone of the primary vertebral body is now fully chondrified, and consists of isodiametric cells with a considerable quantity of brightly blue-stained intercellular substance (figs. 23 and 24, *a.iv.*, *os.z.*, *p.v.b.*, *s.v.b.*). The opisthospondylous zone of the primary vertebral body is likewise chondrified, but its cells are elongated and preserve their former arrangement, which is tangential with respect to the notochordal position.

The caudal bulkier half of the interventrals has lost its prechondral character, and consists of dense red-stained connective tissue, with an insignificant quantity of intercellular substance. This formation represents the external portion of the secondary intervertebral body (fig. 24, *p.iv*).

The external portion of the atlas-body has fused with the axis-body (fig. 25, *at.b.*, *ax.b.*). In sagittal section the atlas-intercentrum exhibits an elongated triangular shape (fig. 23, *at.ic*). Laterally it passes over into the lateral parts of atlas-basiventrals, forming with the latter a half-ring embracing ventrally and laterally the primary vertebral body of atlas, at the same time remaining separated from the latter. The primary vertebral body of the atlas (= odontoid process of axis) also remains separated from the basal portions of the basidorsals, which are fused with the upper ends of the basiventrals.

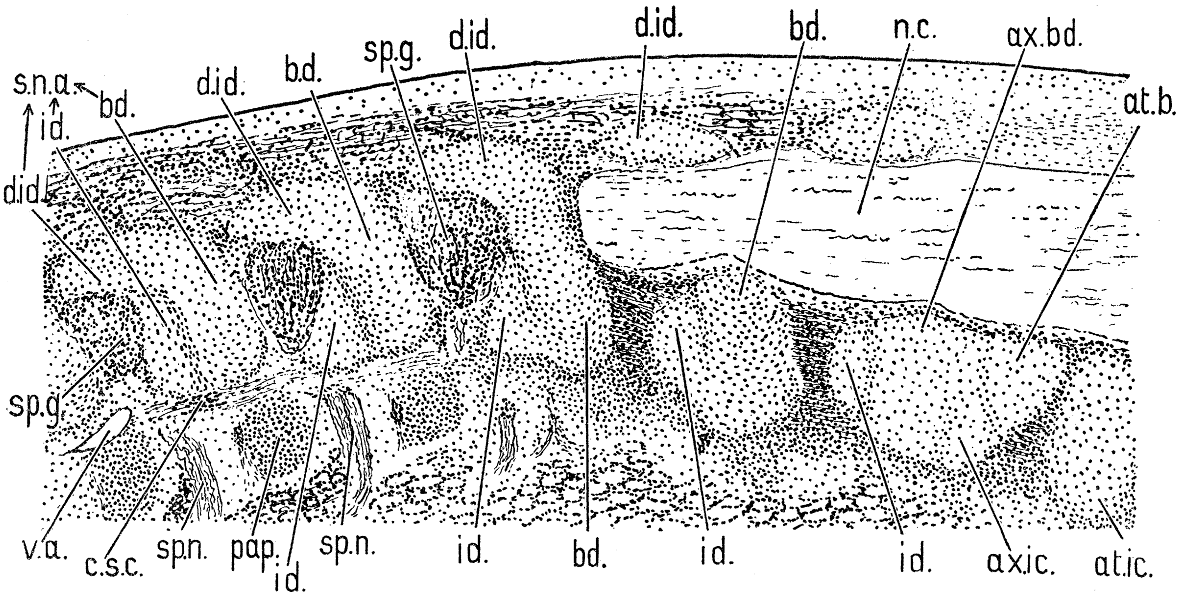


FIG. 25.—Specimen and region as in fig. 23. Lateral sagittal section through the region of the neural arches. Anterior end of section to the right. Abbreviations as in figs. 23 and 24, except *ax.bd.*, axis-basidorsal; *ax.ic.*, axis-intercentrum; *c.s.c.*, collateral sympathetic cord; *d.id.*, dorsal interdorsal; *pap.*, parapophysis; *s.n.a.*, secondary neural arch; *sp.g.*, spinal ganglion; *sp.n.*, spinal nerve; *v.a.*, vertebral artery.

The axis-intercentrum is commencing to fuse with the axis- as well as with the atlas-bodies (figs. 23, 24, 25, *ax.ic.*, *ax.b.*, *at.b.*).

Extracervical Regions.

The secondary dilatations at both ends of the vertebral body are not yet plainly expressed in the extracervical regions. The moniliform differentiation of the notochord in the caudal region is scarcely noticeable. The caudal end of the notochord is completely vacuolised. The formation of the secondary vertebral bodies has reached the hinder half of the tail. The end portions of the secondary vertebral bodies of the caudal region are not yet swollen.

The thoracic intercentra have undergone complete atrophy. The paired intercentra of the synsacral region show beginnings of chondrification, appearing in frontal section as palish blue-coloured areas in the violet-stained tissue of the ventral aspect of the intervertebral body (fig. 26, *ic.*).

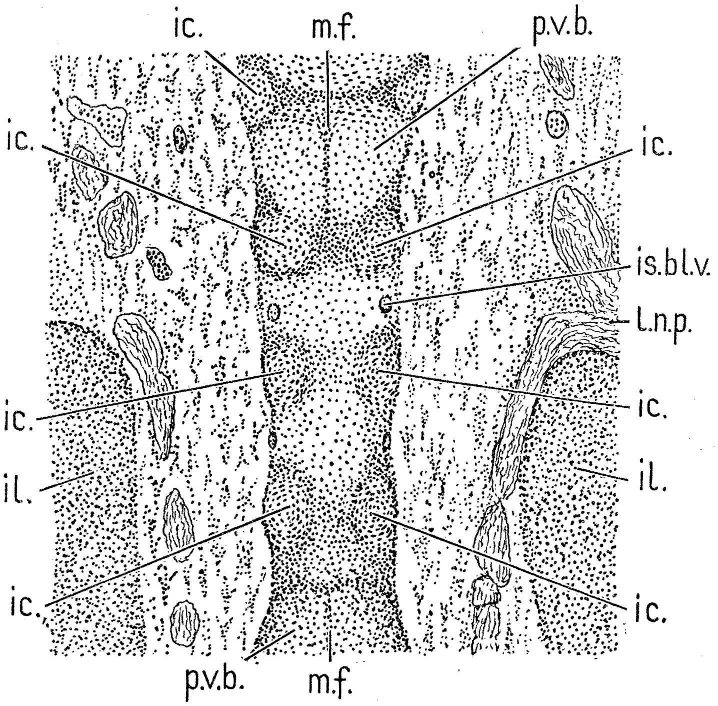


FIG. 26.—Frontal section of the lumbo-sacral region of a 6-day Gull embryo. Owing to the curvature in the sagittal plane the section has passed through the intercentra in its middle portion, while its anterior and posterior ends have passed through the primary vertebral bodies. Anterior end of section above. *i.c.*, intercentrum; *il.* ilium; *is.bl.v.*, intersclerotomic blood vessel; *l.n.p.*, leg nerve plexus; *m.f.*, median fissure dividing the vertebral body into right and left halves; *p.v.b.*, primary vertebral body.

The unpaired intercentra of the caudal region show progressive development, having increased in size. Those of the middle portion of the tail are the largest and they are chondrified.

The vertebral bodies of the synsacral region show a distinctly expressed tendency to split into a right and a left half. This is caused by a sagittal fissure appearing in the dorsal and ventral walls of the vertebral body (fig. 26, *m.f.*, *p.v.b.*).

EMBRYO OF *Larus Canus*, AGED ABOUT 8 DAYS.—CERVICAL REGION.

The slight secondary dilatations at both ends of the vertebral body exhibited by 6-day *Larus* have increased in size. The large middle dilatation occupying in 6-day *Larus* nearly the whole extent of the vertebral body has become considerably shortened (fig. 27, *s.dil.d.*). The constricted portions of the notochord surrounded

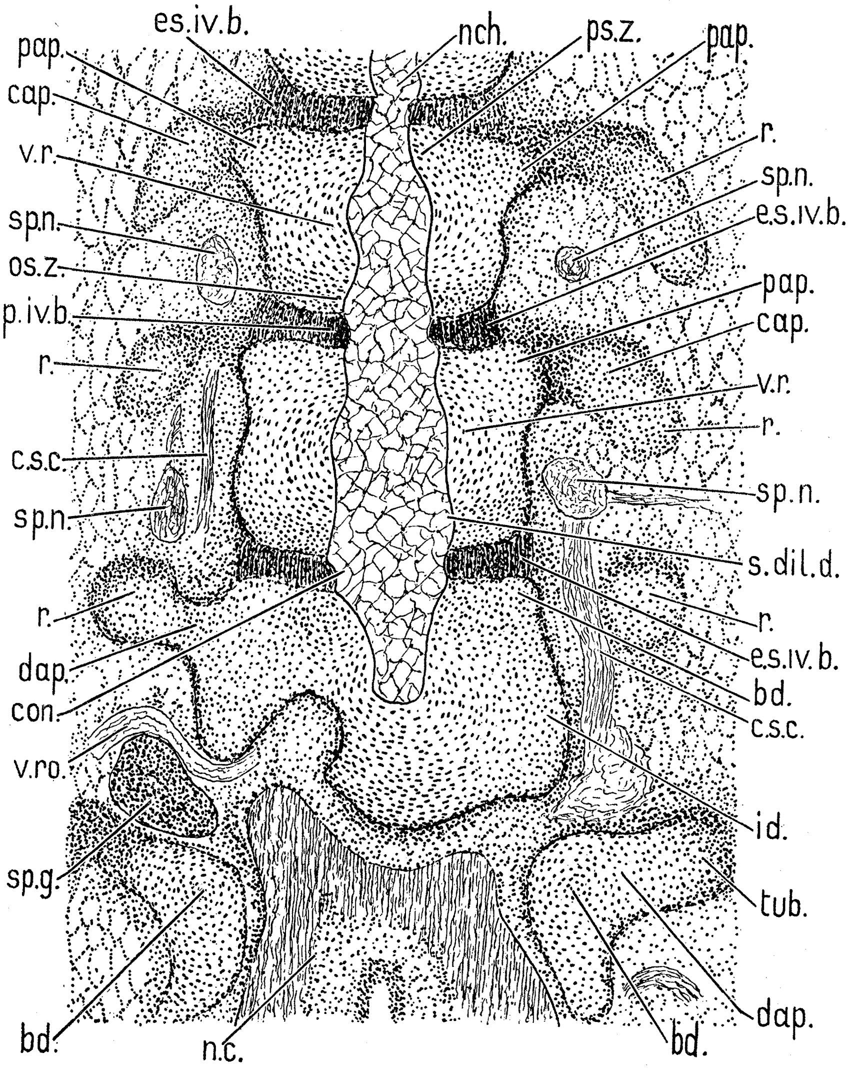


FIG. 27.—Frontal section through the cervical region of an 8-day Gull embryo. The anterior end of the section (above in the figure) is at a lower plane than the posterior end. Anterior end of section above. *bd.*, basidorsal; *cap.*, capitular portion of the rib; *con.*, constricted portion of the notochord; *c.s.c.*, collateral sympathetic cord; *dap.*, diapophysis; *e.s.iv.b.*, external portion of secondary intervertebral body; *id.*, interdorsal; *n.c.*, neural cord; *nch.*, notochord; *os.z.*, opisthospondylous zone; *pap.*, parapophysis; *p.iv.b.*, primary intervertebral body; *ps.z.*, prospondylous zone; *r.*, rib; *s.dil.d.*, secondary dilatation of dilated portion of notochord; *sp.g.*, spinal ganglion; *sp.n.*, spinal nerve; *tub.*, tubercular portion of rib; *v.r.*, vertebral ring; *v.ro.*, ventral (motor) root of spinal nerve.

by the intervertebral bodies have become shorter (fig. 27, *con.*, *p.iv.b.*). The network of the notochordal tissue has become looser. The chordal sheath is well discernible. The dorsal membrana reuniens shows beginnings of chondrification.

The upper portions of the interdorsals, concrescent with the posterior aspect of the middle division of the basidorsals, have expanded in dorsal direction. As a result of this the middle portion of the neural arch has assumed greater craniocaudal dimensions.

The emancipation of the posterior end of the dorsal-interdorsal from the anterior aspect of the next caudally disposed basidorsal, more or less pronounced in 6-day *Larus*, is definitely completed. The dorsal-interdorsals appear in the form of fully chondrified caudally directed hook-like processes of the dorsal ends of the basidorsals, joined by strands of dense connective tissue with the rudimentary anterior zygapophyses* of the neural arch immediately behind them.

The parapophyses and the ribs are fully chondrified. A strip of violet-stained prechondral tissue separates the parapophysis from the capitular and the diapophysis from the tubercular portion of the rib (fig. 27, *pap.*, *r.*).

The cranial face of the vertebral body is in frontal section slightly concave, the caudal slightly convex. The atlas- and axis-bodies have undergone partial fusion. The fusion is more complete in their lateral than in mesial portion. This is caused by the earlier chondrification of the external portion of the secondary intervertebral body disposed between atlas and axis in comparison with its internal portion (= primary intervertebral body).

The axis-intercentrum has coalesced with the bodies of atlas and axis, thus contributing to the fusion of the latter. The ribs of atlas and axis remain in a prechondral condition, whilst all other (cervical) ribs are chondrified.

Extracervical Regions.

The moniliform differentiation of the notochord in the tail region is fully expressed and exhibits essentially the same character as in the cervical region. The segment of the perichordal tube enveloping the utmost end of the tail is not differentiated into vertebral and intervertebral bodies, although it consists of early cartilaginous tissue.

The interdorsals and the dorsal- (supraganglionic) interdorsals of the caudal region are, in comparison with other regions, considerably reduced. The dorsal portions of the basidorsals of the caudal region are directed cranialwards with regard to the vertebral bodies, not caudalwards as in other regions. The chondrification of the dorsal membrana reuniens has proceeded to the anterior portion of the tail.

The intercentra of the synsacral region, showing signs of beginning chondrification in 6-day *Larus*, are now almost all atrophied. Those of the middle portion of the caudal

---

* The anterior zygapophysis appears as an outgrowth of the anterior face of the basidorsals.

region, on the contrary, are well expressed and have undergone chondrification (fig. 28, *ic.*).

The intervertebral bodies of the tail region, in comparison with the vertebral bodies of the same region, are very much bulkier than those of other regions (fig. 28, *p.iv.b.*, *p.v.b.*).

EMBRYO OF *Larus Canus*, AGED ABOUT 10 DAYS.—CERVICAL REGION.

The moniliform differentiation of the notochord exhibits, in comparison with 8-day *Larus*, considerable alterations. This depends upon a very considerable enlargement of the secondary dilatations of the notochord enclosed by both ends of the vertebral body (fig. 29, *s.dil.d.*). At the same time, the primary dilatation comprised in the middle portion of the vertebral body (or, more exactly, in the former vertebral ring) has been greatly reduced. The latter appears in the form of an insignificant dilatation occupying a very short area in the equatorial zone of the vertebral body (fig. 29, *dil.*).

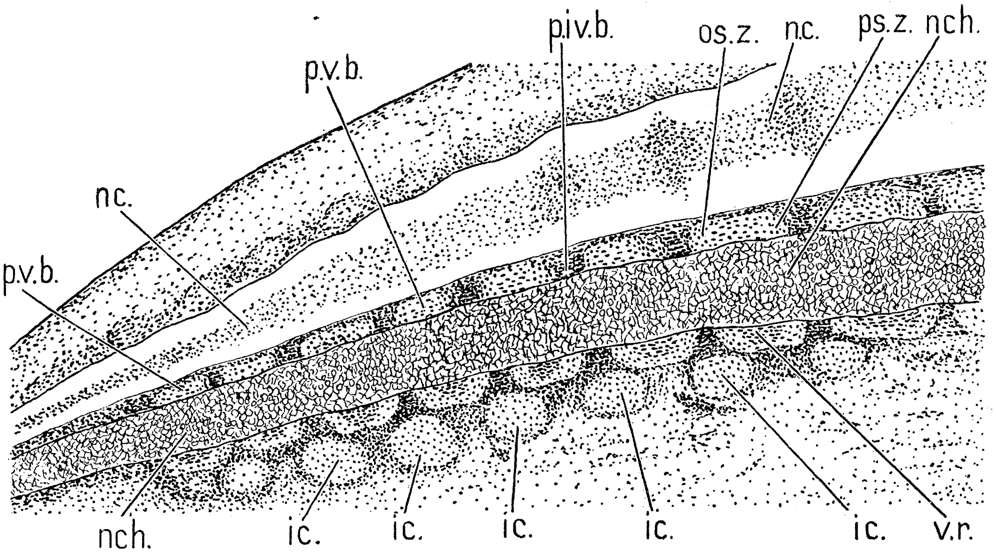


FIG. 28.—Median sagittal section of the middle portion of the tail of an 8-day Gull embryo. Anterior end of section to the right. Abbreviations as in fig. 27 except *ic.*, intercentrum ; *p.v.b.*, primary vertebral body.

The reduction of the primary dilatation of the notochord is caused by the intense growth in thickness of that portion of the vertebral body which corresponds to the vertebral ring (fig. 29, *v.r.*). Its cartilaginous cells have become swollen and the spaces containing them greatly inflated. The chondrified substance enclosing these spaces appears more differentiated and shows, in contrast to the light blue-coloured end portions of the vertebral body and the neural arch, a deep blue stain. The constricted areas of the notochord confined to the regions of the intervertebral bodies have completely disappeared on account of the considerable reduction in length of the intervertebral bodies (fig. 29, *con.*, *s.iv.b.*). A result of this is that the maximally dilated regions of the notochord occupy secondarily an intervertebral or intrasclerotomical position, as was primarily the case in 3- and 4-day *Larus* (fig. 29, *s.dil.d.*).

The intravertebral portions of the notochord are greatly reduced. The notochord, on the whole, reveals an intervertebral development, and the vertebral body as a whole exhibits an amphicœlous character (fig. 46, *nch.*).

The interdorsals have by intense dorsally directed growth reached the ventral aspect of the anterior portion of the dorsal-interdorsals and have fused with the latter. The result of this process is the formation of the definitive or *secondary neural arch*, having a much greater extension in a cranio-caudal direction than the primary one, the proximal portion of which consisted only of basidorsals. The secondary neural arch is thus a compound formation, its cranial portion consisting of basidorsals, the caudal one of interdorsals and dorsal-interdorsals. The caudally directed posterior portion, that is,

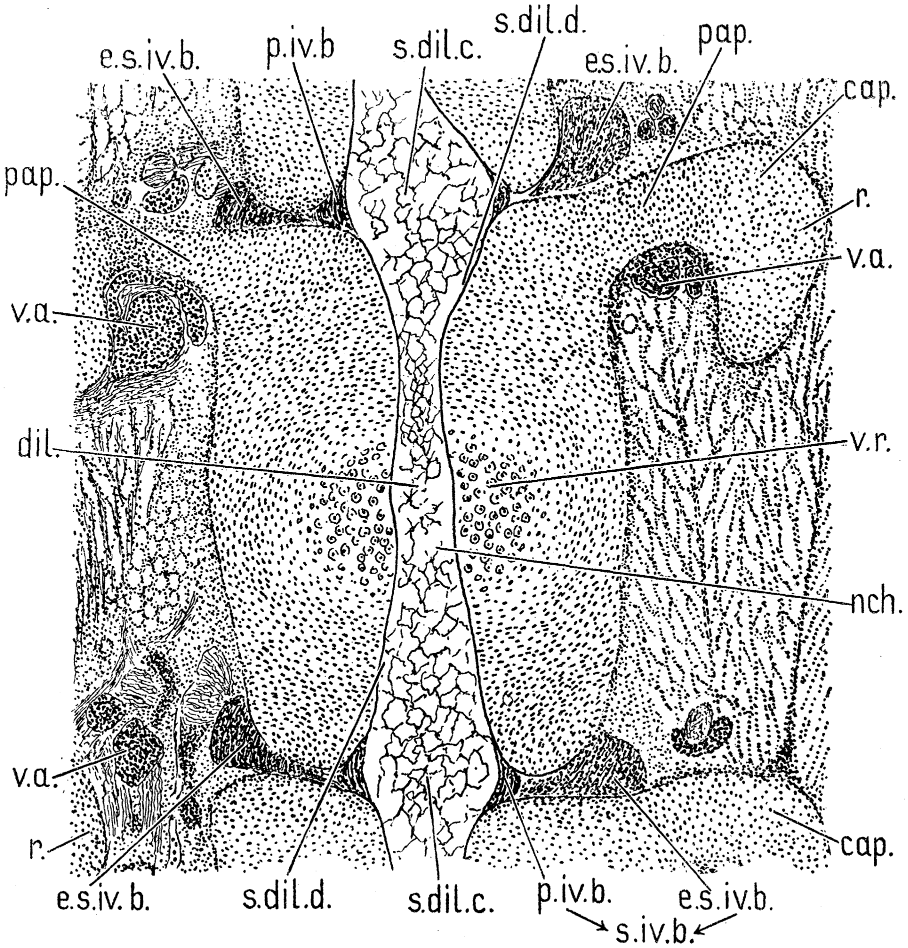


FIG. 29.—Frontal section of a vertebra from the cervical region of a 10-day Gull embryo. The section has passed through the middle portion of the notochord. Anterior end of section above. Abbreviations as in fig. 27, except *s.dil.c.*, secondary dilatation of constricted portion of notochord; *v.a.*, vertebral artery.

the dorsal-interdorsals, gives rise to the posterior zygapophysis. The dorsal membrana reuniens is completely chondrified. The zone of the prechondral tissue separating the cartilaginous diapophysis from the cartilaginous tuberculum of the rib and the cartilaginous parapophysis from the cartilaginous capitulum has undergone complete chondrification (fig. 29, *pap.*, *cap.*, *r.*).

The concavity of the cranial face and the convexity of the caudal one, exhibited by the vertebral body of 8-day *Larus* on frontal section, is here differently developed. It is well expressed in the subchordal portion of the vertebral body and scarcely, or not at all, displayed in the frontal zone of the middle portion of the notochord because of the above-described amphicœlous character of the vertebra in that region.

The primary intervertebral body closely surrounding the notochord shows signs of temporary chondrification (fig. 29, *p.iv.b.*). The external portion of the intervertebral body consists of violet-stained connective tissue composed of spindle-shaped cells without any stainable intercellular substance (fig. 29, *e.s.iv.b.*). The inner portion of the secondary intervertebral body (= primary intervertebral body) probably represents the incipient ligamentum suspensorium, the external portion probably the rudiment of the intervertebral meniscus.

Extracervical Regions.

The primary dilatation of the middle portion of the vertebral body, still expressed in the cervical region, is absent in the thoracic and synsacral regions, its place being occupied by the maximally constricted portion of the notochord. The constrictions are caused, as in the cervical region, by the growth of the walls of the vertebral rings.

The successive vertebral bodies of the synsacral region are fused as a result of the beginning of the chondrification of the intervertebral bodies. The external portion of the secondary vertebral body (intervertebral meniscus) chondrifies first of all, while the internal portion (primary intervertebral body-suspensory ligament) chondrifies somewhat later.

In the synsacral region the dorsal portions of the successive neural arches have become secondarily fused. In frontal section, passing through the dorsal portion of the neural cord, the fused neural arches appear in the form of sinuous bands of cartilage flanking the neural cord on both sides. The lower portions of the arches remain separated.

The neural arches and the vertebral bodies of the 4–5 hindermost caudal vertebræ are fused, forming the common neural arch of the pygostylic vertebræ.

DISCUSSION.

Notochord.

According to FRORIEP (FRORIEP, 1883, p. 190), the first change in the form of the notochord appears in the cervical region of chick at the end of the 5th day of incubation.

This change is represented in the form of constrictions coinciding with the regions of the perichordal rings (der aufgelockerte perichordale Teil des Wirbelbogens), alternating with the intersomitic dilatations belonging to the intravertebral regions of the notochord. FRORIEP (1883, p. 220) corroborates the observation of GEGENBAUR recording the remarkable fact that during the 7th and 8th day of incubation the dilatations of the notochord are arranged intervertebrally and the constrictions intravertebrally. SCHAUINSLAND (1906, p. 546) also gives a text-figure showing that the dorsal (thoracic) vertebræ in 8-day chick bear amphicœlous character.

It is evident that all above-mentioned authors agree in this, that the first deformation of the notochord observed in the chick embryo is represented by intervertebral constrictions and intravertebral dilatations, and that these deformations do not appear earlier than on the 5th day of development. This, in connection with the fact that none of the later investigators known to the writer, who deal with the early development of the chick or of other birds, have described a stage in the evolution of the form of the notochord earlier and different from these just mentioned, renders the observation of intrasclerotomic dilatations and intersclerotomic constrictions on the notochord of the 3- and 4-day *Larus* very interesting.

The fact that the shape of the notochord remains unaltered before the beginning of the formation of the system of the perichordal rings renders it highly probable that the deformation of the notochord is not caused by internal but external forces. The most intimate environmental factor for the developing notochord is, of course, that portion of the series of sclerotomes which closely surrounds the notochord—the perichordal rings or the perichordal tube, consisting of fused perichordal rings. The moniliform differentiation of the notochord during the 3rd and 4th day may be explained by the unequal growth of the different segments of the perichordal tube. It may be assumed that the perichordal rings once formed protect the underlying notochord from compression and diminution of volume. On the contrary, the portions of the notochord enclosed by the rapidly growing mass of mesenchymatous tissue filling up the intervals between successive perichordal rings become constricted.

During the period between the 4th and 5th day of incubation of *Larus*, when the completion of the formation of the perichordal tube and its differentiation into primary vertebral and intervertebral bodies occurs, the zones of growth are displaced from the vertebral to the intervertebral bodies. The result of this is the constriction of the intervertebral portion of the notochord contained in the intervertebral bodies. Such a condition of things in *Larus* lasts till the 8th day of incubation and is fully similar to that described by the above-named authors for the corresponding stages in the chick.* It is of interest to notice that the inversion in the disposition of the dilatations and constrictions of the notochord described by GEGENBAUR and FRORIEP in 8-day chick could not be observed in *Larus* at a corresponding age.

---

* The fact that the chick hatches on the 21st and *Larus canus* on the 23rd day of incubation makes it probable that the corresponding stages of development in both birds are almost simultaneous. This renders the comparison of developmental stages in both birds easier and the conclusion drawn therefrom more certain.

The stage of 3 dilatations and 4 constrictions described by GEGENBAUR and FRORIEP in chick from the 9th and 10th day onwards is also represented in *Larus*, but it begins on the 8th day of incubation—somewhat earlier than might be expected in comparison with the chick. GEGENBAUR and FRORIEP assert that this stage in the case of chick lasts at least till the end of the incubation period of the egg. But *Larus* offers a remarkable deviation from this course of development. Approximately, on the 10th day of incubation the middle large dilatation enclosed by the vertebral body becomes greatly reduced, whilst the smaller dilatations at both ends of the vertebral body grow in dimensions. As a result of this process the vertebral body assumes an amphicœlous shape, the notochord becoming constricted at the waist portion of the vertebral body and dilated at both ends of it. This stage corresponds morphologically but not chronologically to that described by GEGENBAUR and FRORIEP in 7- and 8-day chicks, if we abstract from the above-described slight dilatation in the middle of the constricted waist portion of the vertebral body.

The earliest stage of *Struthio* that was at the disposal of the writer is aged about 7 days, and corresponds chronologically with $4\frac{1}{2}$-day *Larus*. This specimen is of special interest in presenting a transitional stage in the moniliform differentiation of the notochord connecting the earlier stages, which show the dilated intrasclerotomic notochord, to the next following stages, in which we find the constricted intrasclerotomic (= intervertebral) notochord. The specimens of 8, 10, 12 and 14 days display intrasclerotomic (= intervertebral) constrictions and intersclerotomic (= intravertebral) dilatations.

On the 14th day of incubation the ends of the vertebral body of *Struthio* exhibit in the region of the pro- and opistho-spondylous segments very slight indentations, which are homologous with those of 8-day *Larus* and of the chick on and after the 9th day.

It is interesting to see how with advancing age the gradual shortening of the constricted portions of the notochord goes hand in hand with the lengthening of the dilated segments of the latter. The lengthening of the intersclerotomic or intravertebral portions of the notochord is probably causally connected with the development of the vertebral rings and of the pro- and opistho-spondylous segments fused with the latter. The portion of the notochord included in the vertebral body is for a while protected by the latter exactly in the same way as was the intrasclerotomic segment of it by the fully developed perichordal ring.

Perichordal Tube.

FRORIEP (1883) studied the development of the cervical vertebræ in chick. The material of which this portion of the vertebral column is composed is represented, according to FRORIEP, by the mesoblastic tissue surrounding the notochord and filling up all spaces between the notochord on one side and the neural cord, myotomes, spinal ganglia with nerves and aorta on the other. The first indications of the vertebræ appear at the end of the 4th developmental day in the form of metamerically arranged condensations in the continuous connective-tissue matrix surrounding the notochord and the neural cord. These condensations, called by **Froriep** " primitive Wirbelbögen," are best developed in the ventral region of the notochord, pass between the spinal ganglia and in a latero-caudal direction extend into the intermuscular septa separating the successive myotomes.

About the middle of the 5th day the inner, or perichordal, portion of the " primitiver Wirbelbogen," closely applied to the notochord, loses its former dense consistency and is converted into a formation tightly enclosing the notochord and consisting of short longitudinally disposed fibres (kurze Längsfaser). This formation, termed by **Froriep** " perichordaler Faserring " in regard to its spacial relations (intrasclerotomic position) and characteristic structure, corresponds to the perichordal ring in *Larus* and *Struthio.*

The " perichordales Bindegewebe " described by **Froriep** (1883, p. 192) in chick at the close of the 5th developmental day, and consisting of longitudinally arranged cells disposed between successive perichordal rings, is evidently identical with the intersclerotomic thin-walled portions of the perichordal tube in *Larus* and *Struthio.*

In the ventral wall of this " perichordales Bindegewebe " there is laid down, according to **Froriep**, a condensation of cells representing the incipient vertebral body (" die erste Andeutung des Wirbelkörpers "). This unpaired cluster of cells grows into a horseshoe-shaped formation surrounding the notochord from below upwards, and is transformed during the 6th developmental day into the cartilaginous ring surrounding the notochord. This ring, representing the primordium of the cartilaginous vertebral body, soon fuses with the subchordal portion (" subchordale Spange ") of the " primitiver Wirbelbogen." The result of this fusion is a definite vertebral body.

It is of importance to emphasise the considerable difference in the method of formation of the vertebral body in chick as described by **Froriep**, and in *Larus* and *Struthio,* as observed by the present writer. In *Larus* as well as in *Struthio* there is nothing to be seen of an unpaired cartilaginous structure in the ventral wall of the perichordal tube. The incipient nucleus of the vertebral body appears at the very beginning in the form of a ring (vertebral ring), consisting of *sui generis* prechondral tissue composed of radially flattened cells with peculiar elongated nuclei. That the primordium of the vertebral body in birds arises in the form of a ring is also maintained by **Sonies** (1907, p. 417) on the ground of observations made by him in duck, chick and starling.

In the cervical and thoracic (dorsal) regions this ring remains of almost equal thickness, whilst in the pelvic (synsacral) region the lateral portions become thicker than the ventral and dorsal ones, and the whole formation exhibits a tendency to separating into a right and a left half. This tendency also persists during the first period of chondrification. This, in connection with the splitting of the synsacral centra, and to a less degree also of the thoracic and caudal ones by a median sagittal fissure running along their dorsal and ventral walls, has probably given rise to the view that the vertebral centra are laid down in the form of paired (right and left) rudiments, which only secondarily unite round the notochord (**Lillie**, 1919, p. 418).

It seems probable that the formation described by FRORIEP as the unpaired rudiment of the vertebral body represents the ventral portion of the opisthospondylous zone fused with the anterior portion of the interventrals.

The cartilaginous ring developed, according to FRORIEP, from the unpaired rudiment of the vertebral centrum probably represents the whole opisthospondylous zone fused with the vertebral ring disposed in front of it. This portion of the vertebral body arises in *Larus* and *Struthio* as a differentiation of that region of the perichordal tube which comes to lie between the incipient vertebral ring and the primary intervertebral body. It is composed of voluminous cells arranged tangentially with regard to the notochord and forms the hinder end of the primary vertebral body, as the prospondylous ring furnishes the cranial end. The fact that FRORIEP insists on the development of the vertebral body from an unpaired ventral cluster of cells may be explained by the observation made by the present writer in *Larus* and *Struthio*, that the ventral wall of the opisthospondylous zone at its first origin is somewhat thicker than the corresponding wall of the prospondylous zone.

The pro- and opistho-spondylous zones have no phylogenetic significance. They represent adaptive structures formed in order to meet the mechanical requirements existing between successive vertebræ. This explains the weaker development of the ventral portion of the prospondylous zone in comparison with the much-better-expressed ventral portion of the opisthospondylous zone. The function of the ventral portion of the prospondylous zone is performed by the basiventrals. With the gradual reduction of the basiventrals, the ventral and ventro-lateral portions of the prospondylous zone attain their full development. The absence or rudimentary condition of the pro- and opistho-spondylous zones of the incipient atlas-centrum can be interpreted by the same principle.

SCHAUINSLAND (1906, p. 544, fig. 318) in his comprehensive account on the development of the vertebral column gives an illustration of a frontal section of *Puffinus cuneatus* embryos, showing clearly the presence of the perichordal mesenchymatous tube in this bird. The tube is also thinner intersclerotomically and thicker intrasclerotomically, but it does not yet show any sign of differentiation into the primary vertebral and intervertebral bodies. It exhibits conditions roughly corresponding to the conditions represented by 4-day *Larus* and 7-day *Struthio*.

Giving a detailed description of the development of the vertebral column in *Hatteria*, and referring to the work of FRORIEP on the development of cervical vertebræ in chick, he expresses the hope that in future more detailed investigations in birds will prove that the evolution of the vertebral column in birds in general follows the same plan as in reptiles. It is therefore of interest to compare the development of the vertebral column in birds with the evolution of that organ in *Hatteria* as investigated by SCHAUINSLAND (1900), especially with regard to the formation to the perichordal tube and its derivatives.

The formation of the perichordal tube (perichordale Zellschicht of SCHAUINSLAND, 1906, p. 525) follows almost the same lines in *Hatteria* as in *Larus*. As in *Larus* the material from which the tube is formed is a derivative of those portions of the sclerotomites which are flanking the notochord on both sides. As in *Larus* the perichordal mesenchymatous layer is at its very first formation segmented, the segments (perichordal rings) coinciding with the sclerotomes.

As in *Larus* and *Struthio* the segments (perichordal rings) fuse completely into a continuous tube, leaving but very little trace of their original segmentation. In close resemblance to *Struthio* and *Larus* the middle zone of perichordal rings of which the perichordal tube is formed increases in thickness and becomes histologically different from the neighbouring portions of the tube.

The middle zone of that thickened portion of the " perichordale Zellschicht " (perichordal tube) represents, as in *Larus* and *Struthio*, the incipient intervertebral body (= primärer Zwischenwirbelkörper). The remaining portions of the perichordal tube represents the primary vertebral bodies (primärer Wirbelkörpers). The zones of the perichordal tube lying immediately cranially and caudally from the incipient intervertebral body are differentiated in *Struthio* and *Larus* into the pro- and opistho-spondylous zones of the primary vertebral body.

That formations homologous with the pro- and opistho-spondylous zones of *Larus* and *Struthio* were noticed by SCHAUINSLAND also in the case of *Hatteria* is evident from this passage : " Die mittleren Teile der wulstförmigen Verdickungen der Perichordalschicht in der Gegend der Intervertebralspalte der Sklerotome,—die sich vorn und hinten daran (*i.e.*, primary intervertebral body) anschliessen (*i.e.*, zones of the thickened portions of the " perichordale Zellschicht ")—gehören bereits dem Ende des vorhergehenden und dem Anfang des nachfolgenden primären Wirbelkörpers an—stellen die späteren intervertebralen Partien der Wirbelsäule, die Zwischenwirbelscheiben (Menisci, Fibrocartilagines intervertebrales) dar " (SCHAUINSLAND, 1906, p. 525).

Agreeing in almost all points concerning the genesis and the differentiation of the perichordal tube with *Hatteria*, *Larus* and *Struthio* differ only in one aspect from the latter. SCHAUINSLAND asserts that the primary intervertebral body (primitiver Zwischenwirbelkörper) in *Hatteria* represents the incipient intervertebral disk (Zwischenwirbelscheibe, meniscus or fibrocartilago intervertebralis). In *Larus* and *Struthio* the primitive intervertebral body, being a derivative of the perichordal tube, probably gives rise to the innermost portion of the intervertebral apparatus—the ligamentum suspensorium of JÄGER. The intervertebral disk developed mainly in the lateral aspect of the intervertebral apparatus is most probably derived from the external layer of the secondary intervertebral body formed of the posterolateral portion of the cranial sclerotomite.

The chondrification of the primary vertebral body in *Hatteria* (SCHAUINSLAND, 1906, p. 530) commences after the chondrification of the neural arch. The process starts on both ends of the vertebral body at the base of the neural arch, proceeding hence towards the middle of the primary vertebral body. In *Larus* and *Struthio* the chondrification of the vertebral ring composing the middle portion of the primary vertebral body takes place quite independently of the chondrification of the neural arch. The processes of chondrification of the vertebral body and of the neural arch in *Larus* and *Struthio* are effected almost simultaneously. The chondrification of the pro- and opistho-spondylous zones forming the anterior and posterior ends of the primary vertebral body begins slightly later than that of the vertebral ring and primary neural arch (basidorsals).

The membranous vertebral ring in *Larus* and especially in *Struthio* for some time after its formation shows an anterior and posterior half as an indication of its genesis from the caudal portion of one perichordal ring and the cranial portion of the next caudally disposed perichordal ring.

Sclerotomes.

As was mentioned above, REMAK was the discoverer (in chick) of the resegmentation of the developing vertebral column. He introduced the idea of the differentiation of the sclerotomes and of the formation of the definitive vertebra by means of recombination of the sclerotomal halves.

The formation of the sclerotomes in *Larus* is effected exactly in the same way as was described by REMAK in chick. The inner core of the somite (REMAK's Urwirbelkern), concrescent with the ventral wall of the latter, begins to increase in size and fuses with the mesial as well as with the anterior and posterior walls of the somite, producing the so-called " Wirbelkernmasse " of REMAK. It is evident that the " Wirbelkernmasse " represents the main bulk of the sclerotome which is separated from the dermato-myotome (REMAK's tafelförmige Rückenwand) by the myocœle.

Attention must be drawn to the presence of the homogeneous membrane (sclerotheca) covering the sclerotomes of *Larus* in their earliest stages of development and not yet described in birds.

The origin and the fate of the intersclerotomic fissure in *Larus* and *Struthio* is the same as was described by REMAK in chick. The intersclerotomic fissures were described by REMAK (1851, p. 42) as " schmale spaltenförmige Lücken " between successive sclerotomes. Those fissures arise as clefts dividing the dorsal portions of the originally undivided masses of mesoderm into the somites. The intersclerotomic fissures become completely obliterated at the end of the 4th day in *Larus* and during the 5th day in chick and the 7th in *Struthio*.

The intrasclerotomic fissure was discovered by v. EBNER (1888, 1892) in the embryos of *Tropidonotus*, and its presence was proved by SCHAUINSLAND also in birds (1903). The intrasclerotomic fissures are laid down as transverse clefts dividing the originally compact sclerotomes into cranial and caudal halves (sclerotomites). About the extension of the intrasclerotomic fissure in birds in its different stages of development very little is known. This fissure in *Larus* seems to occupy a larger area at its earlier stages of development than later on, being then chiefly confined to the horizontal level of the notochord, the lower portion of the neural cord and spinal ganglia. It is stated by EBNER that in *Tropidonotus* the intrasclerotomic fissure is clearest in the horizontal zone of the spinal ganglia, whilst more dorsally it disappears. In *Tropidonotus* it extends ventrally to the level of the notochord. In reptiles the intrasclerotomic fissure appears at the first origin to be in communication with the myocœle. In birds the communication between the myocœle and the intrasclerotomic fissure is a secondary phenomenon, according to the observations of SCHULTZE (1896). In *Larus* even the secondary communication between the myocœle and the intrasclerotomic fissure does not occur because of the early differentiation of the myotome. In *Larus* and in *Struthio* the intrasclerotomic fissure, as was mentioned above, undergoes complete obliteration, and the final intervertebral (synovial) cavity separating successive vertebræ in the adult represents a new formation entirely independent of this fissure.

FRORIEP discusses and rejects the view of REMAK as to the resegmentation of the incipient vertebral column in chick. The primordia of the vertebral bodies in chick, according to FRORIEP, arise, as was already alluded to, in the form of the so-called "primitive Wirbelbögen." The position of the latter with regard to the spinal ganglia and the interprotovertebral (intersomitic) blood vessels proves decisively that the "primitive Wirbelbögen" of FRORIEP are truly intrametameric formations. The comparison of these formations with the structural relations found in *Larus* and *Struthio* shows that they are homologous with the mesial (axial) portions of the sclerotomes in the form, as the latter appear in *Larus* and *Struthio* immediately after the obliteration of the intrasclerotomic fissure. Further proof for the assumption that the "primitiver Wirbelbogen" of FRORIEP represents that portion of the sclerotomes which contains the obliterated intrasclerotomic fissure and consists in its chordal portion of the caudal sclerotomite fused with the posterior portion of the cranial sclerotomite, is furnished by its spatial relation to the perichordal ring. The perichordal ring of FRORIEP arises as a differentiation of the innermost perichordal portion of his "primitiver Wirbelbogen." The perichordal ring of *Larus* and *Struthio* also becomes enclosed, after its formation, between the sclerotome and the corresponding intrasclerotomic portion of the notochord.

Chondrification of the Sclerotomal Derivatives.

GEGENBAUR did not draw any precise limit between the membranous (prechondral) and cartilaginous stage in the development of the vertebral column in birds. This is clear from the assertion that the vertebral bodies in birds arise ". . . aus einer die Chorda umgebenden Knorpelmasse." If GEGENBAUR by the term "Knorpelmasse" understood not the definitive cartilaginous tissue, but a kind of prechondral tissue intermediate between the connective tissue and cartilage, the writer must completely agree with this view of a continuous "Knorpelmasse" enclosing the notochord and representing the matrix from which the future vertebral and intervertebral bodies are formed. In 4- and 5-day *Larus* and in 8- to 10-day *Struthio*, there is clearly expressed a phase in the development of the vertebral column, where the perichordal tube fused with the cranial and caudal sclerotomites is represented by a continuous mass of prechondral tissue surrounding the notochord. In this continuous tube of prechondral tissue there develop in 5–6-day *Larus* and 10–12-day *Struthio* the definitive vertebral as well as intervertebral bodies.

A more precise distinction between the membranous and the cartilaginous stages of the developing vertebral column in chick was given by FRORIEP (1883).

His " primitiver Wirbelbogen " giving off the mesenchymatous elements for the formation of the perichordal ring from its inner aspect is already a prechondral formation. At the end of the 5th day the " primitiver Wirbelbogen " undergoes complete chondrification, giving rise to the " Bogenknorpel." The latter consists of two (right and left) symmetrically disposed pieces connected subchordally by an unpaired cartilaginous clasp. The latter was called by FRORIEP " hypochordale Spange " and homologised with the ventral half of the atlas ring (RATHKE'S " ventrales Schlussstück "). At the end of the 6th day the Bogenknorpel commences to fuse with the cartilaginous vertebral body (Körperknorpel) meanwhile formed. The " Bogenknorpel " leaning on the " Körperknorpel " by their bases represent the neural arches, and during the 7th and 8th day undergo further growth, whilst the " subchordale Spange " gradually decreases in size and disappears. The dorsal ends of the right and left limb of the neural arches meet and coalesce in a transverse direction, whereas in a longitudinal direction they grow caudalwards over the spinal ganglia, giving rise to the posterior zygapophyses. The bases of the neural arches produce lateral outgrowths representing the transverse processes.

The " Bogenknorpel " of FRORIEP in their earlier stage, when they have not yet developed the rudiments of the transverse processes, correspond exactly to the basidorsals of *Larus* and *Struthio*. Both structures are formed of the same material, namely, of the caudal halves of the sclerotomes disposed between successive spinal ganglia and spinal nerve roots. Their bases fuse with the prospondylous zone of the differentiated perichordal tube, thus contributing to the formation of the external layer of the cranial end of the secondary vertebral body. As to the material and mode of formation of the posterior articular processes, the writer cannot agree with FRORIEP. The posterior zygapophyses arise, according to FRORIEP, as caudally directed outgrowths of the upper ends of the neural arches. In *Larus* and *Struthio* the posterior zygapophyses do not represent derivations of the upper ends of the incipient basidorsals, but are formed *in loco* from the supraganglionic portion of the cranial halves of the next caudally disposed sclerotomes. The primordia of the posterior zygapophyses (= dorsal-interdorsals) thus do not belong genetically to the caudal halves of the sclerotomes, but are derivatives of the cranial halves of the latter.

Similarly, a portion of the subganglionic division of the cranial sclerotomite (= interdorsal) partakes in the formation both of the neural arch as well as of the dorso-lateral portion of the secondary vertebral body.

SCHAUINSLAND'S supposition that the neural arches in birds are not products of a single metamere but belong like the vertebral bodies to two different sclerotomes, which he endeavoured to prove by fragmentary embryological evidence, can thus be confirmed by a continuous series of embryological facts. The principle of resegmentation thus holds true not only in the case of vertebral bodies but also in the vertebral arches.

Observations made on *Larus* and *Struthio* prove that the nature of the " subchordale Spange " of FRORIEP is not so elementary as was described by him for the cervical region of the vertebral column in chick. The material from which is formed the " subchordale Spange " of FRORIEP is furnished by the ventral portion of the hoop-like " primitiver Wirbelbögen," or in other terms by the subchordal portion of the sclerotomes. The latter in *Larus* and *Struthio* consists of an anterior portion derived from the cranial sclerotomite (= interventral) and a posterior portion produced by the caudal sclerotomite (= basiventral). Despite the obliteration of the intrasclerotomic fissure separating in earlier stages both components of the subchordal sclerotome, they, nevertheless, can be distinguished by their different structure and stain. At the same time each subchordal sclerotomal component, the cranial as well as the caudal, becomes differentiated during the 4th and 5th day in *Larus* and the 7th and 8th day in *Struthio* into a median swollen unpaired portion and a paired symmetrically disposed lateral portion. The differentiation described is at its highest at the middle of the membranous (prechondral) stage. The transverse groove between the cranial and the caudal components of the subchordal division of the sclerotome (" subchordale Spange " of FRORIEP), clearly expressed during the 4th day, becomes less obvious during the 5th day and disappears.

The fate of the different portions of the " subchordale Spange " of FRORIEP in *Larus* and in *Struthio* is different. The swollen median unpaired portions of the fused inter- and basi-ventrals (= intercentra) never reach the cartilaginous stage, except those of atlas, axis, and in *Larus* of some caudal vertebræ. After having attained a certain degree of development in their prechondral condition, they undergo gradual involution and disappear. Support of the statement, that in the cervical region of birds only the atlas- and axis-intercentra (= ventral-most unpaired portions of the inter- + basiventrals) undergo chondrification, is also furnished by the observation made by SONIES (1907, p. 411) on the development of the atlas and axis and other cervical intercentra in the duck.

The caudal divisions of the lateral portions of the " subchordale Spange " of FRORIEP, representing the basiventrals of *Larus* and *Struthio*, fuse with the prospondylous zone of the differentiated perichordal tube. The basiventrals thus contribute to the formation of the external layer of the ventro-lateral and ventral halves of the anterior end of the vertebral body, as the bases of the basidorsals do with regard to the dorsal half of the latter. The lateral divisions of the basiventrals also give rise to the parapophyses or ventro-lateral prominences of the anterior end of the secondary vertebral body to which the capitula of the ribs are attached.

The cranial divisions of the lateral portions of FRORIEP'S " subchordale Spange " represent the precartilaginous interventrals of *Struthio* and *Larus*. The anterior division of the interventrals contribute to the formation of the caudal end of the secondary vertebral body in covering the ventro-lateral and ventral portions of the opisthospondylous zone. The caudal division of the interventral furnishes the external portion of the secondary intervertebral body as material from which is probably formed the intervertebral meniscus (= ligament).

It must be emphasised that the anterior division of the interventrals is very inconspicuous. It is represented by a thin layer of cartilage covering the lower half of the caudal end of the primary vertebral body. The main bulk of the interventrals is represented by their posterior portion forming, as was stated above, the external portion of the secondary vertebral body and the anterior portion of the corresponding intercentrum.

The chondrification of the prechondral vertebræ of *Hatteria* commences, according to SCHAUINSLAND (1906, p. 529), with the formation of the dorsal arcualia and thus precedes the chondrification of the primary vertebral body (primitiver Wirbelkörper). In *Hatteria* there appear in the caudal region simultaneously two pairs of incipient dorsal arcualia (Bogenanlagen). The anterior pair is more conspicuous and is formed at the dorso-lateral aspect of the anterior end of the primary vertebral body from the caudal portion of the sclerotome. The posterior pair of dorsal arcualia is smaller and is formed from the cranial half of the sclerotome.

In *Struthio* and *Larus* the basidorsals as regards their position and origin correspond exactly to the anterior pair of arches in *Hatteria*. But there is a difference in the chronology of the chondrification. In *Larus* and *Struthio* the chondrification of the basidorsals occur, as has already been mentioned, almost simultaneously with that of the vertebral ring, whilst in *Hatteria* the chondrification of the dorsal arcualia precedes that of the vertebral ring.*

The posterior pair of dorsal arcualia in *Struthio*, and to a certain degree also in *Larus*, does not arise in the form of an undivided structure, as in *Hatteria*. In the former the elements of the posterior cartilaginous dorsal arcualia arise in a matrix belonging to the cranial half of the sclerotome, but in two topographically independent regions. The upper portion of the posterior half of the neural arch or the dorsal-interdorsal arises from the portion of the cranial sclerotomite which lies partly dorso-laterally, partly dorsally, from the spinal ganglion. This portion of the caudal aspect of the neural arch gives rise to the posterior zygapophysis of the definitive vertebra.

The lower portion of the posterior dorsal arcualia or the interdorsals in *Struthio* appears in the form of a conspicuous prechondral formation, extending from the posterior aspect of the lower portion of the basidorsals slantingly backwards and downwards and covering the dorso-lateral face of the vertebral ring, which represents the middle portion of the primary vertebral body. It is thus evident that in *Struthio* the basal portion of the inter-

---

* In the chick, according to JÄGER (1924, p. 22), the chondrification of the neural arch is effected later than that of the vertebral body. The same is stated by SONIES regarding the duck embryo (1907, p. 411).

dorsals contribute in a very efficient manner to the formation of the dorso-lateral region of the secondary vertebral body.

The incipient interdorsals of *Larus* are not so clearly shaped as in *Struthio*, but they can nevertheless be traced in the corresponding region of the vertebral body as ridges of prechondral, or cartilaginous, tissue covering the same region of the primary vertebral body as in *Struthio*.

A comparison of the text-fig. 301, p. 527, given by SCHAUINSLAND in O. HERTWIG'S "Handbuch der Entwicklungsgeschichte der Wirbeltiere," with the fig. 16 in the descriptive part of this paper once more proves the identity of the interdorsals in *Hatteria* and in *Struthio*. There is, however, a difference as regards the relative time of chondrification of the dorsal arcualia in *Hatteria* and in *Struthio*. In *Hatteria*, as was already alluded to, the basidorsals and interdorsals are chondrified simultaneously, whilst in Struthio the chondrification of the interdorsals and of the dorsal-interdorsals is somewhat delayed as compared with that of the basidorsals.

The basal portion of the basidorsals in *Larus* and *Struthio* coalesce with the dorso-lateral face of the prospondylous zone of the primary vertebral body. The basidorsals thus contribute to the formation of the lateral aspect of the cranial end of the secondary vertebral body. The basal portions of both pairs of dorsal arcualia (basi- + inter-dorsals) on each side undergo fusion, in *Larus* earlier than in *Struthio*, and together contribute to the formation of the dorso-lateral part of the definitive cartilaginous vertebral body. Exactly the same occurs, according to SCHAUINSLAND, in *Hatteria*, when the "Bogenbasen" fuse and cover the dorso-lateral aspect of the "primärer Wirbelkörper" and thus give rise to the formation of the "sekundärer Wirbelkörper" of GOETTE and SCHAUINSLAND.

In *Hatteria* the middle and dorsal portions of the basi- and inter-dorsals also undergo fusion and furnish the neural arch, although there remains between them a slight superficial groove, even after the ossification of the arch, indicating the double origin of the latter. In *Struthio* and *Larus* the fusion of the basidorsals with the dorsal-interdorsals and interdorsals is much more complete, even in the cartilaginous stage.

The similarity in the evolution of the vertebra in *Hatteria* and birds is accentuated by the fact that, as in *Larus* and *Struthio*, there is also in *Hatteria* a stage in the development of the neural arches where the upper ends of the successive neural arches become coalescent, so that the whole system of these arches on each side of the neural cord appears in the form of a series of vault-like formations enclosing the spinal ganglia. The single difference is that in *Hatteria* the temporary coalescence of the upper ends of the neural arches occurs in the cartilaginous stage, whilst in *Larus* and *Struthio* it comes about in the late prechondral stage. In *Larus* and *Struthio*, as in *Hatteria*, the temporary union of the neural arches is very soon broken, the zones of union being transformed into the incipient articular faces and ligaments between the posterior and anterior zygapophyses of successive vertebræ.

SCHAUINSLAND (1906, p. 532) identifies the intercentra with the basiventrals, and the latter with the "hypochordalen Spangen" of FRORIEP. From the above discussion of the morphological value of FRORIEP's "subchordale Spange" it follows that the latter does not represent *pure* basiventrals, but also contains the posterior portion of the interventrals. It is then very likely that the intercentra* of *Hatteria* do not represent derivatives of caudal sclerotomal halves only, as SCHAUINSLAND asserts, but in their production there participate also the posterior portions of the cranial sclerotomal halves, which at the level of the notochord and subchordally give rise to the interventrals. From this point of view the intervertebral position of the intercentra in *Hatteria* is not a secondary but primary phenomenon.

In *Larus* and *Struthio* true cartilaginous intercentra occur only in the atlas and axis, and in the case of *Larus* also in the caudal region.† But incipient intercentra, *i.e.*, intercentra in their mesenchymatous and prechondral stages in *Larus* and *Struthio*, occur in all regions of the vertebral column. They are laid down in the subchordal portion of the sclerotomes and originally comprise elements of cranial as well as of caudal sclerotomites. In the cervical and in the anterior thoracic regions, where the differentiation of the interventrals from the cranial sclerotomites and of the basiventrals from the caudal sclerotomites is effected early, the intercentra are formed from the ventral-most portion of the basiventrals fused with the corresponding portion of the interventrals. In the pelvic and caudal regions, where the formation of the basi- and inter-ventrals from the corresponding sclerotomites is retarded, the intercentra are formed directly from the ventral ends of the sclerotomites resulting from the fusion of the subchordal portions of the cranial sclerotomites with the corresponding caudal ones.

From the above it is evident that each incipient intercentrum is primarily an intervertebral (= intrasclerotomic) formation in contrast to *Hatteria*, where its intervertebral position is described by SCHAUINSLAND, as already mentioned, as a secondary one.

Whilst in *Hatteria* the intercentra represent permanent formations, the intercentra of the cervical (except atlas and axis), anterior thoracic and pelvic regions in *Struthio* and *Larus* and the caudal ones of *Struthio* are temporary formations. These intercentra, after having reached a more or less advanced prechondral stage, undergo complete atrophy. In the pelvic region of *Larus* they show signs of chondrification before the beginnings of their reduction. In the cervical and thoracic regions the process of reduction of the intercentra commences at their anterior or interventral portion, hence proceeding to the posterior or basiventral division. The interventral portion of the intercentra disappears comparatively earlier in *Larus* than in *Struthio*.

GADOW and ABBOTT (1895, pp. 185–219) deny the existence of the intrasclerotomic fissures altogether. They explain the resegmentation of the vertebral column and the

---

* The intercentra are known under very different names : chevron bones, wedge bones, os en chevron, Zwischenwirbelbeine, Gabelknochen. They occur among the Amniota in reptiles, birds and in the tail of some mammals (Marsupialia, Edentata, Cetacea). They are also described in the lumbar region of Erinaceus, Talpa (LULL, 1922, p. 314) and Atherura (BEDDARD, 1902, p. 24).

† That, of the cervical intercentra, only those of atlas and axis undergo chondrification has been proved by SONIES (1907, p. 411) for Gallus and Anas, and by JÄGER (1924, p. 3) for Gallus.

occurrence of more than one pair of dorsal and ventral arcualia in one metamere by the fact that the protovertebral plates curve like an S and overlap. Each protovertebra consists of a myotome and two sclerotomes, of which one is ventral and one dorsal. The dorsal half of a protovertebra is bent medianwards and caudalwards, the ventral half lateralwards and cranialwards. The reconstruction of a series of sections through the tail of a 7-mm. embryo of *Scyllium catulus* shows that: "(1) The dorsal half of sclerotome 2 grows downwards and comes to lie behind the ventral half of sclerotome 1. (2) The ventral half of sclerotome 2 lies in front and below the dorsal half of sclerotome 3. (3) The formation of a physiological unit is effected by the combination and fusion of the unequally numbered sclerotomic halves, so that the dorsal half lies behind and above the ventral half." "If A and B mean two successive sclerotomes, a and b their dorsal, α and β their respective ventral halves, then the new scleromere is composed of $b+\alpha$, and not of $\frac{A+B}{2}$, because $b+\alpha$ is the same as $\frac{\text{B dorsal}}{2}+\frac{\text{A ventral}}{2}$." From this is evident that a vertebra (scleromere) is formed by the combination of alternating dorsal and ventral halves of sclerotomes. The ventral half of sclerotome A is termed the *basiventral* by GADOW, the dorsal half of sclerotome B the *basidorsal*.

In forms where four pairs of arcualia occur in each segment, the second dorsal and ventral pairs are formed as outgrowths from the basalia (basiventralia and basidorsalia). Each pair of basiventrals extends with its apices above the notochord and gives rise to pairs of condensations of cells representing the interdorsals. Similarly, the rudiments of the basidorsals grow down and below the notochord found the primordia of the interventrals.

These conclusions, drawn from the observations made on *Selachians* and interpreting the resegmentation of the notochord and the occurrence of four pairs of arcualia, are applicable according to GADOW and ABBOTT also in the case of other vertebrates.

Observations made on *Larus* and *Struthio* show that GADOW'S and ABBOTT'S theory cannot be applied to the ontogenetic evolution of the vertebral column in birds. The intrasclerotomic (= intervertebral) fissure, the existence of which the above authors deny, is distinctly developed in both birds. The dorso-ventral axis of the somites does not exhibit any S-shaped curving, but is straight and disposed vertically with regard to the long body axis. The basidorsals and basiventrals of a vertebra do not arise from two successive sclerotomes, but belong to the same sclerotome. The basidorsals are formed from the dorsal (= neural), the basiventrals from the ventral (= chordal), portion of the caudal half of a sclerotome. Similarly the system of the interdorsals and the interventrals of the same vertebra do not belong genetically to two different sclerotomes, but are both derived from the cranial half of the same sclerotome. The supra- as well as the infra-ganglionic* portions of the interdorsals represent derivatives of the dorsal (= neural) division of the cranial sclerotomite, the ventral division of the latter giving rise to the interventrals.

---

* *I.e.*, spinal ganglion.

On the basis of the above-mentioned investigation of Froriep (1883), Gadow (1897, pp. 43–45 and pp. 49–51) tried to show that the vertebral body of a bird, with regard to its ontogeny, belongs to the " gastrocentral " type. If the centrum of a gastrocentral vertebra consists mainly of the interventrals, a bird-vertebra does not belong to this group. Observations made on *Struthio* and *Larus* show that the main bulk of the lateral divisions of the interventrals gives rise to the external portion of the secondary intervertebral body. Only the thinner cranial portion of the interventrals covering the opisthospondylous zone takes part in the formation of the vertebral centrum. The share of the interventrals in the building up of a vertebral centrum in birds is even less conspicuous than that of the lateral portions of the basiventrals. A comparison in *Struthio* and *Larus* of the dorsal and ventral arcualia, in regard to the degree of their participation in the formation of the secondary vertebral body, shows that the dorsal arcualia surpass the ventral ones. From the comparison it also follows that the share of the interdorsals in the building up of a definite cartilaginous vertebral centrum is greater than the part played in this regard by the basidorsals.

Arriving at the end of our discussion of the evolution of the vertebral centrum, it is of great interest once more to emphasise the fact that the cartilaginous centra of *Larus* and *Struthio* consist of two genetically and structurally different portions. The inner portion or the " primary vertebral body " immediately surrounding the remainder of the notochord consists of more or less flattened concentrically disposed cells and develops from the perichordal tube. The outer portion is represented by the bases of the dorsal and the ventral arcualia which consist of irregularly disposed isodiametric cells and arise from the secondary sclerotomes.

The histological difference between the inner and outer portions of the cartilaginous vertebral body in chick embryo was noticed by Gegenbaur (1862, p. 55) and also described by Schwark (1873, p. 570). Froriep denied the existence of a difference between the " chordaler Wirbelkörper " (= primary vertebral body) and the " Belegungsmasse " (= bases of arcualia) established by Hasse and Schwark (1873, pp. 23–28). According to Lillie, (1919, p. 418), " the distinction between the primary vertebral body formed by chondrification within the perichordal sheath and a secondary vertebral body formed by the basal ends of the arches surrounding the primary is not a clear one in the case of the chick."

Intervertebral Body.

The intervertebral discs, according to Remak, are formed in the shape of dark strips of tissue dividing the inner portion (" Blastem ") of the sclerotome (primitiver Wirbel) into two halves. At the same time, Remak, on the ground of observations made on later stages, assumed that the intervertebral disc belongs genetically to the caudal half of the " primitiver Wirbel " (sclerotome) and consequently to the anterior end of the definitive vertebral body.

This statement of Remak was accepted by later authors.

It can be shown in *Larus*, as well as in *Struthio*, that the material from which is formed the intervertebral body is derived from two sources. The inner portion of the intervertebral body (= primary intervertebral body) is formed as a differentiation of the middle zone of the thickened portion of the perichordal tube (Blastem). The outer, or lateral, portion of the definitive or secondary intervertebral body originates from the latero-posterior portion of the interventrals.

It seems to the writer that REMAK has described, in 5-day chick, only the inner portion of the incipient secondary intervertebral body (or in other terms, the primary intervertebral body) arising, as was alluded to above, from the middle zone of the intrasclerotomic portion of his " Blastem " (perichordal tube). In later stages, he observed, on the contrary, only the formation of the outer portion of the secondary intervertebral body: " Die Anlagen der Zwischenwirbelscheiben gehen, wie der weitere Verlauf lehrt, aus dem Schwanzteile des primitiven Wirbelkörpers, oder, was dasselbe ist, aus dem Kopfteile des sekundären Wirbelkörpers hervor."

REMAK supports his statement about the origin of the outer portion of the definitive intervertebral body by the observation that the intervertebral disc (Zwischenwirbelkörper) adheres to the anterior portion of the secondary vertebral body when we try to isolate it. But this fact iself is no valid argument in favour of its origin from the anterior aspect of the secondary vertebral body. Careful study of the development of the postero-lateral portion of the chordal division of the cranial sclerotomites (interventrals) in 12- and 14-day *Struthio*, and 5- and 6-day *Larus*, shows distinctly that this formation gives rise to the outer layer of the secondary intervertebral body from which is probably formed the intervertebral disc or ligament.

JÄGER (1859) showed that the intervertebral apparatus in birds consists of a central and a lateral portion. The central portion, or the suspensory ligament, according to JÄGER, arises " . . . aus einer die Chorda dorsalis umhüllenden Substanzbrücke zwischen zwei Wirbelkörpern " (p. 554). The lateral portion, or intervertebral ligament (= meniscus) " entwickelt sich wahrscheinlich als Abhebung von der oberen Fläche des Wirbelkörpers " (p. 554). It is highly probable that the " Substanzbrücke " enclosing the notochord and furnishing material for the formation of the suspensory ligament represents, in the case of *Larus* and *Struthio*, the middle zone of the thickened portion of the perichordal tube (respectively perichordal ring). As to the origin of the intervertebral ligaments (= menisci) JÄGER maintains the above-discussed view of REMAK.

Rib.

FRORIEP (1883, p. 204–205) describes the incipient cervical rib in a 6-day chick as a prechondral plate disposed laterally from the " hypochordale Spange," and connected with the latter. The dorsal portion of the incipient rib is concrescent with the neural arch. In 9-day chick (p. 210) the rudiment of the rib has undergone chondrification and completely fused by its dorsal portion with the neural arch by its ventral division with the vertebral body. From this it is evident: that according to FRORIEP, the cervical rib, in its membranous stage, is a derivative of the ventral (= chordal) portion of the sclerotome. As each sclerotome consists of a cranial and a caudal half, it remains undecided whether the cervical rib of a chick arises from the cranial or the caudal sclerotomite, or from both together. FRORIEP did not decide the question whether the rib has an independent centre of chondrification in regard to the vertebral body or not. GADOW (1897, pp. 49 and 50) regards the ribs of all vertebrata as lateral or pleural outgrowths of the basiventrals. The tuberculum and its attachment is, according to GADOW, a secondary acquisition, but it is not clear whether the tubercular portion of the rib takes its origin from the ventral half of a sclerotome or from the dorsal half of the sclerotome next behind it. GEGENBAUR (1898, p. 275) regards the ribs of Amniota in general as formations " . . . die ihr Material von dem die unteren Bogen herstellenden Material beziehen." It is thus probable that, according to GEGENBAUR, a bird's rib takes its origin from the ventral (= chordal) portion of the caudal sclerotome.

SONIES (1907, p. 414), describes the incipient cervical and thoracic ribs in duck embryo as *prima origine* independent of the corresponding vertebræ formations. They chondrify almost synchronously with the vertebral bodies and arches. With further development, the vertebral ends of the ribs are shifted close to the vertebral bodies and bifurcate. The dorsal end of the rib enters into relation with the diapophysis—the ventral—with the cranial border of the vertebral body.

According to LILLIE (1919, p. 424) the primary costal process is an outgrowth of the membranous centrum, corresponding in position to the capitulum of the definitive rib. The tuberculum arises from the primary costal process, while the latter is still in the membranous condition and grows dorsalwards to unite with the neural arch in the region of the transverse process. The centres of chondrification of the cervical and thoracic ribs " . . . arise a short distance laterally to the vertebral centres, with which they are connected only by the intervening membrane."

In *Struthio* and *Larus*, the membranous rib is a derivative of the lateral (muscular) portion of the ventral (= chordal) division of the caudal sclerotomite. In 5-day *Larus* and 8-day *Struthio*, this rib-producing portion of the caudal sclerotomite becomes partly separated by the incipient vertebral artery and collateral sympathetic cord from the mesial portion of the ventral (= chordal) division of the caudal sclerotomite, the latter giving rise to the basiventrals. The proximal portion of a prechondral cervical and thoracic rib in *Larus* and *Struthio* becomes differentiated into a ventral and dorsal limb.

The ventral limb is continuous with the dorso-lateral portion of the basiventrals, which represent the parapophysis. This ventral limb of the vertebral portion of the incipient rib represents its capitular division. The dorsal limb attached to the diapophysis (ventro-lateral outgrowth of the basidorsals), and represents the tubercular portion of the prechondral rib.

It follows from the above that in *Larus* and *Struthio* the prechondral capitulum and the tuberculum of a rib arise simultaneously from a common rudiment, in contrast to the chick, where, according to LILLIE, the tubercular portion represents a secondary excrescence of the capitular as the primary portion of the rib.

The chondrification of the capitular and tubercular portions of cervical and thoracic ribs comes about quite independently as compared with the chondrification of the parapophyseal portion of the basiventrals and the diapophyseal portion of the basidorsals. The chondrification commences simultaneously in capitulum and tuberculum, and hence proceeds distally. The chondrification of the ribs is effected somewhat later than of the corresponding vertebræ.

Ontogenetical Stages and Phylogeny.

The analysis of the data furnished by the ontogenetic evolution of the vertebral column in birds allows us to distinguish four main stages in its membranous and cartilaginous conditions. As *Principia Classificationis* are taken the evolution of the form of the notochord, the absence or presence of the perichordal and vertebral rings, of the intrasclerotomic fissure and of the intercentra. The two earlier ones of these stages—the *pre- and proto-spondylous* stages—represent the evolutionary steps of the vertebral column in its mesenchymatous and early prechondral condition. The two later ones—the *meso- and meta-spondylous* stages—display the developmental phases of the vertebral column in its late-prechondral and cartilaginous condition.

1. *Prespondylous Stage.*—The notochord persists in its original cylindrical shape. The perichordal rings are not yet formed or are presented by single mesenchymatous cells detached from the primary sclerotomes and surrounding the notochord. The sclerotomes are divided by the intrasclerotomic (= intervertebral) fissures into the cranial and caudal sclerotomites.

2. *Protospondylous Stage.*—The notochord exhibits intrasclerotomic dilatations and intersclerotomic constrictions. The intrasclerotomic dilated segments of the notochord are enclosed at the beginning by mesenchymatous perichordal rings, which later on fuse into the perichordal tube. Each perichordal ring is flanked on both sides by a pair of sclerotomites derived from the same sclerotome. Each sclerotome becomes divided into a dorsal (= neural) and ventral (= chordal) half. The ventral (= subchordal) ends of the cranial and caudal components of a sclerotome undergo fusion in a longitudinal direction, and in the regions other than synsacral also in transverse direction.

3. *Mesospondylous Stage.*—The notochord displays intersclerotomic (= intravertebral) dilatations and intrasclerotomic (= intervertebral) constrictions. The vertebral column consists of vertebral bodies (centra + arches), intercentra, intervertebral bodies. The inner portion of the centrum enclosing the dilated division of the notochord represents the primary vertebral body (= prospondylous zone + vertebral ring + opisthospondylous zone). The outer portion of the centrum is represented by the bases of the arcualia dorsalia (basi- + inter-dorsals) and ventralia (basi- + inter-ventrals). The intercentra, consisting of subchordally fused ventral-most portions of the inter- and basiventrals, are present in all regions of the vertebral column. The intervertebral apparatus

consists of the primary intervertebral body flanked laterally by the caudal portion of the interventrals.

4. *Metaspondylous Stage.*—Secondary dilatations appear at both ends of the centra. Whilst these secondary dilatations increase in size, the main dilatation placed in the middle portion of the centra becomes reduced. As a result of this, the notochord becomes intervertebrally dilated and intravertebrally constricted, and the vertebral body assumes an amphicœlous character. At the end of this stage the vertebral body loses its amphicœlus character, the notochord becomes pinched in and atrophies intervertebrally.* The centra and neural arches become considerably elongated and undergo final chondrification. The cervical (except atlas and axis) dorsal and synsacral intercentra are atrophied. The atlas, axis, and caudal intercentra (if the latter persist—as in *Larus*) undergo chondrification. The intervertebral apparatus shows signs of differentiation into the primordia of the suspensory and intervertebral ligaments.

A comparison of the above-established ontogenetic stages with the vertebræ of different fossil and recent lower forms leads to the following suggestions: The prespondylous stage can be paralleled with the embolomerous type of vertebra occurring in fossil and recent Amioidei and in some Carboniferous Stegocephalia. In the prespondylous stage as well as in the first period of the protospondylous, the vertebral centra bear a decidedly arcogenous character and consist of a distinctly expressed cranial and caudal half. The lower (= chordal) portion of the caudal sclerotomites is comparable with the anterior arch—bearing half of an embolomerous vertebra. The portion of the cranial sclerotomite disposed below the spinal ganglion can be compared with the caudal half of an embolomerous centrum.

The protospondylous stage, where each sclerotome is differentiated into dorsal (= neural) and ventral (= chordal) divisions, which give rise to dorsal and ventral prechondral arcualia, presents a parallel to the more primitive forms of rhachitomous vertebra, which consists of 2 pairs of dorsal and 2 pairs of ventral arcualia (Archegosaurus). The membranous basidorsals with the dorsal-interdorsals correspond to the neural arch, whilst the basiventrals can to a certain extent be compared with the hypocentra. The interdorsals find their equivalents in the dorsal pleurocentra and the interventrals in the ventral ones. It is probable that in fossil forms with temnospondylous vertebræ a layer of pliable tissue corresponding to the perichordal rings (resp. tube) was interposed between the osseous arcualia and the notochord.

The mesospondylous stage, remarkable for the presence of the intercentra developed from the subchordal portions of the sclerotomes, can be compared with the type of vertebræ represented by certain Cotylosauria and Rhynchocephalia. The temporary and constant intercentra of *Larus* and *Struthio* are very likely homologous with the intercentra and chevron bones of the above-mentioned reptiles. This supposition is supported by the intervertebral and subchordal position of the intercentra and chevrons both in

---

* This occurs in 12-day *Larus*, a stage not described in the descriptive part of this paper and which shows the first beginnings of ossification of the centra.

reptiles and birds. That, on the other hand, the homologies between the components of the vertebral centra in *Hatteria* and in birds are very considerable has already been sufficiently pointed out.

The metaspondylous stage, characterised by the absence of the trunk intercentra and by the amphicœlous form of the centra, vividly recalls the vertebræ of some Mesozoic toothed birds, which are amphicœlous and devoid of intercentra.

SUMMARY.

(1) The newly formed somites and those which show the very first beginnings of the differentiation into dermato-myotomes and sclerotomes are surrounded by a very thin homogeneous membrane, which may be termed *somatheca* or *sclerotheca* (fig. 30, *A*).

(2) Each sclerotome is divided by a narrow transverse cleft, the *intrasclerotomic* (= *intervertebral*) *fissure*, passing through the whole dorso-ventral extent of the sclerotome, into a cranial and a caudal half—*the cranial and the caudal sclerotomite* (fig. 30 *A*, A^1, *B*, B^1).

(3) The intrasclerotomic fissure (= sclerocœle) appears in sclerotomes whilst they are still surrounded by the sclerotheca (fig. 30, *A*).

(4) The rupture and dissolution of the sclerotheca starts partly in the angle between the notochord and the aorta, partly on the anterior and posterior faces of the sclerotomes.

(5) From the ventro-mesial aspect of the sclerotomes, through the points of rupture of the sclerotheca, emigrate loose mesenchymatous cells, covering first the ventral and lateral and later on also the dorsal face of the notochord. In the caudal region the production of the mesenchymatous perichordal tissue commences before the formation of the intrasclerotomic fissure.

(6) The notochord, which primarily has a uniform diameter throughout, undergoes moniliform differentiation. Faint dilatations are confined to the middle portion of the sclerotomes, while the constrictions occur in the intersclerotomic regions (fig. 30, *A*, A^1, *B*, B^1).

(7) As the production of the mesenchymatous cells is most intense in the middle portion of the sclerotome divided by the intrasclerotomic fissure, the dilated divisions of the notochord confined to this portion of the sclerotome become enclosed by ring-like formations consisting of mesenchyme—the *perichordal rings*. The sclerotomes (sclerotomites) which have not yet produced the perichordal rings, represent the *primary sclerotomes* and *sclerotomites*. After the formation of the perichordal rings the sclerotomes (resp. sclerotomites) represent the *secondary sclerotomes* and *sclerotomites* (fig. 30, *A* and *B*).

(8) Owing to the obliteration of the intrasclerotomic (= intervertebral) fissure at the level of the dorsal half of the neural cord, as well as in the subchordal portions of the sclerotomes, the dorso-ventral extension of the intrasclerotomic fissure becomes confined solely to the portion of the sclerotomes flanking laterally the notochord and the ventral half of the neural cord (fig. 30, C^1).

(9) Each sclerotome becomes differentiated into a dorsal curved portion situated above the median horizontal prominence of the myotome and a ventral straight portion. The curved or *neural* portion extends round the latero-ventral portion of the neural cord. The lower straight or *chordal* portion stretches ventrally between the mesenchymatous perichordal ring and the ventral half of the corresponding myotome.

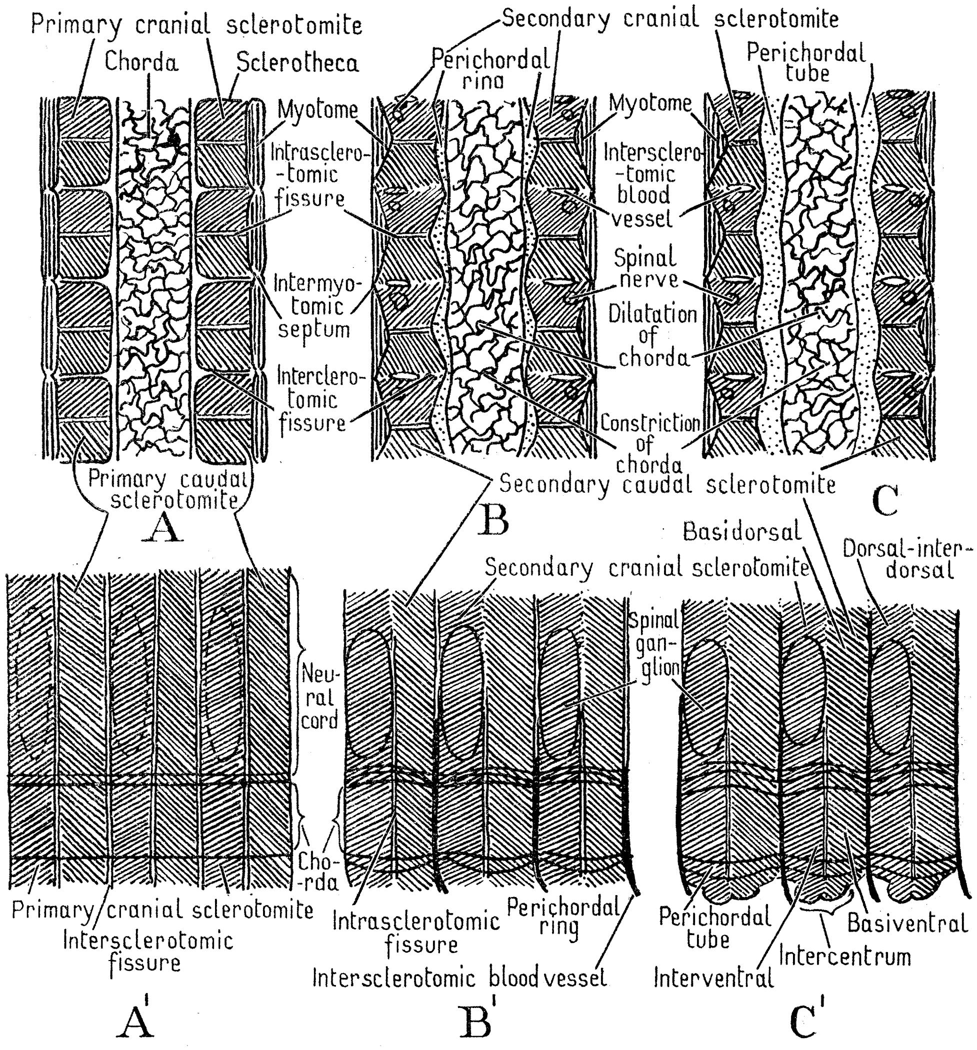


FIG. 30.—Diagrams illustrating successive stages in evolution of cervical vertebræ in birds. *A—C*, frontal sections through middle of notochord; A^1—C^1, superimposed sagittal and parasagittal sections.

(10) The successive perichordal rings fuse into a moniliform tube enclosing the notochord —the *perichordal tube* (fig. 30, *C* and C^1).

(11) The prechondral *basiventrals** develop from the chordal and subchordal divisions of the subchordally fused pairs of caudal sclerotomites, and are laid down in the form of arches bounding the ventral and ventro-lateral faces of the caudal halves of former perichordal rings (fig. 30, C^1).

---

* In cervical and thoracic regions.

(12) The prechondral *basidorsals* arise from the neural divisions of the caudal sclerotomites, situated between successive spinal ganglia, surrounding the neural cord on both sides and passing laterally into the intermyotomic septa. The basal portions of the basiventrals representing their most advanced parts, lean against the dorsolateral faces of the caudal halves of former perichordal rings (fig. 30, C^1).

(13) The prechondral *interventrals** arise from the chordal and subchordal divisions of the subchordally fused pairs of cranial sclerotomites. They are laid down in the form of arches bounding the ventral and ventro-lateral faces of the cranial halves of former perichordal rings. The interventrals consist of a less advanced form of perichordal tissue than the corresponding basiventrals and basal portions of basidorsals (fig. 30, C^1).

(14) The prechondral *intercentra* (= hypocentra) represent derivatives of the ventral-most portion of the basiventrals fused with the ventral-most portion of the interventrals. In the cervical and thoracic regions the interventral portion of an intercentrum is smaller and consists of less advanced prechondral tissue than its basiventral portion (fig. 30, C^1).

In the synsacral and in caudal regions where the differentiation of the basi- and inter-ventrals from corresponding sclerotomites is retarded, the intercentra are formed directly from the ventral ends of the sclerotomes, resulting from the fusion of the cranial sclerotomites with the corresponding caudal ones.

(15) The intercentra of the cervical, dorsal and caudal regions are laid down as unpaired formations. The intercentra of the synsacral region arise in the form of paired formations.

(16) In the synsacral and caudal regions the part played by the cranial component of an intercentrum is the same as that of the caudal one.

(17) The dorsal (= supraganglionic) portion of the prechondral interdorsal arises in the form of an independent cell-condensation in the dorsal (= supraganglionic) end of the neural division of the cranial sclerotomite. The incipient *dorsal-interdorsal* very early becomes fused with the upper end of the next cranially situated basidorsal (fig. 30, C^1).

(18) The inter- and intra-sclerotomic fissures undergo complete obliteration. The obliteration of the intersclerotomic fissure precedes that of the intrasclerotomic.

(19) The earlier intrasclerotomic position of the dilated portions of the notochord is gradually changed into an intersclerotomic one. On the contrary, the former intersclerotomic localisation of the constricted areas of the notochord becomes by degrees intrasclerotomic (fig. 31, D, D^1).

(20) The perichordal tube becomes differentiated into two kinds of structurally different segments alternating regularly with each other. One system of these segments—the *vertebral rings*—is disposed intersclerotomically (= intravertebrally) and surrounds the dilated portions of the notochord. The vertebral rings represent the nuclei of the *vertebral centra*—at least the internal and waist-like portions of the latter. As the intersclerotomic portions of the perichordal tube arise by the fusion of the ends of successive perichordal rings, each vertebral ring must be looked upon at its

earliest stage as a compound formation. Its anterior half is formed by the caudal end of one perichordal ring, whilst the posterior half is developed from the cranial end of the perichordal ring immediately behind (fig. 31, *D*, *D*¹).

(21) The other system of segments formed from the perichordal tube—*the interstitial bodies*—occupy an intrasclerotomic (= intervertebral) position and enclose the constricted portions of the notochord (fig. 31, *D*, *D*¹).

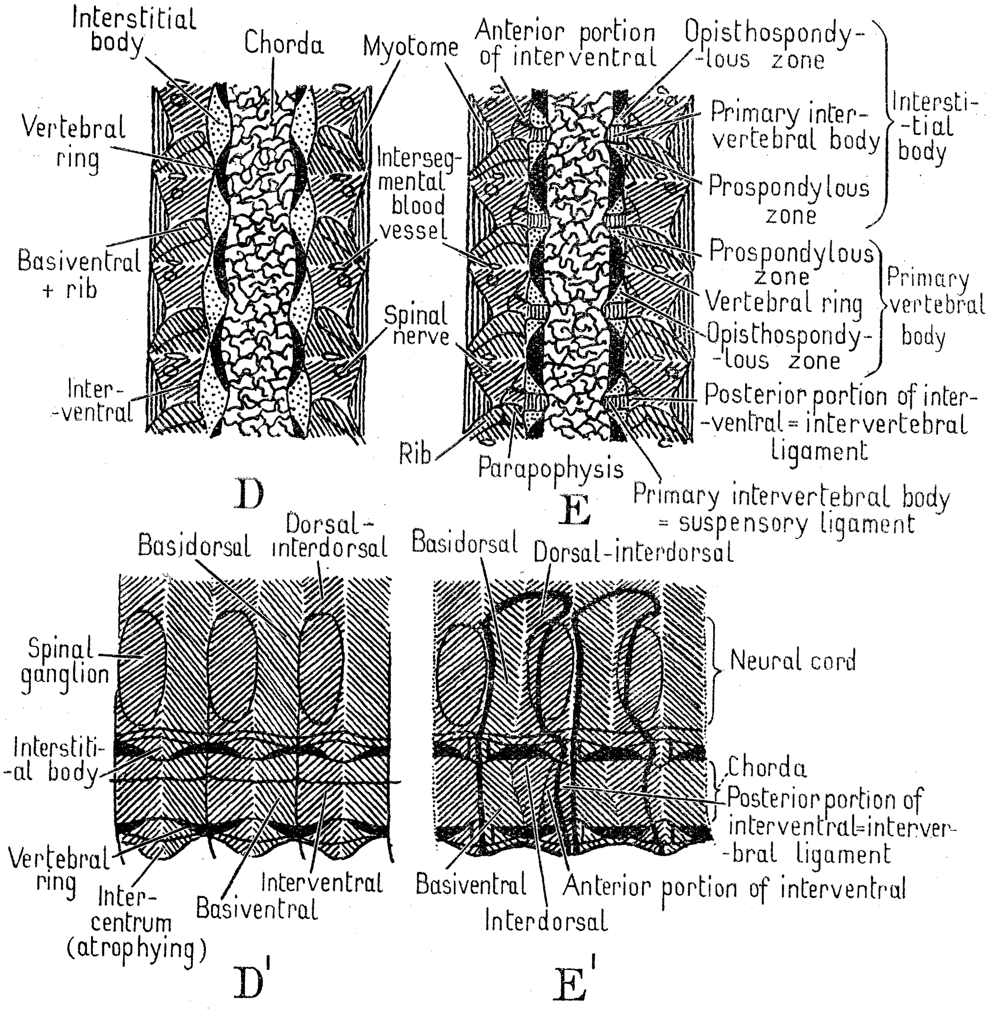


FIG. 31.—Diagrams in continuation of fig. 30. *D*, *E*, frontal sections through middle of notochord; D^1, E^1, superimposed sagittal and parasagittal sections.

(22) Besides the connection of the dorsal-interdorsals with the next cranially disposed basidorsals, the dorsal-interdorsals become temporarily fused with the dorsal ends of the next caudally located basidorsals. In this stage the dorsal arcualia on each side of the notochord look like a system of curved pillars (= basidorsals) disposed between the spinal ganglia and dorsally connected by a system of vaults (= dorsal-interdorsals) roofing over the spinal ganglia.

(23) The interstitial bodies become differentiated into three different portions: a cranial, a middle and a caudal one. The middle portion corresponds exactly to the middle zone of the former perichordal rings and consists of closely set spindle-shaped cells directed transversely with but traces of stainable intercellular substance. This portion represents the *primary intervertebral body* (fig. 31, *E*).

(24) Cranially and caudally from the incipient primary intervertebral body are differentiated areas of advanced prechondral tissue consisting of cells directed tangentially with regard to the notochord and with abundant intercellular substance. These divisions of the interstitial bodies are closely applied to the tapering ends of the adjacent vertebral rings and become concrescent with the latter. These formations may be called the *pro- and opistho-spondylous segments* of the primary vertebral body. The vertebral ring with the prospondylous zone at its cranial and the opisthospondylous zone at its caudal end represents the *primary vertebral body* (fig. 31, *E*).

(25) The primary vertebral bodies of the synsacral region show during the prechondral and the first period of its chondral stages a tendency to split along the median sagittal plane passing through their dorsal and ventral walls into right and left halves.

(26) The lateral extension of basiventrals placed immediately below the collateral sympathetic cord and the vertebral artery represents the incipient *parapophysis* (fig. 32, *B*).

(27) The prechondral *diapophysis* arises from the ventro-lateral portion of the dorsal (= neural) division of the caudal sclerotomite. It is placed above the incipient foramen transversarium, and is finally represented in the form of an outgrowth of the ventro-lateral portion of the basiventrals (fig. 32, *B*).

(28) The lateral portion of the ventral (= chordal) division of the caudal sclerotomite extending from the incipient foramen transversarium along the meso-caudal face of the corresponding myotome lateralwards, caudalwards, and ventralwards, gives rise to the incipient prechondral rib (fig. 31, *E*).

(29) The proximal portion of an incipient cervical and thoracic rib consists of a dorsal and a ventral limb. The dorsal limb connected with the ventro-lateral portion of the basiventrals—the incipient diapophysis—represents the tubercular portion of the rib. The ventral limb continuous with the dorso-lateral portion of the basiventrals—rudiment of the parapophysis—represents the capitular portion of the rib.

(30) During the prechondral stage, till the beginning of chondrification, there is neither any histological difference nor a perceptible boundary line between the capitular and tubercular portions of the rib and the rudiments of the par- and di-apophysis.

(31) The cervical (except atlas and axis) and thoracic intercentra never reach the cartilaginous stage but undergo atrophy. Their reduction sets in with the atrophy of the anterior (= interventral) portion of the formation and hence proceeds to its posterior (= basiventral) division. The atlas and axis intercentra become chondrified.

(32) The basidorsals and the primary vertebral body undergo chondrification. The chondrification of both formations comes about almost simultaneously. The chondrifi-

cation of the pro- and opistho-spondylous zones begins slightly later than that of the vertebral ring.

(33) The anterior and middle portion of the dorsal-interdorsals undergo chondrification. The dorsal-interdorsals remain in chondrified connection with the cranially disposed basiventrals. The caudal ends of the dorsal-interdorsals do not chondrify.

(34) The interventrals undergo differentiation into an anterior and a posterior portion. The less conspicuous anterior portion becomes chondrified and fuses with the hinder end of the chondrified primary vertebral body, thus contributing to the formation of the outer portion of the hinder end of the secondary vertebral body (fig. 31, E^1, and fig. 32, A, A^1, D, E). The posterior bulkier portion of the interventrals* can be discriminated into a ventral unpaired and lateral paired portions. The ventral unpaired portion of the interventrals represents the anterior portion of the intercentrum. The lateral paired portion fuses with the primary vertebral body. The structure resulting from this fusion may be called the *secondary intervertebral* body (fig. 32, E, A, A^1, and 31, E^1).

(35) In *Struthio*, the *interdorsal* is laid down in the basal portion of the neural division of the cranial sclerotomite covering the dorso-lateral face of the vertebral ring (= median zone of the primary vertebral body). It extends from the base of the basidorsals slantingly backwards and downwards, and forms the main bulk of the dorsolateral aspect of the definitive cartilaginous vertebral body. In *Struthio*, the ventral interdorsal exhibits in the late-prechondral, as well as in the chondral, stage a very distinct individuality, if compared with neighbouring parts. In *Larus* and in the synsacral and caudal regions of *Struthio*, the interdorsal can be clearly distinguished only in its chondral stage. It appears in the form of an indistinctly shaped ridge of cartilaginous tissue occupying the same position as in *Struthio*, and contributing greatly to the formation of the dorso-lateral portion of the vertebral body (figs. 31, E^1, and 32, A, A^1, C).

(36) With the final atrophy of the basiventral portion of the cervical (except atlas and axis) and thoracic intercentra, the remaining (latero-ventral) portions of the basiventrals grow round the ventral face of the prospondylous zone, and contribute to the formation of the ventral border of the anterior end of the vertebral body, instead of the atrophied parts (fig. 32, B).

(37) The interventral (anterior) components of the atlas and axis intercentra probably undergo atrophy. The basiventral (posterior) portions of the atlas and axis intercentra remain and become chondrified.

(38) The paired intercentra of the synsacral region also undergo atrophy. This occurs in *Struthio* comparatively earlier than in *Larus*. In *Larus* the synsacral intercentra exhibit signs of chondrification before the commencement of reduction.

(39) The unpaired caudal intercentra of *Larus* undergo chondrification. In *Struthio* they do not reach beyond the membranous stage and undergo reduction.

(40) The definitive cartilaginous neural arch consists genetically of a cranial and a caudal division. The cranial division or the *primary neural arch* is formed from the

* In cervical and thoracic regions.

basidorsals. The caudal division of the definitive or *secondary neural arch* arises from a dorsal and a ventral portion. The dorsal portion is represented by the dorsal-interdorsals (= epiganglionic interdorsals) the ventral by the interdorsals (= hypoganglionic interdorsals). The *definitive or secondary neural arch* is formed by further growth and mutual fusion of the above-named components. The prechondral dorsal membrana

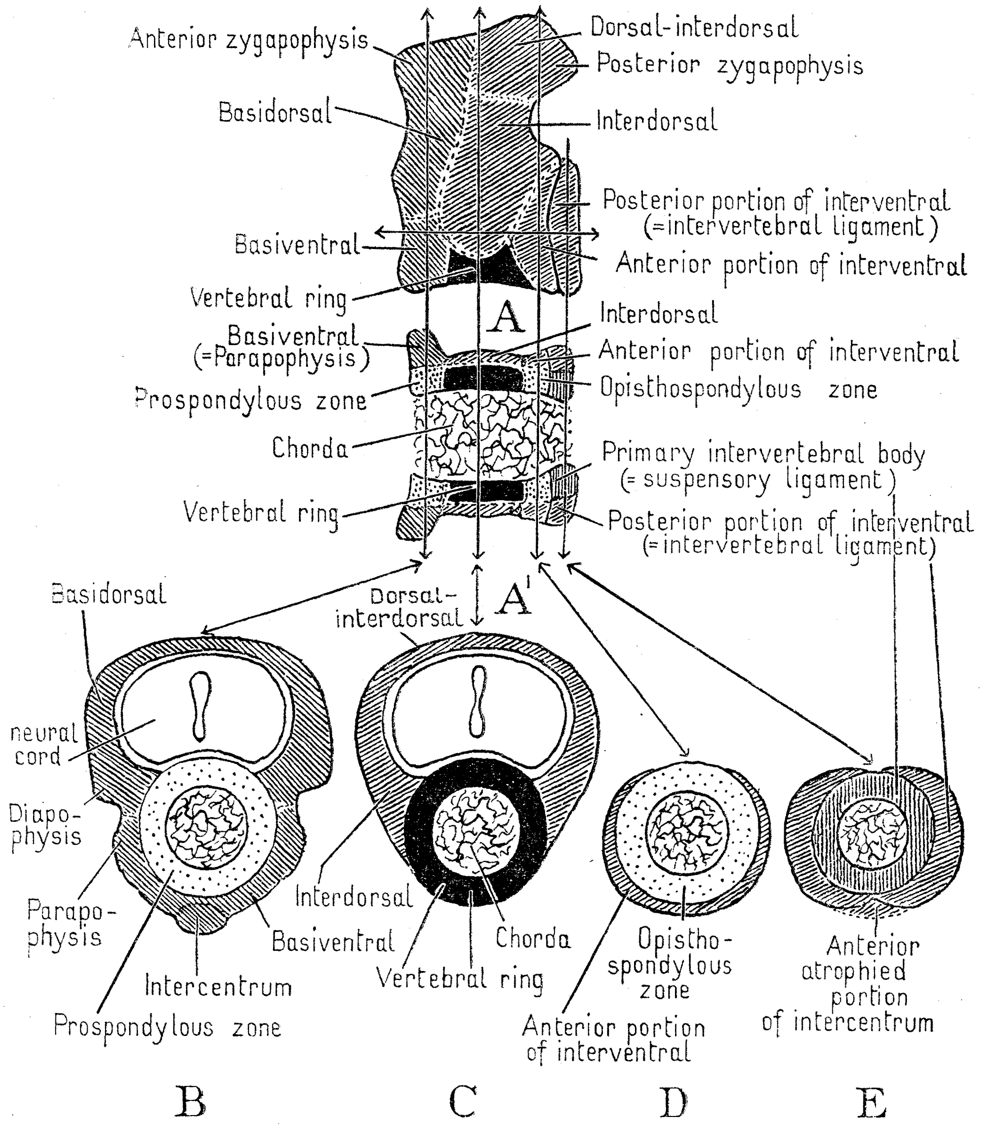


FIG. 32.—Diagram illustrating the composition of a cartilaginous bird vertebra. A side view of vertebra and intervertebral body. *A'* frontal section of vertebra *A* in the direction indicated by horizontal double-arrow; *B–E* represent transverse sections of vertebra *A* through regions indicated by vertical double-arrows.

reuniens connecting both halves of the neural arch undergoes chondrification (figs. 31, E^1, and 32, *A*, *B*, *C*).

(41) The dorsal half of the cartilaginous atlas ring, in contrast to the secondary neura.

arches of other cervical vertebræ, represents a primary neural arch, *i.e.*, it consists only of basidorsals.

(42) The ventral half of the cartilaginous atlas ring is a composite formation consisting of three parts. The lateral portions are homologous with the lateral portions of the basiventrals of other cervical vertebræ. The ventral unpaired portion connecting the lateral portions has a double origin. Its anterior portion is derived from the ventral-most portion of the interventrals, whilst its posterior portion represents the ventral-most division of the basiventrals.

The intercentrum of atlas is homologous with the incipient (membranous) intercentra of other vertebræ and with the cartilaginous intercentra of the caudal region in *Larus*.

(43) The cartilaginous secondary vertebral body represents a combination of the chondrified primary vertebral body (= prospondylous zone + vertebral ring + opisthospondylous zone) with the chondrified basal portions of the dorsal arcualia (= basidorsals and interdorsals) and with portions of the chondrified ventral arcualia (lateral divisions of the basiventrals and anterior divisions of the interventrals) (figs. 31, *E*, E^1, and 32, *A*, A^1, *B*, *C*, *D*).

(44) The share of the dorsal arcualia, especially of the interdorsals, in the formation of a definitive centrum is much greater than that of the ventral ones (fig. 32, *A*, *B*, *C*, *D*).

(45) At the anterior and posterior ends of the secondary vertebral body appear secondary dilatations enclosed by the pro- and opistho-spondylous zones.

(46) The differentiation of the *secondary intervertebral body* into an inner and outer portion becomes more sharply pronounced. The inner portion is represented by the *primary intervertebral* body, which is a derivative of the middle portion of the interstitial body. The *primary intervertebral body* probably gives rise to the *suspensory ligament.* The outer portion of the secondary intervertebral body is mainly developed on its lateral aspects and is a derivative of the posterior division of the lateral portions of the interventrals. This portion probably gives rise to the *intervertebral ligament or meniscus* (figs. 31, *E*, E^1, and 32, *A*, A^1, *E*).

(47) The chondrification of the capitular and tubercular portions of cervical and thoracic ribs is effected independently of the chondrification of the parapophyseal portion of the basiventrals and the diapophyseal portion of the basidorsals.

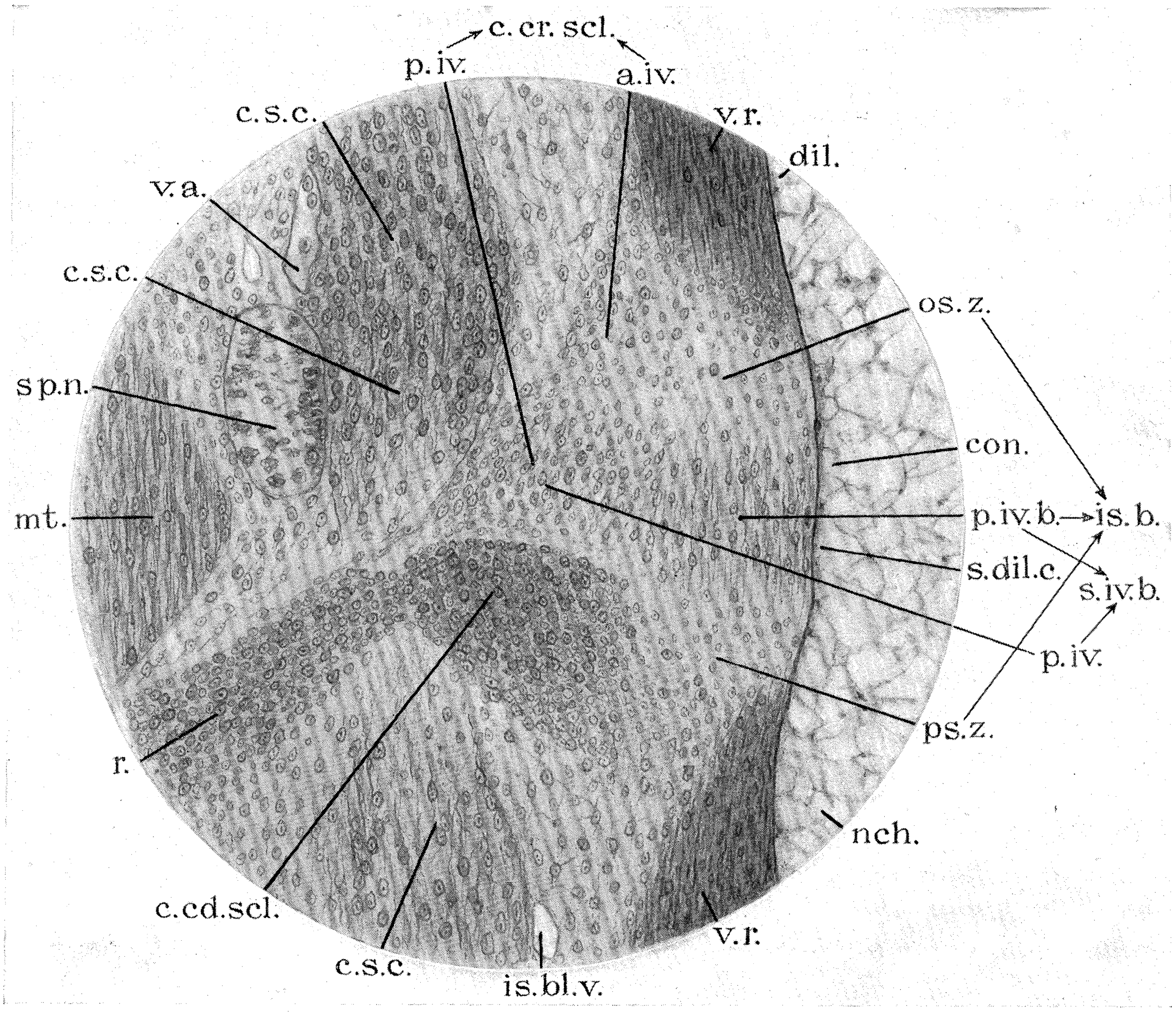
LITERATURE LIST.

ABEL, O. (1919). "Die Stämme der Wirbeltiere." Berlin and Leipzig, pp. 221-232.

BEDDARD, F. E. (1902). "Mammalia." 'The Cambridge Natural History.' Vol. 3, p. 24.

FRORIEP, A. (1883). "Zur Entwicklungsgeschichte der Wirbelsäule, insbesondere des Atlas und Epistropheus und der Occipitalregion. I. Beobachtungen an Hühnerembryonen." 'Arch. Anat. Entw.,' pp. 190–205.

GADOW, H. (1897). "On the Evolution of the Vertebral Column in Amphibia and Amniota." 'Phil. Trans.,' B, vol. 187, pp. 43–55.


c. cr. scl.
p. iv.
a. iv.
c. s. c.
v. r.
dil.
v. a.
c. s. c.
os. z.
sp. n.
con.
mt.
p. iv. b.
is. b.
s. dil. c.
s. iv. b.
p. iv.
ps. z.
r.
nch.
c. cd. scl.
v. r.
c. s. c.
is. bl. v.

Idem (1896). "On the Evolution of the Vertebral Column in Fishes." 'Phil. Trans.,' B, vol. 186, Part I, pp. 185–189.

Gegenbaur, C. (1862). "Untersuchungen zur vergleichenden Anatomie der Wirbelsäule bei Amphibien und Reptilien." Leipzig, pp. 52, 53.

Idem (1898). "Vergleichende Anatomie der Wirbeltiere, mit Berücksichtigung der Wirbellosen." Band 1. Leipzig, p. 275.

Hasse, C., und Schwark, W. (1873). "Studien zur vergleichenden Anatomie der Wirbelsäule, insbesondere des Menschen und der Säugetiere." 'Anatomische Studien (Herausgeg. v. Hasse).' Bd. 2. Leipzig, 1873, pp. 23–28.

Jäger, I. (1924). "Ueber die Segmentierung der Hinterhauptregion und die Beziehung der Cartilago acrochordalis zur Mesodermkommissur. (Ein Studium bei Vögeln)." Gröningen, p. 22.

Jäger, C. (1858). "Das Wirbelkörpergelenk der Vögel." 'Sitzungsber. Akad. Wien.' Bd. 33, pp. 527–554.

Lillie, F. R. (1919). "Development of the Chick." New York, pp. 418–424.

Lull, R. S. (1922). "Organic Evolution." New York, p. 314.

Remak, R. (1851). "Untersuchungen über die Entwicklung der Wirbeltiere." I. "Über die Entwicklung des Hühnchens im Ei." Berlin, pp. 41–47.

Schauinsland, H. (1906). "Entwicklung der Wirbelsäule nebst Rippen und Brustbein." 'Handbuch der vergl. und exper. Entw.-lehre der Wirbeltiere.' Bd. 3. T. 2, Jena, pp. 525–546.

Schwark, W. (1873). "Beiträge zur Entwicklungsgeschichte bei den Vögeln." 'Anat.-Studien (Herausgeg. v. Hasse).' Bd. 1, p. 570.

Sonies, F. (1907). "Petrus Camper," Dl. 4, Afl. 4, pp. 414–417.

Zittel, v. K. (1923). "Grundzüge der Paläontologie," II Abt., Vertebrata. München und Berlin, pp. 171–174.

DESCRIPTION OF PLATE.

Plate 18.

Cervical region of a 10-day Ostrich embryo. Enlarged middle frontal section through the intervertebral region. Anterior end of section above. *a.iv.*, anterior portion of the interventrals; *c.cd.scl.*, chordal portion of the caudal sclerotomite; *c.cr.scl.*, chordal portion of the cranial sclerotomite; *con.*, constricted portion of the notochord; *c.s.c.*, collateral sympathetic cord; *dil.*, dilated portion of the notochord; *is.b.*, interstitial body; *is.bl.v.*, intersclerotomic blood vessel; *mt.*, myotome; *nch.*, notochord; *os.z.*, opisthospondylous zone; *p.iv.*, posterior portion of the interventral; *ps.z.*, prospondylous zone; *r.*, rib; *s. dil.c.*, secondary dilatation of constricted portion of notochord; *s.iv.b.*, secondary intervertebral body; *sp.n.*, spinal nerve; *v.a.*, vertebral artery; *v.r.*, vertebral ring.

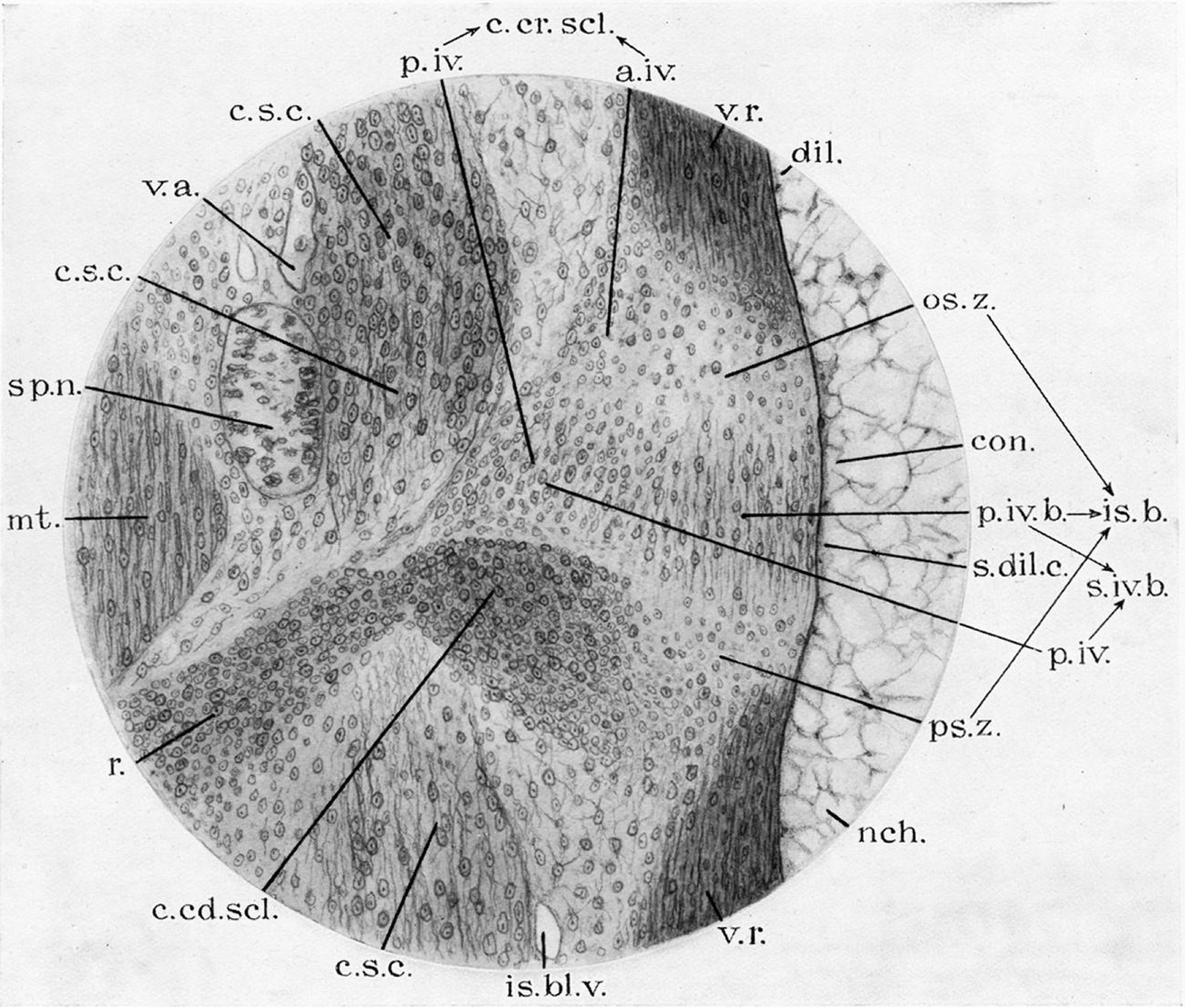


Plate 18.

Cervical region of a 10-day Ostrich embryo. Enlarged middle frontal section through the intervertebral region. Anterior end of section above. *a.iv.*, anterior portion of the interventrals; *c.cd.scl.*, chordal portion of the caudal sclerotomite; *c.cr.scl.*, chordal portion of the cranial sclerotomite; *con.*, constricted portion of the notochord; *c.s.c.*, collateral sympathetic cord; *dil.*, dilated portion of the notochord; *is.b.*, interstitial body; *is.bl.v.*, intersclerotomic blood vessel; *mt.*, myotome; *nch.*, notochord; *os.z.*, opisthospondylous zone; *p.iv.*, posterior portion of the interventral; *ps.z.*, prospondylous zone; *r.*, rib; *s. dil.c.*, secondary dilatation of constricted portion of notochord; *s.iv.b.*, secondary intervertebral body; *sp.n.*, spinal nerve; *v.a.*, vertebral artery; *v.r.*, vertebral ring.