The Early Development of the Chondrocranium of the Lizard.

By

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With 28 Text-figures.

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I. INTRODUCTION.

THE embryonic skull of the lizard was one of the first to be studied by modern critical methods, and now the morphology of the chondrocranium of the Lacertilia may be regarded as well known, thanks to the work of Gaupp on Lacerta agilis (31 mm. stage (1900) and 47 mm. stage (1906)), of Rice (1920) on Eumeces (various stages), and of Pearson (1921) on Lygosoma. However, with the exception of Leydig's (1872) work on Lacerta and Anguis, Parker's (1879) on Lacerta, and Sewertzoff's paper (1900) on Ascalabotes, none of which are very detailed, practically no investigations have been made into the embryology of the lacertilian chondrocranium. The present paper is an attempt to fill this gap, as a result of a study of some two dozen embryos of Lacerta agilis of varying stages of development, prepared according to van Wijhe's method (1902), as amended (1922), using victoria blue.

The material was obtained and preserved by Professor E. S. Goodrich in Naples, and I wish here to record my gratitude to him for very kindly turning some of it over to me for this work. The embryos were removed from their shells, and only those which were living and healthy were fixed and used. Unfortunately, it was impossible to determine the respective ages of embryos of the different stages, and it was necessary to have recourse solely to measurements. The shape of the lacertilian embryo is such that the body from the tip of the snout to the tip of the tail is coiled twice on itself, with the result that the so-called 'greatest length', from the prominence of the mid-brain to the root of the tail, is very variable, and depends on the degree of tightness of the coil. For comparative purposes, therefore, measurements of greatest length are of little use, and the investigator is driven to adopting the head-length as his standard of comparison. The various stages figured and described in this paper are enumerated below.

Stage.	*Embryo.*	*Head-length.*
		mm.
1	X	2·25
2	A	2·5
3	G	3·5
4	H	4
5	I	4
6	B	4·5
7	C	5
8	D	5·25
9	E	5·25
10	F	5·5

The most advanced stage described in this paper leads on conveniently to the younger of those which Gaupp worked at. Gaupp's model, reproduced in wax by Ziegler, was used as a standard of comparison and as a check to the interpretation of the drawings which were made directly from the preparations under a camera lucida. In addition, a number of sets of serial sections of Lacerta at various stages were used to confirm the reconstructions. It should be remembered that the victoria-blue method of van Wihje is specific for chondrin to the exclusion of procartilage, with the result that embryos prepared by this method may appear to be unduly delayed in their chondrification as compared with reconstructions made from sections of the same stages. In the latter case, it almost always happens that the line of demarcation between cartilage and procartilage is interpreted very liberally for the cartilage. In any case, the differences are slight, and the matter is of little importance.

The work was done in the Department of Zoology and Comparative Anatomy of the Oxford University Museum, in which I enjoyed the unfailing encouragement of Professor Goodrich.

II. Description of Stages.

Stage 1 (embryo X, H.L. 2·25 mm., Text-fig. 1).—The first part of the cartilaginous skeleton to chondrify is Meckel's cartilage, and some of the embryos of this stage show no other visible skeleton. In others, however, it is possible to make out a thin film of cartilage on each side of the notochord, beneath the hind-brain, and continuous posteriorly with a small uprising occipital arch on each side. All the roots of the hypoglossal nerve emerge freely in front of the occipital arch of their own side, passing over the parachordal. In such embryos, the chondrification of Meckel's cartilage is obviously more advanced than that of the parachordal and occipital arch. The lizard must therefore be counted among those forms in which the splanchnocranium develops before the neurocranium.

Stage 2 (embryo A, H.L. 2·5 mm., Text-figs. 2 and 3).—The chief difference between this and the previous stage is the fact that the auditory capsule has put in its appearance, as a thin film of cartilage moulded round the lateral surface of the utricle. It must also be noticed that the hindmost of pair roots of the hypoglossal nerve has been enclosed in a foramen by a bar of cartilage which projects sideways and upwards from the para-

Text-fig. 1.

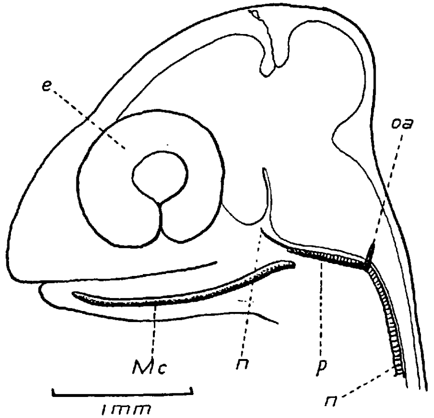

Fig. 1.—Lateral view from the left side of embryo X, stage 1, H.L. 2·25 mm.

Explanation of Lettering.

a, aditus conchae ; *ac*, auditory capsule ; *bc*, basicapsular commissure ; *bd*, basidorsal cartilage ; *bf*, basicapsular fenestra ; *bt*, basitrabecular process ; *c*, eye ; *ca*, columella auris ; *cb1*, cornu branchiale primum (1st ceratobranchial) ; *cb2*, cornu branchiale secundum (2nd ceratobranchial, distal portion) ; *cb2a*, 2nd ceratobranchial, proximal portion ; *cc*, cavum conchale ; *ch*, cornu hyale (ceratohyal) ; *co*, concha nasalis ; *cp*, crista parotica ; *cr*, crista sellaris ; *cs*, sphenethmoid commissure ; *dgl*, duct of lateral nasal gland ; *dl*, dental lamina ; *en*, external nostril ; *fa*, foramen apicale ; *fb*, basicranial fenestra ; *fbr*, fore-brain ; *fe*, foramen epiphaniale ; *fep*, fenestra epioptica ; *ff*, foramen faciale ; *fl*, fenestra lateralis nasi ; *fm*, fissura metotica ; *fmo*, fenestra metoptica ; *fo*, fenestra optica ; *fol*, fenestra olfactoria ; *fp*, fenestra prootica ; *fs*, fenestra septalis ; *fsu*, fenestra superior nasi ; *g*, gland ; *gl*, lateral nasal gland ; *hc*, hypochordal commissure ; *hf*, hypoglossal foramen or foramina ; *hh*, hypohyal cartilage ; *hy*, hypophysial fenestra ; *in*, internal nostril ; *ip*, incisura prootica ; *Jo*, Jacobson's organ ; *lta*, lamina transversalis anterior ; *Mc*, Meckel's cartilage ; *mp*, meniscus pterygoideus ; *n*, notochord ; *oa*, occipital arch ; *oc*, cavity of olfactory sac ; *on*, olfactory nerve ; *p*, parachordal cartilage ; *pa*, processus ascendens ; *pac*, pila accessoria ; *pan*, planum antorbitale ; *pao*, pila antotica (prootica) ; *pc*, paraseptal cartilage ; *pe*, processus entoglossus ; *pm*, pila metoptica ; *pmp*, processus maxillaris posterior ; *pp*, chordal to join the occipital arch behind it, on each side. The bar of cartilage in question may be regarded as a preoccipital arch, similar to that which has been demonstrated in Scyllium and in Amblystoma by Goodrich (1911 and 1918), and in Lepus by de Beer and Woodger (in the press). In Lacerta there are eventually (see Text-figs. 7 and 8) three such arches on each side, in front of the occipital arch. Between them these arches will enclose the three roots of the hypoglossal nerves in

TEXT-FIGS. 2, 3.

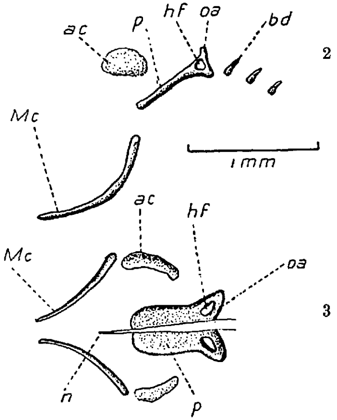

Fig. 2.—Lateral view from left side of the skull.
Fig. 3.—Dorsal view of embryo A, stage 2, H.L. 2·5 mm.

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processus paroticus; *pr*, processus retroarticularis of Meckel's cartilage; *ps*, planum supraseptale; *pt*, parietotectal cartilage of nasal capsule; *q*, quadrate cartilage; *r*, raphe between lateral and medial nasal processes, leading to aperture of Jacobson's organ; *re*, recessus extraconchalis; *ret*, ramus ethmoidalis of profundus nerve; *rl*, ramus lateralis of ethmoid nerve; *rm*, ramus medialis of ethmoid nerve; *si*, interorbital septum; *sin*, subiculum infundibuli; *sn*, nasal septum; *t*, trabecula cranii; *tc*, trabecula communis; *tl*, true lateral wall of nasal capsule, forming inner wall of cavum conchale; *tm*, taenia marginalis; *tme*, taenia medialis; *ts*, tectum synoticum.

separate foramina. This condition is similar to that which Sewertzoff (1897) observed in Ascalabotes. At the stage in question in Lacerta (stage 2), the two anterior pairs of roots of the hypoglossal nerve are still free.

Stage 3 (embryo G, H.L. 3·5 mm., Text-figs. 4, 5, and 6).—

TEXT-FIGS. 4–6.

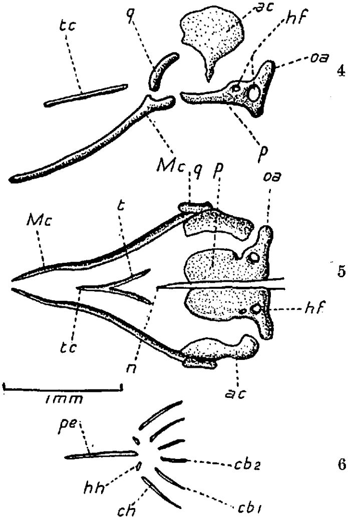


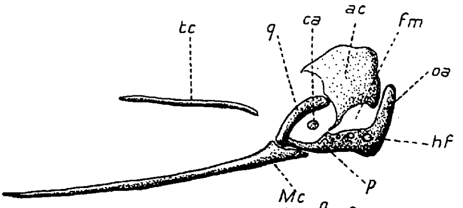
Fig. 4.—Lateral view from left side of the skull.
Fig. 5.—Dorsal view of embryo G, stage 3, H.L. 3·5 mm.
Fig. 6.—Ventral view of hyoid and branchial arches of embryo G.

At this stage, the trabeculae cranii have made their appearance as a pair of bars of cartilage, in front of the parachordals. Posteriorly, the trabeculae diverge from one another, but anteriorly they converge and fuse to form the trabecula communis, which extends forwards for a little way. It has not been possible to find a stage in cartilage at which the trabeculae were not already fused to form a trabecula communis. The auditory capsule shows a fine process directed downwards, and slightly towards the lateral edge of the parachordal of its own side. In front of this process is the quadrate, which is not, as yet, in contact with either Meckel's cartilage or the auditory capsule. Posteriorly, the enclosure of the hypoglossal root is proceeding, but unequally on the two sides. On the left, the second root is definitely enclosed, while, on the right, it runs through a deep notch. In some embryos at this stage the incipient chondrification of the columella auris may be observed.

The so-called 'hyoid' skeleton at this and the subsequent stages is in an interesting condition. There is a median processus entoglossus (or processus lingualis) corresponding to a basihyal and chondrifying independently. On each side of the posterior end of this basihyal is a pair of separate nodules of cartilage which represent the hypohyals, and lateral to them are the ceratohyals in the form of thin rods extending backwards and outwards. Between the ceratohyals are two more pairs of rods of cartilage, chondrifying independently. These are the first and second ceratobranchials. Whereas at these stages all these cartilages are still separate, they eventually all fuse together, as shown in fig. 386 on p. 771 of Gaupp's (1906) description of a 47 mm. embryo. The hypohyal and ceratohyal of each side then form the cornu hyale or anterior horn of the hyoid. Similarly, the first ceratobranchial gives rise to the cornu branchiale primum and the second ceratobranchial to the cornu branchiale secundum. The latter structure represents a chondrification of the skeletal elements of the fourth visceral arch, and it would seem to be incomplete, for, as will be seen below, another cartilage belonging apparently also to the fourth visceral arch appears at later stages.

Stage 4 (embryo H, H.L. 4 mm., Text-figs. 7 and 8).—The trabecula communis has extended forward between the eyes towards the septum separating the nasal sacs, but posteriorly, the hind ends of the trabeculae cranii are still free from the front of the parachordals. Where the anterior edge of the parachordals touches the notochord there has been no advance, but farther to the side a cartilaginous process is directed forward towards the hind ends of the trabeculae cranii. In this way, the front of the parachordals comes to present a hemispherical concavity from the centre of which the notochord projects. This concavity marks the hind border of the future fenestra basicranialis. The lateral edge of the parachordal shows a little prominence which is directed towards the downward projection from the auditory capsule of its own side, but as far as can be made out is still free from it. Behind this prominence all three roots of the hypoglossal nerve are now enclosed in separate foramina on each side. The occipital arches have extended upwards behind the auditory capsules, and it is now possible to outline a space comprised between the auditory capsule, the lateral edge of the parachordal, and the occipital arch, which space will eventually become the fissura metotica. The hind-

TEXT-FIGS. 7, 8.



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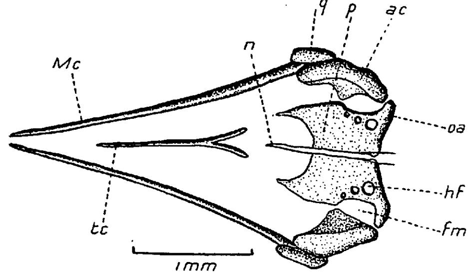

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Fig. 7.—Lateral view from the left side of the skull.
Fig. 8.—Dorsal view of embryo H, stage 4, H.L. 4 mm.

most portions of the parachordal of each side are now extending towards one another beneath the notochord, which will result in the formation of the hypochordal commissure. The chondrification of the auditory capsule is farther advanced, and portions of the roof as well as the septa of the semicircular canals are

TEXT-FIGS. 9, 10.

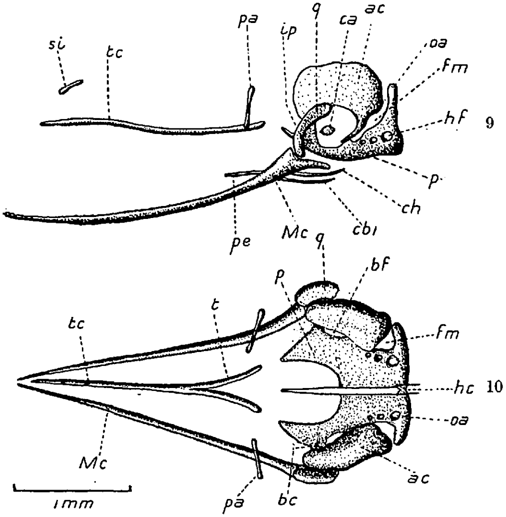


Fig. 9.—Lateral view from the left side of the skull.
Fig. 10.—Dorsal view of embryo I, stage 5, H.L. 4 mm.

present. The walls of the cochlear portion of the auditory capsule are, however, still membranous. Part of the columella auris is now present and can be seen as an independent nodule of cartilage situated behind the quadrate, in the middle of that persistently membranous portion of the side wall of the auditory capsule which will eventually become the fenestra ovalis. This nodule represents the proximal portion of the columella auris, the so-called otostapes. The quadrate is now articulated with Meckel's cartilage ventrally and with the side wall of the auditory capsule dorsally. No cartilaginous connexion between the quadrate and the columella auris was observed at this or any other stage.

Stage 5 (embryo I, H.L. 4 mm., Text-figs. 9 and 10.)—Two new features have appeared at this stage, viz. the interorbital septum and the processus ascendens. The interorbital septum has begun to chondrify as a little strip of cartilage dorsal to the trabecula communis. Each processus ascendens is a bar of cartilage in a more or less vertical position, in front of the auditory capsules on each side, and quite free from any other cartilage. The most interesting features of this stage concern the relations of the auditory capsule to the parachordal, and here, unfortunately, the results are not as definite as in other regions. It may be stated at once that the investigation of the embryology of the chondrocranium of the lizard by means of the van Wijhe technique has been more difficult than in the case of any other type of vertebrate. The extreme fineness of the strips of cartilage and the difficulties attending the dissection of the preparations prior to mounting have been a handicap to the interpretation of the relations in the more complicated regions. This is especially the case in the region in question, principally owing to the apparent superposition of structures seen in a total preparation. However, by careful comparison between several preparations and reference to serial sections, the following points can be made out. The cochlear portion of the auditory capsule becomes chondrified (in continuity with the rest of the capsule) and acquires a connexion with the parachordal. From the earliest of these stages it seems that the facial nerve is enclosed in its facial foramen, and therefore the connexion between the cochlear part of the auditory capsule and the parachordal must be composed of a prefacial commissure as well as an anterior basicapsular commissure.

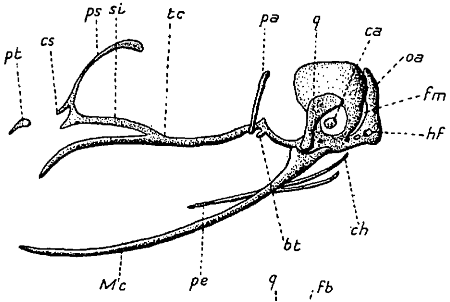
Farther back, the process which at earlier stages was described as projecting towards the prominence on the lateral edge of the parachordal now comes into contact with the latter. It is very important to define this process, and it may be described as the strip of cartilage which forms the lateral and anterior borders of the foramen perilymphaticum of the definitive auditory capsule.

The result of these relations is that between the auditory capsule and its process described in the previous paragraph, the lateral edge of the parachordal, and the anterior basicapsular commissure, there is a gap which at this stage is free from cartilage. Into the upper portion of this gap the proximal end of the columella auris projects, and so this portion of the gap may be regarded as the fenestra ovalis. The lower portion of the gap, however, owes its existence solely to the delay in chondrification of the floor of the cochlear portion of the auditory capsule. While the van Wijhe preparations show a clear space in this region, sections reveal the presence of procartilage in an early stage of histological differentiation, and this procartilaginous floor of the auditory capsule is in contact with the lateral edge of the parachordal. These relations are of importance in view of the question of the relation of the fenestra ovalis of the auditory capsule to the so-called basicapsular fenestra of other forms. At the present stage in the development of the lizard, the fenestra ovalis is present, and it is continuous with a space which may be called the basicapsular fenestra and which represents merely the as yet unchondrified floor of the auditory capsule.

Anteriorly, the parachordals are still free from the trabeculae, while posteriorly they have met beneath the notochord to form a hypochordal commissure.

Stage 6 (embryo B, H.L. 4·5 mm., Text-figs. 11 and 12).—The hind ends of the trabeculae cranii have now established connexion with the anterior projections of the parachordals, with the result that a large pear-shaped gap is enclosed in the floor of the skull. This gap represents the conjoined fenestra basicranialis and fenestra hypophyseos of later stages, which have not yet become separated from one another. Opposite the base of each processus ascendens is a small lateral projection from the hindmost region of each trabecula cranii, forming the basitrabecular process. Farther forward, the interorbital septum is now more extensive and has become connected with the trabecula communis below, and with a new structure, the

Text-figs. 11, 12.



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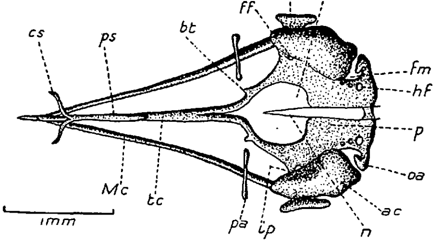

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Fig. 11.—Lateral view from the left side of the skull.
Fig. 12.—Dorsal view of embryo B, stage 6, H.L. 4·5 mm.

planum, supraseptale above. The latter is really a paired structure of which the two members have met in the middle line dorsal to the interorbital septum and beneath the brain. Anteriorly the planum supraseptale is continuous with a pair of processes which project to each side: the rudiments of the sphenethmoid commissures. In front of this again, the roof of the nasal capsule is beginning to chondrify in the form of the parietotectal cartilage. The trabecula communis now extends between the paired nasal sacs and gives rise in this region to the nasal septum.

As regards the auditory capsule, the floor has now become cartilaginous, with the result that the fenestra ovalis has a median border. The walls and roof of the capsule are now well formed, and the quadrate abuts against a prominence formed by the lateral semicircular canal.

TEXT-FIGS. 13, 14.

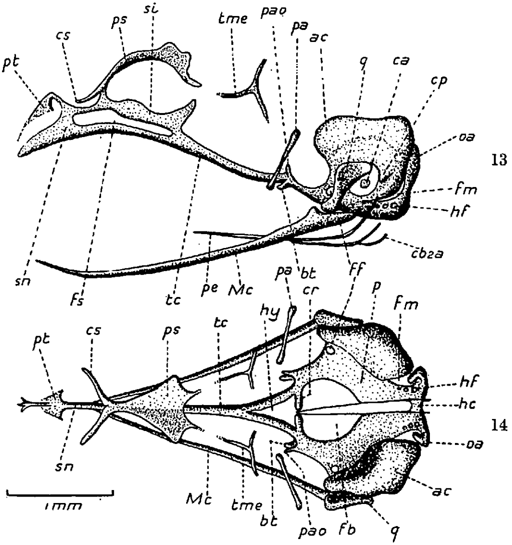


Fig. 13.—Lateral view from the left side of the skull.
Fig. 14.—Dorsal view of embryo C, stage 7, H.L. 5 mm.

It is interesting to note that at this stage the trabeculae make a fairly sharp angle with the parachordals.

Stage 7 (embryo C, H.L. 5 mm., Text-figs. 13 and 14).—The nasal and interorbital septa are now more extensive, although unchondrified gaps remain in the form of septal foramina. Anteriorly, the parietotectal cartilages, which form the roof and part of the side of the nasal capsule, grow out of the nasal septum. The sphenethmoid commissures still end freely in front, but the planum supraseptale has enlarged to form a plate immediately underlying the end-brain. In the orbitotemporal region, the rudiments of the side wall of the skull are appearing in the form of a few struts, in which part of the taenia medialis (taenia parietalis media) can be recognized. The basitrabecular processes are further developed and immediately above them is the small rudiment of the pila antotica.

At the place where the trabeculae and parachordals met, there is from the point of junction on each side a process projecting inwards towards its fellow of the opposite side, and tending to divide the original large pear-shaped gap in the floor of the skull into an anterior fenestra hypophyseos and a posterior fenestra basicranialis. These processes form the rudiment of the crista sellaris, and its paired origin is unexpected. As far as can be made out, the space between the two halves of the crista sellaris in the middle line is occupied by the anterior end of the notochord. The angle between the planes of the trabeculae and of the parachordals, which was marked at the previous stage, has now been smoothened out to a considerable extent.

The side wall of the auditory capsule bears a projection which juts out from the prominence for the lateral semicircular canal, behind the head of the quadrate. This is the crista parotica, to which, as Gaupp (1900 and 1906) showed, a structure which was in blastematous continuity with the columella auris and known as the processus paroticus, becomes attached. This processus paroticus eventually chondrifies, as will be seen in stage 9.

As regards the splanchnocranium, the posterior or dorsal portion of the skeleton of the fourth visceral arch has now chondrified, as a pair of rods lying between the hind ends of the first ceratobranchials.

Stage 8 (embryo D, H.L. 5·25 mm., Text-figs. 15 and 16).—

The chief advance which this stage shows concerns the side wall of the skull in the orbitotemporal region. The rudiment of the taenia medialis of the previous stage is now connected with the trabecula communis by means of the pila metoptica, and dorsally it is continuous by means of the pila accessoria with the taenia marginalis which extends forward as a slender strip of cartilage from the roof of the auditory capsule. Neither the taenia marginalis nor the taenia medialis have yet established cartilaginous connexions with the planum supraseptale,

TEXT-FIGS. 15, 16.

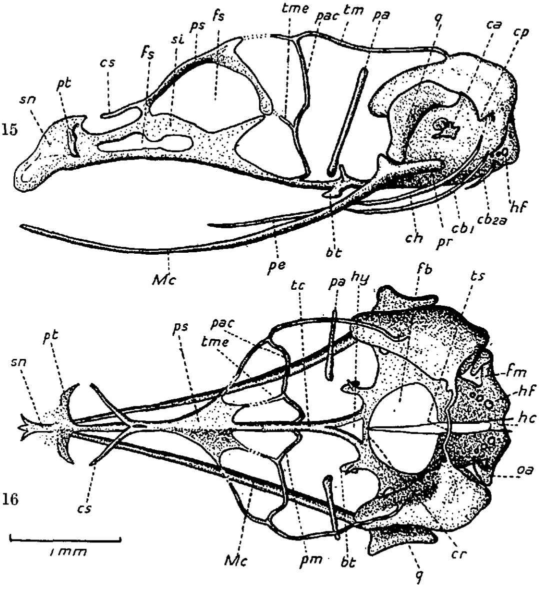


Fig. 15.—Lateral view from the left side of the skull.
Fig. 16.—Dorsal view of embryo D, stage 8, H.L. 5·25 mm.

although the position of these future connexions is evident from the appearance of projections from the planum supraseptale itself. The hinder portion of the interorbital septum projects upwards and backwards towards the hinder part of the planum supraseptale, with which however it does not fuse.

In the nasal capsule the parietotectal cartilages are now more extensive, while the auditory capsules are now joined to one another above the brain by means of a slender bar of cartilage forming the tectum synoticum. This structure passes immediately behind the large and prominent endolymphatic sacs.

The crista sellaris is now a complete bar, separating the fenestra hypophyseos from the fenestra basicranialis. The distal end of the columella auris bears a process which extends forward in the tympanum, and which corresponds to the pars inferior of the hyostapes of Versluys's (1898) descriptions. At this stage, at least on one side of embryo D, this pars inferior is separate from the conical proximal portion of the columella auris, which confirms Versluys's statement (1903) that the proximal and distal ends of the columella auris have separate centres of chondrification.

The wall of the auditory capsule has now closed in round the footplate of the proximal end of the columella auris, with the result that the fenestra ovalis is reduced to its definitive size and that its aperture is blocked by the above-mentioned footplate. It is, however, important to remember that the columella auris arose as a separate cartilage without any connexion with the wall of the auditory capsule.

Stage 9 (embryo E, H.L. 5·25 mm., Text-figs. 17 and 18).—This is the last stage of which a complete description of the chondrocranium will be given, for it may be compared directly with the earlier of the stages described by Gaupp (1900). The side wall of the skull in the orbitotemporal region is now as complete as it will ever be. The taenia marginalis extends from the planum supraseptale to the roof of the auditory capsule; the pila metoptica joins the taenia medialis, which in turn is connected with the planum supraseptale in front, the pila accessoria above, and the pila antotica behind and beneath.

TEXT-FIGS. 17–20.

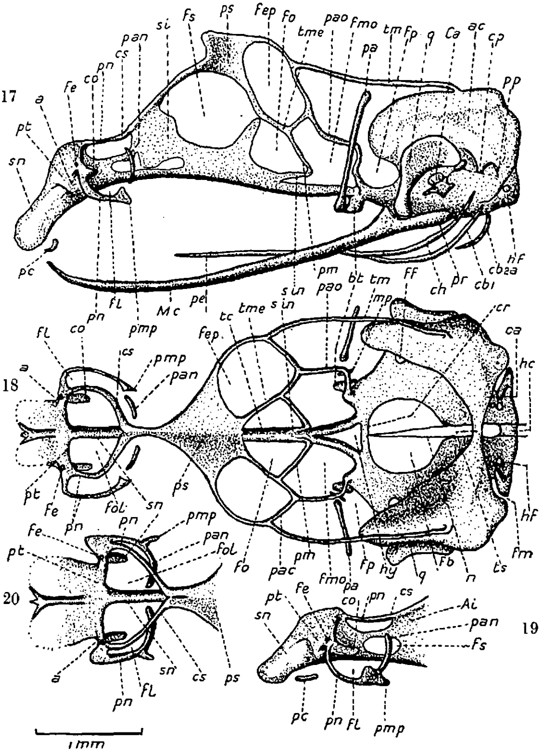


Fig. 17.—Lateral view from the left side of the skull.
Fig. 18.—Dorsal view of embryo E, stage 9, H.L. 5·25 mm.
Fig. 19.—Lateral view from the left side of the nasal capsule.
Fig. 20.—Dorsal view of embryo F, stage 10, H.L. 5·5 mm.

In this way the side wall of the skull shows four large openings on each side in this region: the fenestrae optica, epioptica, metoptica, and prootica. The relations of the various nerves to these different apertures have been described by Gaupp (1900).

The basitrabecular processes are now large structures, and a feature of considerable interest is the appearance of a small independent piece of cartilage between the basitrabecular process and the base of the processus ascendens. This is the so-called meniscus pterygoideus of Howes and Swinnerton's (1901) description of Sphenodon, and the cartilago articularis ossis pterygoidei of Gaupp's (1900) description of Lacerta. A similar structure has been reported in Emys by Kunkel (1912). In his earlier work, Gaupp (1891) showed that the cartilago articularis was connected with the base of the processus ascendens in early stages, and subsequently (1902) he regarded it as the representative of the basal process of the palatoquadrate. This is probably correct. The processus ascendens is still an isolated cartilage, and it is to be noticed that the pterygoid process at its base has not yet developed (cf. stages described by Gaupp). In sections of an embryo slightly older than that here described it has been possible to confirm Broom's (1924) observations (on the lacertilians Zonurus, Eremias, and Mabuia) that the strand of dense tissue which connects the base of the processus ascendens with the quadrate (described by Gaupp, 1891) sometimes undergoes chondrification. The quadrate cartilage of Lacerta is therefore not always free at this stage.

As regards the columella auris, the pars inferior of the distal end is now fairly well developed, and the proximal and distal ends have joined to form a single rod, expanded at each extremity. Dorsal to the columella a small cartilage is seen lodged between the head of the quadrate and the crista parotica. Sections show that this little cartilage is in blastematous connexion with the columella auris, of which it represents the processus dorsalis, or intercalary, or processus paroticus. As already mentioned, this structure eventually becomes joined on to the crista parotica, as Gaupp (1900), Versluys (1903), and Goodrich (1916) described.

The fissura metotica is still open posterodorsally, for the occipital arches have not yet fused on to the hind wall of the auditory capsules. Otherwise, the fissura metotica has assumed its definitive form and bears the usual relations to the foramen perilymphaticum of the auditory capsule (de Beer, 1929). The foramen perilymphaticum is merely an unchondrified portion of the hinder part of the floor of the auditory capsule.

Perhaps the most interesting features which this stage presents are connected with the nasal capsule. The parietotectal cartilages have extended right and left of the nasal septum, and by now a considerable portion of the roof and side walls of the capsule have been formed. Attached to the posterolateral corners of the parietotectal cartilages a new element has appeared on each side. This is the paranasal cartilage.

The paranasal cartilage is shaped like a crescent with the convex side turned forward, and the two horns pointing backward, one above and the other below. The upper horn is attached to the free anterior end of the sphenethmoid commissure, and, slightly in front of this, the paranasal cartilage is attached to the parietotectal cartilage. In this way a pair of apertures is enclosed. Each of these apertures, which are the fenestrae olfactoriae, is bounded medially by the nasal septum, posterolaterally by the planum supraseptale and the sphenethmoid commissure, anterolaterally by the paranasal cartilage, and anteriorly by the parietotectal cartilage.

Near the point of attachment of the paranasal cartilage to the parietotectal cartilage is the foramen epiphaniale, through which the lateral branch of the ethmoid nerve leaves the cavity of the nasal capsule, and the position of this foramen is of importance. Immediately beneath the foramen epiphaniale the paranasal cartilage forms as it were a duplication of the side wall of the capsule, for it is situated laterally to that hindmost portion of the side wall which is formed by the parietotectal cartilage. Between these two cartilaginous walls there is therefore a space, the cavum conchale, which ends blindly behind, but opens forward by the so-called aditus conchae, and lodges the lateral nasal gland. The whole structure, which is shaped somewhat like a cone with the point directed backward, is known as the concha, and it projects into the cavity of the definitive nasal capsule. The lower horn of the paranasal cartilage projects freely backward as the processus maxillaris posterior.

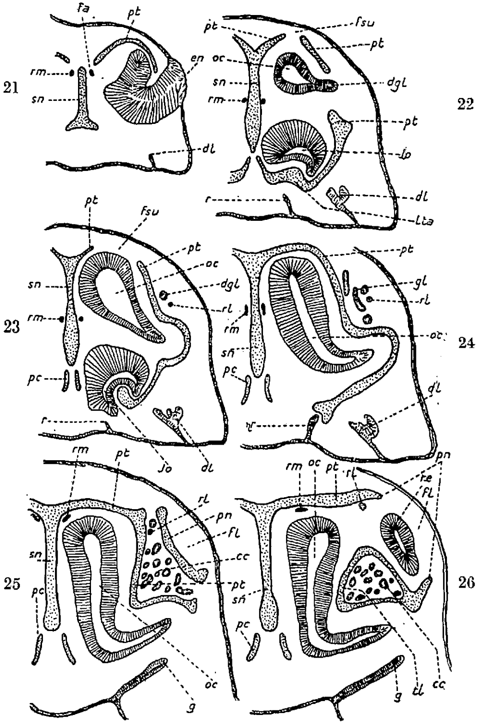
The hind wall of the nasal capsule is represented by an independent paired cartilage, the planum antorbitale, situated at the side of the nasal septum, between the root of the sphenethmoid commissure and the processus maxillaris posterior. The floor of the nasal capsule is represented only by the isolated rudiments of the paraseptal cartilages, which extend for only a short way beneath the ventral edge of the nasal septum.

Stage 10 (embryo F, H.L. 5·5 mm., Text-figs. 19 and 20).—The main portions of the skull of this stage show no appreciable advance over that of the previous one ; only in the nasal capsule have important advances been made. There, the lower posteriorly directed horns of the paranasal cartilages have become attached to the planum antorbitale of their own side. The latter has, however, not yet established connexion with the sphenethmoid commissure. When that has happened, there will still be a large lateral opening in the hinder part of the side wall of the nasal capsule : the fenestra lateralis, through which it is possible to see the concha as it projects backward into the cavity of the nasal capsule. This condition is illustrated in figs. 3 and 13 of Gaupp's (1900) description of the skull of an embryo of Lacerta 31 mm. in length, and Born's (1879) fig. 1, Pl. VI, of an embryo of Lacerta ready to hatch.

Although Gaupp's descriptions of the nasal capsule are excellent, they are somewhat difficult to follow, and it is not easy to visualize the geometrical relations without a series of transverse sections. For this reason, a few sections through selected regions of the nasal capsule of an embryo of Lacerta slightly younger than the earliest of Gaupp's have been added (Text-figs. 21–8).

Text-fig. 21 passes through the external nostril and the fenestra narina through which the nasal sac communicates with the exterior. The roof of the capsule is formed by the front part of the parietotectal cartilage, and the section passes through the

TEXT-FIGS. 21–6.



Selected transverse sections. Series Jenkinson D.
Fig. 21, section 1–2–2; fig. 22, section 1–3–14; fig. 23, section 1–4–5; fig. 24, section 2–1–4; fig. 25, section 2–2–7; fig. 26, section 2–2–15.

small foramen apicale, through which the medial branch of the ethmoid nerve emerges.

Text-fig. 22 shows the hinder portion of the fenestra narina through which the duct of the lateral nasal gland leaves the olfactory sac to run back laterally to the wall of the capsule. The roof of the capsule is here perforated by the fenestra superior, which appears to have no morphological significance.

The floor is formed by the lamina transversalis anterior, which is connected with the ventral edge of the parietotectal cartilage and was connected with the ventral edge of the nasal septum a few sections farther forward.

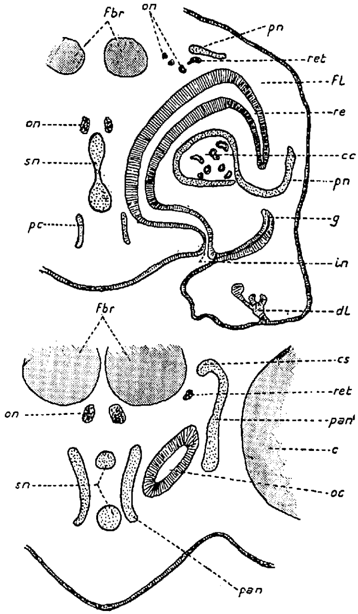
Text-fig. 23 is behind the lamina transversalis anterior, and Jacobson's organ is seen descending towards its opening into the buccal cavity. The fenestra superior is still shown, as are the paraseptal cartilages. Lateral to the true side wall of the capsule (formed by the parietotectal cartilage) may be seen the lateral branch of the ethmoid nerve and the duct of the lateral nasal gland.

Text-fig. 24 is behind the fenestra superior, and so the roof of the capsule is complete. The section passes through the anterior acini of the lateral gland, which are accommodated in a groove in the wall of the capsule. The lateral branch of the ethmoid nerve is still lateral to the side wall of the capsule.

Text-fig. 25 passes through the anterior region of the paranasal cartilage. It is lateral to the lateral nasal gland, which in turn is (together with the lateral branch of the ethmoid nerve) lateral to the true side wall. The gland therefore finds itself enclosed by cartilage in the cavum conchale, which the duct and the nerve have entered by its anterior opening : the aditus conchae.

In Text-fig. 26 the paranasal cartilage has become attached to the parietotectal cartilage, but it does not form a complete cartilaginous wall because of the large fenestra lateralis. The lateral branch of the ethmoid nerve is now median to the paranasal cartilage, and has entered the cavity of the nasal capsule (through its own small foramen epiphaniale). It is important to realize that the cavity of the concha (the cavum conchale) is really a part of extracapsular space, and it is lined throughout by what are really external capsular walls. The concha may be descriptively regarded as having been pushed into the cavity of the capsule at the spot where the paranasal cartilage becomes attached to the parietotectal. Or, alternatively (and with a greater degree of probability), it may be said that the concha owes its existence to the fact that the paranasal cartilage has been reflexed forward, outside the side wall of the capsule

TEXT-FIGS. 27, 28.



27

28

Fig. 27, section 2–4–4 ; fig. 28, section 2–5–8.

formed by the parietotectal cartilage. The result is that the cavity of the capsule bulges out and forward over the concha, and this bulge accommodates the recessus extraconchalis. The cause of this bulge is probably associated with the enormous size of the eyes, which press on the hind wall of the nasal capsule, causing it to find the necessary accommodation for its contents in the manner described.

In Text-fig. 27 the recessus extraconchalis is still open to the side through the fenestra lateralis. The lateral and median branches of the ethmoid nerve are now united, dorsal to the branches of the olfactory nerve, forming the ramus ethmoidalis of the profundus branch of the trigeminal nerve.

In Text-fig. 28 the fenestra lateralis is no longer seen, for the planum antorbitale (itself attached to the lower horn of the paranasal cartilage) has established connexion with the spheneth-moid commissure (itself attached to the upper horn of the paranasal cartilage). The paraseptal cartilage has also run into the median portion of the planum antorbitale, and, a few sections farther back, the planum antorbitale will be seen forming a complete hind wall to the cavity of the nasal capsule.

III. Discussion.

The only other lacertilian of which the earliest stages of development have been studied is Ascalabotes, by Sewertzoff (1900), and it must be noted that there are considerable differences between the conditions which he describes and those which are given in this paper. According to Sewertzoff, the trabeculae in Ascalabotes appear wide apart and separate from one another, whereas in Lacerta I have found them to be joined anteriorly to form a trabecula communis from their earliest appearance. Then Sewertzoff describes the appearance at an early stage of a crista sellaris, connected on each side with an ' alisphenoid ' (meaning the pila antotica) and unconnected either with the trabeculae in front or the parachordals behind. In Lacerta, however, as described in this paper, the chondrification of the crista sellaris and pila antotica occurs comparatively late, and in continuity with the cartilages of the floor of the skull. In this respect, my observations are partly in agreement with Parker's (1879) on Lacerta. His earliest figured stage (Pl. XXXIX, fig. 1) shows the trabeculae attached to the parachordals, and diverging freely anteriorly. On the other hand, in his next stage (Pl. XXXIX, fig. 2) the trabeculae have fused to form a trabecula communis but there is no crista sellaris.

The comparison between the chondrocranium of Lacerta and that of other reptiles so far known is reserved for a later section of this discussion. It may, however, be noted here that Shaner (1926), who studied early stages of development of Chrysemys, found conditions comparable to those described by Sewertzoff for Ascalabotes; the trabeculae were free anteriorly and a structure was present corresponding to the crista sellaris.

A discussion of the relations of the cartilages to the nerves and blood-vessels is unnecessary here, for they have been summarized in a previous work (de Beer, 1926).

A. The nasal capsule.

The nasal capsule of the lacertilian is a complicated structure, and a welcome light on its interpretation has been thrown by the recently acquired knowledge of the development of the nasal capsule in certain mammals. It has been shown by Terry (1917) in the cat, and confirmed by de Beer and Woodger in the rabbit, that three elements take part in the formation of the nasal capsule. There is (1) the parietotectal cartilage, which is continuous with the dorsal edge of the nasal septum, and forms the anterior part of the roof and side wall of the capsule; (2) the paranasal cartilage, which forms the hind part of the side wall; and (3) the planum antorbitale which forms the hind wall. In the mammals mentioned these elements chondrify independently of one another, and subsequently become connected. Where the paranasal cartilage joins the parietotectal, the foramen epiphaniale remains as a witness of the former space separating them. Further, as the paranasal cartilage overlaps the parietotectal, the posterior edge of the side wall formed by the latter projects into the cavity of the nasal capsule as the so-called crista semicircularis. Now, although in the lizard it has not been possible to find a stage at which the paranasal cartilage was separate from the parietotectal, yet the position of the foramen epiphaniale may be taken as an indication of the line of demarcation between these two elements. Further, this line is also that of the aditus conchae. Allowance has of course to be made for the fact that the paranasal cartilage is widely fenestrated (by the fenestra lateralis) in Lacerta, but this is not the case in Eumeces (Rice, 1920) or in Lygosoma (Pearson, 1921), where this cartilage forms an unbroken wall. Now the median wall of the concha of the lacertilian (representing the posterior portion of the side wall of the capsule formed by the parietotectal cartilage) bears relations which are very comparable to those of the crista semicircularis of the mammal, and the mammalian condition would be still further approached if the cavity of the concha of the reptilian nasal capsule were obliterated by the approximation and fusion of its median and lateral walls, or if the lateral wall of the concha disappeared and the aditus conchae were closed by the paranasal cartilage.

It is not proposed to homologize the reptilian concha with the mammalian crista semicircularis, but an investigation into the causes contributory to the formation of the former might throw some light on the interpretation of the latter. Seydel (1896) considered the concha as an inpushing of the capsular wall due to the development of the lateral nasal gland. Gaupp (1900), however, inclined to the view that the accommodation of the gland in the concha is a passive result of another process, viz. the expansion of the cavity of the nasal capsule resulting in a bulging outward and forward of the side wall over the concha. It seems further not improbable that this process may have been associated with the huge size of the eye in the lacertilian, which presses on the capsule from behind.

However, the latter factor is probably less important in the case of the other reptiles which possess a concha : crocodiles and snakes ; and it can hardly be appealed to in the case of the mammals.

The formation of the concha is therefore probably associated with an expansion of the cavity of the nasal capsule. The recessus extraconchalis of the lizard may be regarded as comparable to the mammalian recessus anterior ; but the concha would not correspond to the mammalian maxilloturbinal as Gaupp (1900) supposes.

Among other reptiles the presence of a concha is reported by Peyer (1912) for Vipera; by Brock (1929) for Leptodeira; and by Shiino (1914) for Crocodilus. In birds Tonkoff (1900) has shown for Gallus that a structure corresponding to the reptilian concha is present.

B. The fenestra ovalis and the basicapsular fenestra.

In many animals the cartilaginous auditory capsule becomes attached to the lateral edge of the parachordal by two commissures known respectively as the anterior and posterior basicapsular commissures (e.g. in the trout, de Beer, 1927). A gap is thus formed between the capsule laterally and the parachordal medially known as the fenestra basicapsularis, and which ultimately becomes obliterated as the chondrification of the floor of the auditory capsule is completed. Now, in several places in his treatise, Gaupp (1906) states that this basicapsular fenestra becomes the fenestra ovalis (=fenestra vestibuli) of the auditory capsule of tetrapods, while it becomes obliterated in the fish (cf. loc. cit., pp. 583, 725). As it stands, this statement is slightly misleading, for it would lead one to suppose that the medial border of the fenestra ovalis (into which the footplate of the columella auris fits) is formed of parachordal and therefore axial cartilage. There is no doubt that the medial border of the foramen ovale is formed of true capsular cartilage. However, as in many forms the chondrification of the floor of the capsule is delayed, the fenestra ovalis has for a time no medial border, and is therefore confluent with the basicapsular genestra. It is therefore hardly legitimate to say that the fenestra ovalis is a remnant of the basicapsular fenestra itself.

When the condition in the tetrapod is compared with that of Selachii, it is clear that the basicapsular fenestra of the latter has no claim to represent any part of the fenestra ovalis. The position of the fenestra ovalis is morphologically indicated by the point of articulation of the hyomandibula, which is a considerable distance lateral to the basicapsular fenestra. In this connexion it is of the greatest interest to note that van Wijhe (1924) has actually found a small fenestra ovalis in Heptanchus, situated where one would expect it, viz. ‘ in the under part of the fossa for the hyomandibula ’.

C. The planum supraseptale, ala orbitalis, and interorbital septum.

Much of the peculiarity of the skull of the lizard is due to the fact that the floor of the cranial cavity in the orbital region is lifted high above the level of the trabecula communis, a tall vertical interorbital septum being intercalated in between. It is clear that this modification is directly related to the large size of the eyes in these animals.

As regards the interorbital septum itself, the conditions in Sphenodon as reported by Schauinsland (1900) and by Howes and Swinnerton (1901) lead to the conclusion that it is really a distinct element, separate from the trabecula communis. Fuchs (1915) approaches the matter from a different point of view in his study of Chelone, for he denies that the trabecula communis extends as far forward as this. The conditions in Lacerta here described lend support to the view that the interorbital septum is an independent structure, which rapidly acquires connexion with the trabecula. At all events the matter seems to be of little importance. The membranous skull (dura mater) is stretched up from the trabecula (as the forebrain is lifted dorsally) and gives rise to a vertical wall between the orbits, in which chondrification sets in.

The formation of the interorbital septum results in important modifications of the orbital cartilage. This structure no longer springs up from two pairs of roots direct from the trabecula. The posterior pair (the pila metoptica) is present, but the anterior pair has been lost. Further, the orbital cartilages in their anterior portion have been pressed together between the orbits so that their medial borders meet in the middle line, forming the planum supraseptale. This explains why the sphenethmoid commissures leave the planum supraseptale near the middle line, and diverge as they run forward. It may be noted that an interorbital septum is present in certain mammals (Primates, Rodents), and in these the orbital cartilage (ala orbitalis) springing from the dorsal edge of the septum approximates to the form of a planum supraseptale.

The posterior portion of the orbital cartilage is in a reduced condition, being represented only by the taenia medialis, taenia marginalis, pila accessoria, pila metoptica, and pila antotica, which form a very slender framework. This region of the skull presents features of interest for comparison with other reptiles, from which interesting conclusions as to the affinities of the lacertilians may be drawn.

D. The phylogenetic position of the Lacertilia in the light of the chondrocranium.

The affinities of the Lacertilia have been a matter of controversy for some time. Long ago Huxley (1871) considered that the Lacertilia had lost the lower temporal bar which is still preserved in Sphenodon. Whether they are regarded, as Huxley would have and as Broom (1924) does, as members of the Diapsida in which the lower temporal fossa has been lost, or, with Williston (1925), as Parapsida which have never possessed a lower temporal fossa, the fact remains that these distinctions are based primarily on the configurations of the temporal arches formed by the dermal bones in the osteocranium. It becomes of interest to inquire whether any independent indications of affinity are given by the chondrocrania of Lacertilia and other reptiles. An attempt at a comparison of this kind is now possible, since investigations have been made by modern methods into the structure of the chondrocranium of all the principal groups of surviving reptiles.

It must be said at once that the snakes must be excluded from any such comparison, for their skulls are so peculiar and specialized as to supply little material for profitable comparison. As Brock (1929) has pointed out, the evidence in favour of the lacertilian origin of the Ophidia is debatable. There remains, then, Sphenodon, the Crocodilia, and the Chelonia, with which the Lacertilia may be compared. In all of these there is the same general form of a tropitrabic skull with a trabecula communis, an interorbital septum, and a planum supraseptale, and in all the posterior portion of the orbital cartilage is more or less reduced. This reduction of the orbital cartilage follows definite lines, and it is interesting to note that the condition in the Lacertilia (Lacerta, Gaupp, 1900; Eumeces, Rice, 1920) is identical in plan with that found in Crocodilia (Shiino, 1914) and in Sphenodon (Schauinsland, 1900; Howes and Swinnerton, 1901). In each case it is easy to identify the four fenestrae: optica, metoptica, epioptica, and prootica; separated from one another by the various taeniae and pilae already described. These cartilaginous struts are more slender in the Lacertilia than in the others, indicating a greater degree of specialization. In the Chelonia the conditions are more variable. In Dermochelys (Nick, 1912) the side wall of the skull in this region is fairly substantial, while in Chelone (Fuchs, 1915) it has reached approximately the same degree of reduction as in the crocodile. Emys (Kunkel, 1912), Chrysemys (Shaner, 1926), and Chelydra (Nick, 1912) show still greater reduction, but the same general plan of structure can be recognized. The fact that the lacertilians conform to this plan suggests that their affinities lie with these animals.

This conclusion is strengthened by a consideration of two other regions of the skull. The concha of the nasal capsule, present in lacertilians, is also present in a precisely comparable condition in the crocodile (Shiino, 1914). (The concha is present in the snakes: Vipera, Peyer, 1912; Leptodeira, Brock, 1929.) The pterygoquadrate presents great similarities in Sphenodon, Crocodilus, and Chelonia, consisting of an otic process connected to the base of an ascending process, from which a pterygoid process projects forward. In the Lacertilia all these elements are present in precisely comparable conditions, although the connexion between the bases of the ascending and otic processes is slender and transient.

As far as the evidence from the chondrocranium goes, it shows that the Lacertilia have several points of similarity with Sphenodon and the crocodiles, that is to say, with Diapsida, and it supports Broom's views concerning the derivation of the Lacertilia from this group.

IV. SUMMARY.

1. The embryology of the chondrocranium has been studied in ten stages of the development of Lacerta agilis.
2. The splanchnocranium chondrifies before the neurocranium.
3. The crista sellaris has a paired and belated origin.
4. The constituents of the nasal capsule of Lacerta agree generally with those of mammals.
5. It is pointed out that the foramen ovale is not a derivative of the fenestra basicapsularis.
6. The otic process of Lacerta has a temporary cartilaginous connexion with the processus ascendens.
7. Points of similarity between the chondrocrania of Lacertilia and of other reptiles lead to the conclusion that the Lacertilia are derived from Diapsid reptiles.

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