The articulations of the neurocranium in the postnatal skeleton of the domestic fowl (*Gallus gallus domesticus*)

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INTRODUCTION

Accurate information concerning the articulations formed by the cranial bones in the domestic fowl is hard to obtain. The reasons for this are several:

Firstly there is a tendency in birds, especially carinates, for the cranial sutures and synchondroses to undergo synostosis and lose their identity in the adult (Goodrich, 1930; de Beer, 1937). As a consequence, illustrations of the adult bird skull in most textbooks either merely indicate approximate areas of bones with no attempt at precise delineation (Bradley, 1960; King & McLelland, 1975) or do not identify the bones separately at all (Chamberlain, 1943; Feduccia, 1975). There are several detailed accounts of prenatal ossification (Hamilton, 1952; Romanoff, 1960), which include diagrams of approximate relationships of the cranial bones during development, but these do not clearly demonstrate the articulations which are formed. The best investigatory approach would seem to be one based on the appearance of the skull soon after hatching when the bones have achieved their recognizable form, but the articulations between them are still distinct. Jollie (1957) used this method and has provided us with some very useful diagrams which have been reproduced with modifications by subsequent authors (Bellairs & Jenkin, 1960; Thomson, 1964), but these do not make it perfectly clear as to what actual articulations are formed subsequently around the fontanelles, and between the prootic and surrounding bones in the basis cranii.

Despite general agreement as to the fact of eventual fusion in the cranium, there is disagreement as to the timing and pattern of fusion, which is variously described as occurring before the chick leaves the egg (Bradley, 1960), at an early age (de Beer, 1937), soon after hatching (King & McLelland, 1975), within the nestling stage (Bellairs & Jenkin, 1960), and in the adult (Goodrich, 1930). Only Jollie (1957) gives information about the timing and sequence of synostosis in the domestic fowl, stating that it begins 75 days after hatching in the occipital region and spreads upward and forward until closure of the frontal sutures occurs at 100 days.

The second reason is one of confused terminology, especially in the older literature and with reference to the cranial base: as yet there is no official avian anatomical nomenclature.

A third reason lies in disagreement about the actual existence of certain skeletal elements around the orbit. Three bones have been described and will, for convenience, be referred to as A, B and C. Bone A is paired and forms portions of the posterior wall of the orbit and lateral wall of the cranium. Bone B is paired and described as being near the midline and dorsal to the optic foramen, while bone C forms the bony interorbital septum. The views of various authors regarding the occurrence and identity of these bones are shown in Table 1.

Table 1. *The views of various authors concerning the existence and identity of three cranial bones in the domestic fowl*

Author	Bone A	Bone B	Bone C
Parker (1869)	Alisphenoid	Orbitosphenoid (anterior and posterior pairs)	Ethmoid
Newton & Gadow (1896)	Alisphenoid	Orbitosphenoid	Ethmoid
Heilman (1926)	Alisphenoid	—	Ethmoid
Goodrich (1930)	Lateral or pleurosphenoid	Orbitosphenoid	Mesethmoid
De Beer (1937)	Pleurosphenoid	Orbitosphenoid	Presphenoid or mesethmoid
Erdmann (1940)	Pleurosphenoid	Orbitosphenoid	Presphenoid
Fujioka (1955)	Pleurosphenoid	—	Orbitosphenoid
Jollie (1957)	Orbitosphenoid	—	Mesethmoid
Bellairs & Jenkin (1960)	Lateral or pleurosphenoid	Orbitosphenoid (in some species)	Mesethmoid
Thomson (1964)	Orbitosphenoid	—	Mesethmoid
King & McLelland (1975)	Orbitosphenoid	—	Mesethmoid

Bone A was termed alisphenoid by early authors; however, according to Goodrich (1930), it is not homologous with the greater wing of the mammalian sphenoid but rather represents the posterior part of the sphenethmoid of lower forms. He therefore proposed that it be termed lateral or pleurosphenoid, a convention maintained by de Beer (1937). Bone B was identified by most of the earlier authors and termed the orbitosphenoid. Goodrich (1930) claimed this to represent the anterior part of the sphenethmoid and described it as fusing to a median ethmoid to form an extensive bony interorbital septum. Jollie's view (1957) was rather different. He terms bone A the orbitosphenoid and describes its development from two centres of ossification, corresponding to the orbitosphenoid and presphenoid of the mammal. In his view Goodrich has assumed the existence of two elements where only one is present. The more recent reviews by Thomson (1964) and King & McLelland (1975) adopt Jollie's view. Bellairs & Jenkin (1960) reproduce Jollie's diagrams but substitute the term lateral or pleurosphenoid for Jollie's orbitosphenoid, and mention an additional orbitosphenoid in some birds.

Bone C is generally termed the ethmoid by earlier authors and mesethmoid by the more recent, though it is alternatively termed presphenoid by de Beer (1937) and Erdmann (1940) and even orbitosphenoid by Fujioka (1955).

The existence of an additional bone, the 'presphenoid' is hinted at by several authors. Parker (1869) describes it as being the anterior of the two pairs of orbitosphenoids lying near the midline. Fujioka (1955) claims that it does not appear until hatching. Jollie (1957), as described above, claims that the equivalent of the mammalian presphenoid does not exist separately in birds, but is represented as one of the centres of ossification in his orbitosphenoid.

The present study examines centres of ossification in the neurocranium (including the interorbital septum) at, and after, hatching, indicates the articulations formed by the various cranial bones, follows the sequence and records the times of fusion of the various articulations.
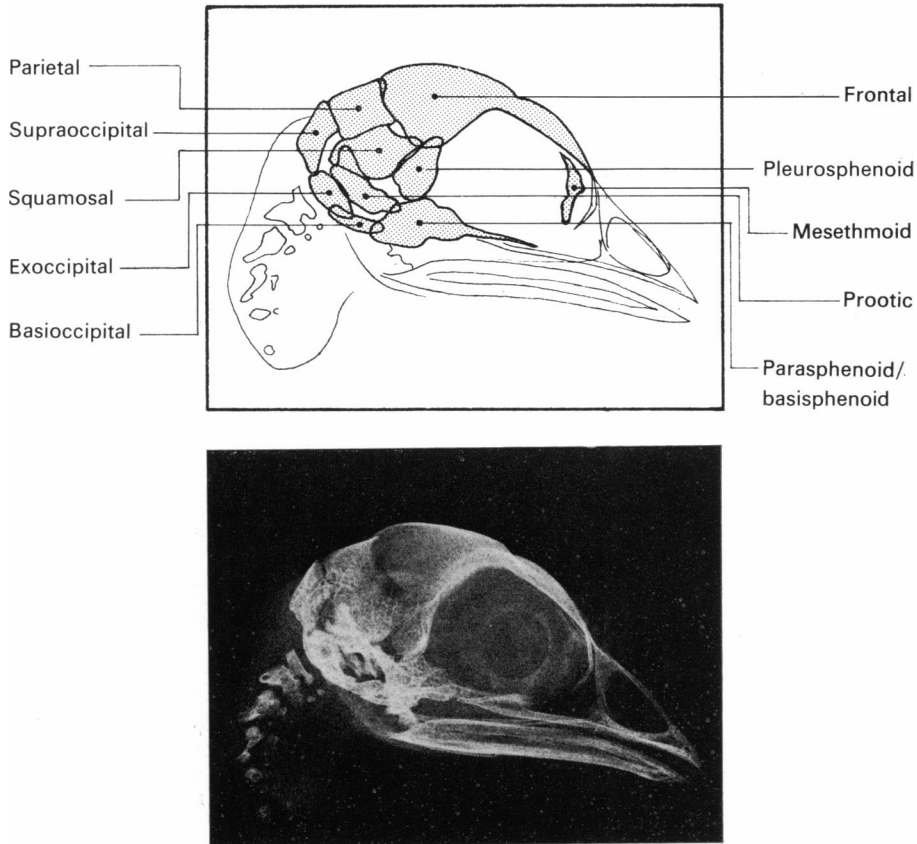
Fig. 1. Lateral view of mid-sagittal section of skull of chick at hatching. Silver nitrate radiography. × 3.

MATERIALS AND METHODS

In all 88 Golden Comet brown egg-laying hybrid pullets were studied. All were from the same hatch and were sampled in groups of four at hatching and then at 7 day intervals until 112 days post-hatching, and then at 14 day intervals until 182 days post-hatching. Chicks were killed by injection of pentobarbitone sodium, and the skulls of two of each group were stained by alizarin red S, using a modification of Dawson's (1926) method. The eyes were removed to facilitate penetration of the stain to the deeply lying bones. One of each pair was sectioned mid-sagittally and in the other the roof of the cranium and the cranial contents were removed. They were then examined under a Zeiss operating microscope with strong transillumination and dissected further as necessary. The various centres present, and the articulations between them, were readily identifiable. The criterion for concluding that a joint was 'open' was a continuous translucent line between adjacent bones.

The remaining two skulls in each group were treated with silver nitrate and radiographed, as described by Hodges (1953). One was sectioned mid-sagittally and lateral views taken and in the other the roof of the cranium and the mandible were removed to minimize superimposition on dorsoventral views. The radiographs were examined with the aid of a hand lens. The method gave contrast adequate for the
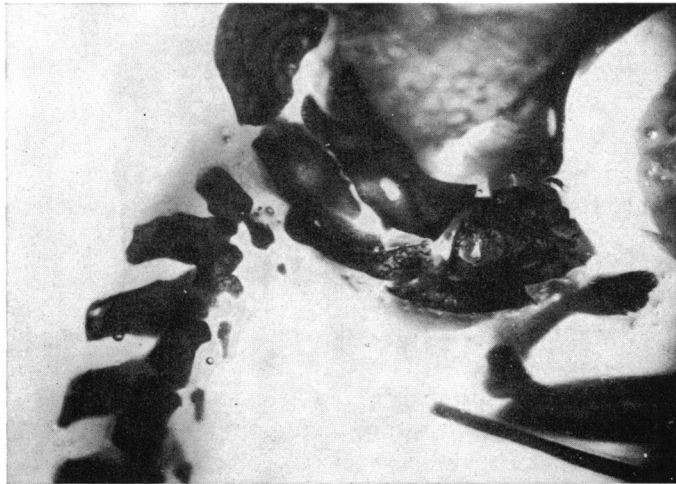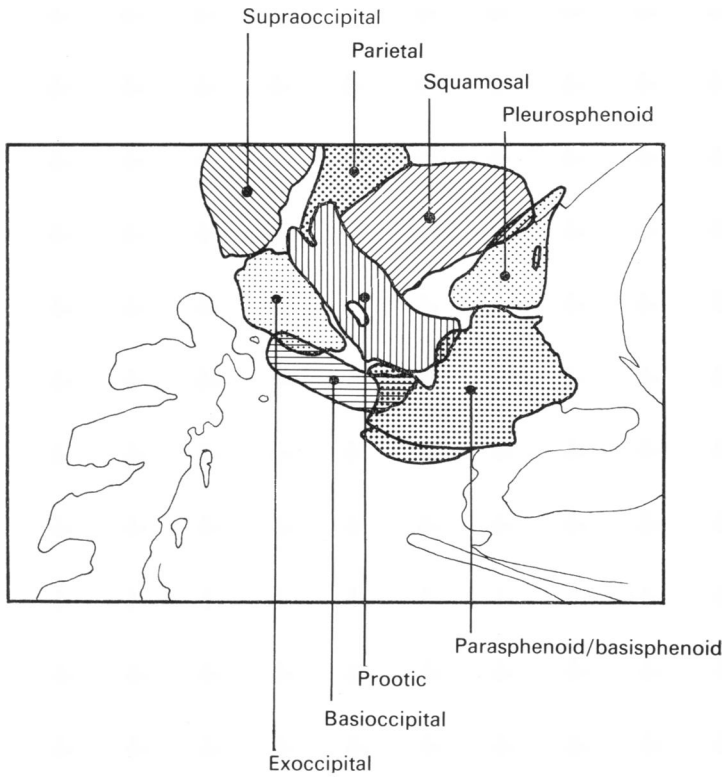
Fig. 2. Medial view of mid-sagittal section of skull of chick at hatching. Alizarin red S. × 10.

identification of the various centres and of most articulations. Those which could not be identified with certainty on the standard views taken are indicated in the Results section of this paper. The criterion for concluding that a joint was 'open' was a continuous radiolucent line between bones.

RESULTS

Centres of ossification

The centres present at hatching are shown in Figures 1–3. They correspond to those shown by Jollie (1957) and are similarly named except that the term pleurosphenoid is substituted for orbitosphenoid (see later).

Examination of the alizarin specimens under the higher powers of the operating microscope revealed no sign of multiple centres within bones, nor did it indicate the separate identities of the parasphenoid and basisphenoid which are, therefore, referred to as parasphenoid/basisphenoid. At 70 days, in one bird examined by radiography and in both stained with alizarin, an additional paired centre was detected. It was found variably at 77 and 84 days, but was present in all birds examined thereafter (Figs. 4, 5). It closely fits the description given by Goodrich (1930) of the orbitosphenoid.

No further centres of ossification were found to appear during the course of investigation.

Articulations

Examination of the skulls of the chicks at hatching and in the neonatal period allowed the articulations of the cranial bones to be determined, with the exception of those of the orbitosphenoid, which were studied at a later stage after their ossification had commenced. The following 27 cranial articulations, many of them paired, were identified and are illustrated in Figures 1–5.

basioccipital–exoccipital
basioccipital–parasphenoid/basisphenoid
basioccipital–prootic
exoccipital–parasphenoid/basisphenoid
exoccipital–prootic
exoccipital–squamosal ·
exoccipital–supraoccipital
frontal–frontal
frontal–mesethmoid
frontal–parietal
frontal–pleurosphenoid
frontal–squamosal
mesethmoid–orbitosphenoid
mesethmoid–parasphenoid/basisphenoid

orbitosphenoid–orbitosphenoid
orbitosphenoid–pleurosphenoid
parasphenoid/basisphenoid–
    pleurosphenoid
parasphenoid/basisphenoid–prootic
parietal–parietal
parietal–prootic
parietal–squamosal
parietal–supraoccipital
pleurosphenoid–prootic
pleurosphenoid–squamosal
prootic–squamosal
prootic–supraoccipital
squamosal–supraoccipital

Many of these joints are obvious and need no elaboration, but the following points are noteworthy:

(i) The supraoccipital and squamosal are at first separated by a fontanelle which is also bordered by the parietal and exoccipital (Fig. 3). Subsequently they approach each other and develop a suture line.
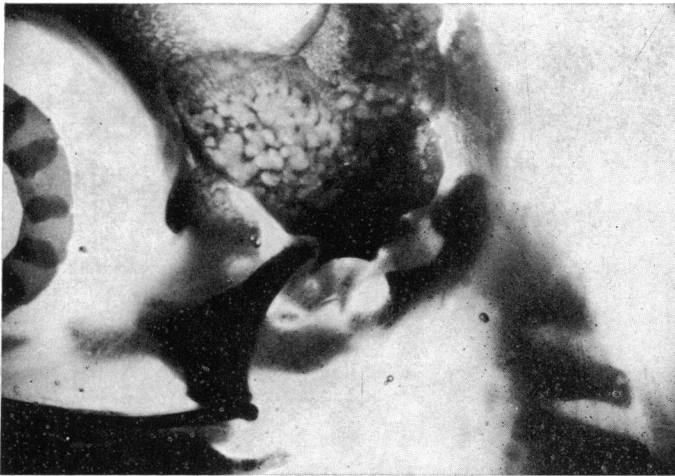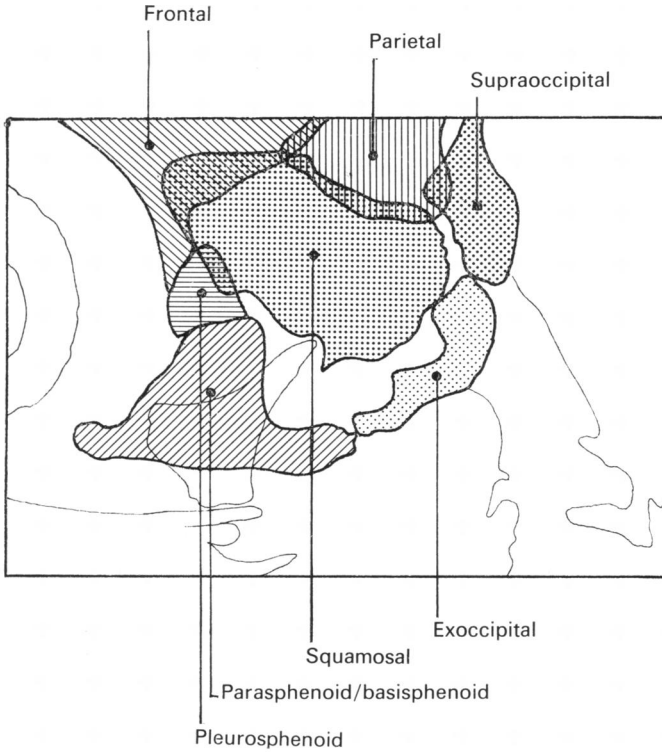
Fig. 3. Lateral view of mid-sagittal section of skull of chick at hatching. Alizarin red S. × 10.

(ii) The superior part of the prootic articulates with the parietal anteriorly and with the supraoccipital more posteriorly: fairly widely separated at first, they eventually approach and fuse to complete the otic capsule. Anteriorly the prootic contacts the pleurosphenoid for a short distance (Fig. 2).

(iii) Because of overlap between the squamosal and the frontal, parietal and pleurosphenoid (Fig. 3), careful angulation of the alizarin specimens was necessary to confirm whether these joints were 'open'.
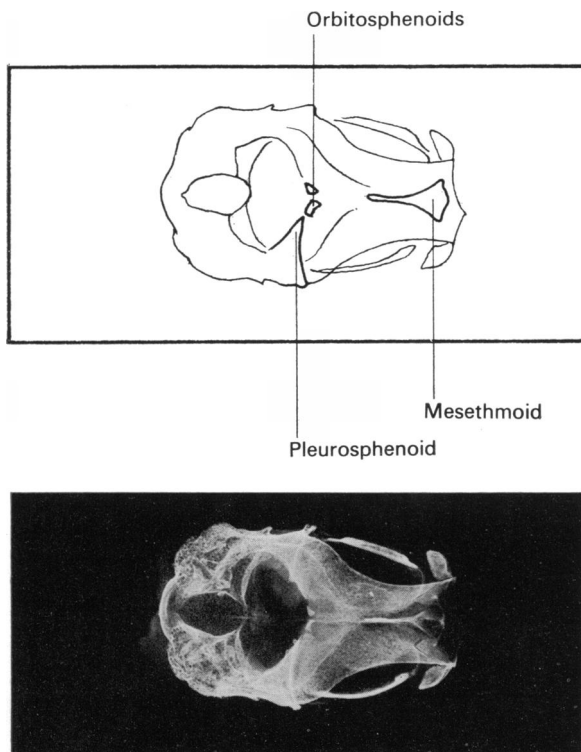
Orbitosphenoids

Mesethmoid

Pleurosphenoid

Fig. 4. Dorsoventral view of roof of cranium of 105 days old bird, sectioned through optic foramina. Silver nitrate radiography. × 1.

(iv) The frontals and parietals meet their fellows of the opposite sides at sutures which are somewhat serrated and overlapping.

(v) The mesethmoid centre, although widely separated from the anterior projection of the rostrum of the parasphenoid at hatching, eventually makes close contact with it, being accommodated in a groove on its dorsal surface.

(vi) The relations of the orbitosphenoid centres after their appearance are seen in Figures 4 and 5. They develop articulations with each other in the midline, and with the pleurosphenoid laterally, and eventually fuse into the interorbital septum as the mesethmoid ossifies caudally.

Fusions

The joints of all available birds in both series were examined and recorded as 'open' or 'closed'. The two birds at each age in the alizarin series were used, although the midline joints clearly could not be studied in the mid-sagittally sectioned specimen. Most joints were only identifiable in one of the two members of the radiographic series, that is, either on the lateral or the dorsoventral projection. Several joints formed by the squamosal (namely the squamosal–supraoccipital, exoccipital–squamosal, pleurosphenoid–squamosal and prootic–squamosal) could not always be identified with certainty on either projection because of overlap and the narrowness of the joint gaps: and so they were studied only on the alizarin specimens. In both series some variation in the times of fusion was encountered so
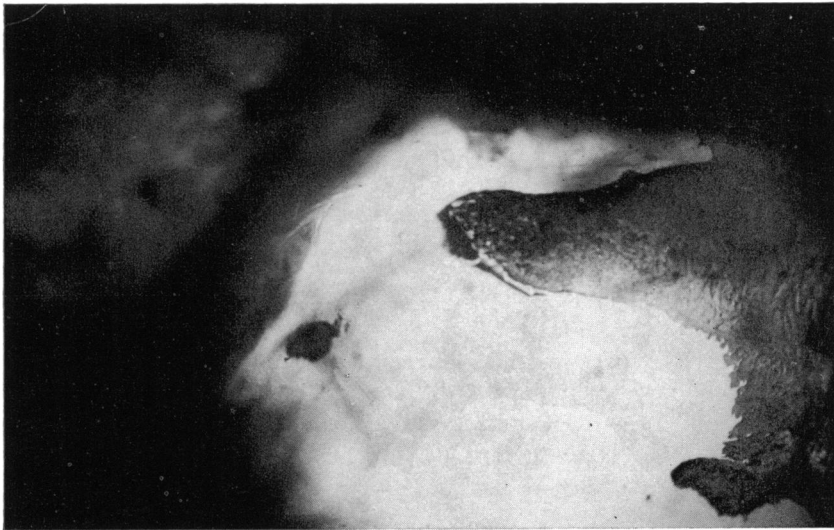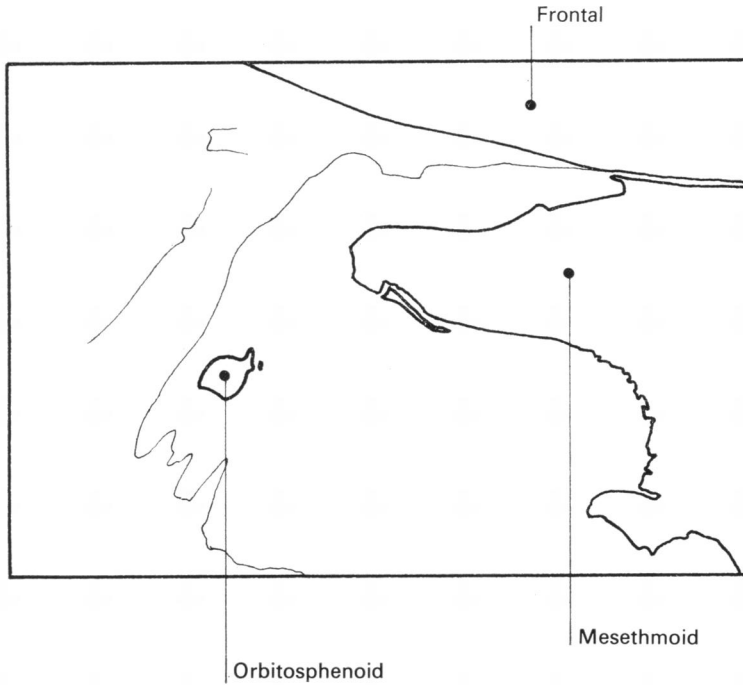
Fig. 5. Right lateral view of interorbital septum from 84 days old bird. Alizarin red S. × 10.

that, for example, if fusion was found to have occurred in a bird of a particular age it might not have occurred in birds sampled 7 days later. In general this variability did not exceed 14 days, although in the case of the basioccipital–exoccipital joint in the alizarin series, fusion was detected in a 14 days old bird, yet the joint was found open in both the 49 days old birds.

The two series of results, which broadly agreed with each other, were pooled and the last age where each joint was invariably 'open' and the first age at which it
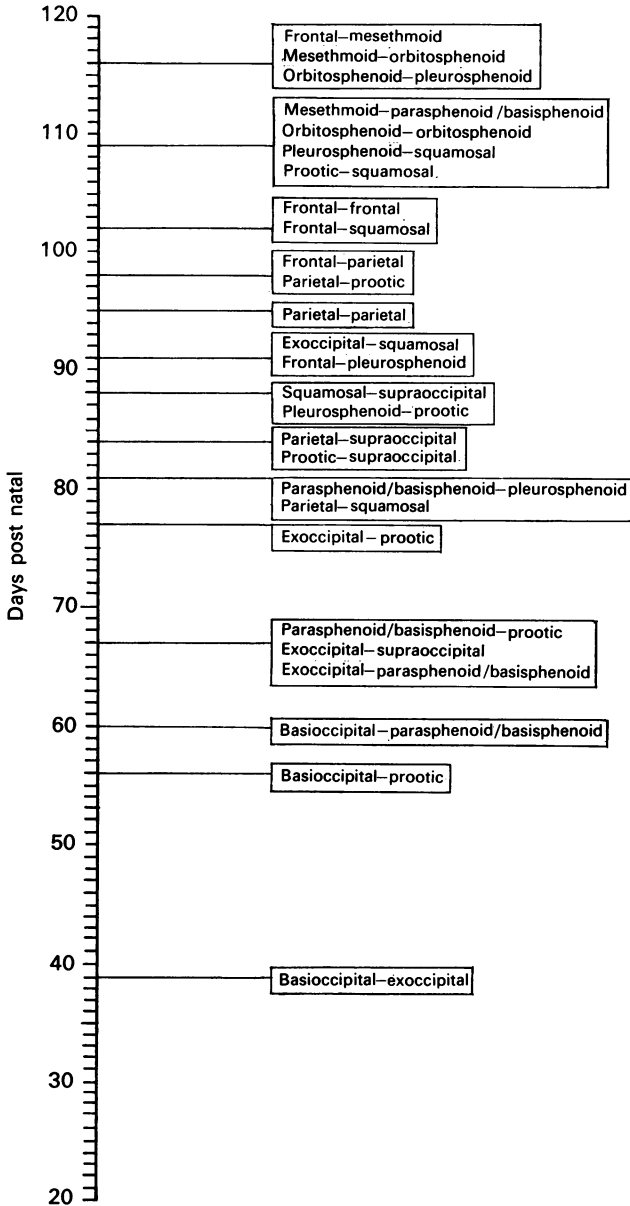
Fig. 6. Sequence and timing of fusions of the articulations of the neurocranium.

was invariably 'closed' were noted. The median between these two ages was calculated and termed the 'mean fusion time'. These are shown in sequential order against a time scale in Figure 6. The earliest was basioccipital–exoccipital at 39 days and the latest were mesethmoid–frontal, mesethmoid–orbitosphenoid and orbitosphenoid–pleurosphenoid at 116 days.

DISCUSSION AND CONCLUSIONS

The centre which does not appear until some time after hatching has the features of the orbitosphenoid as described by Goodrich (1930). Although the earlier authors similarly identified it, Jollie (1957) did not, and his view has been adopted by subsequent authors. No author since Parker (1869) has drawn attention to the fact that this centre appears so much later than all other skull centres, which, including the scleral ossicles, columella and mandible (though not all the hyoid centres) are well ossified by the time of hatching. Jollie included some postnatal birds in his series, but their numbers and the sampling intervals are not quoted. He may have missed out the stage between the appearance of the orbitosphenoid centre and its disappearance by fusion with surrounding bones. Jollie used alizarin red S staining: however, in the present study it was found that this dye penetrates to the orbito-sphenoids very poorly in older birds unless the eyes are first removed.

No extra centres were detected which could be termed 'presphenoids'.

The epiotic fuses to the supraoccipital, and the opisthotic to the exoccipital, soon after their initial ossifications in embryo (Jollie, 1957). No sign of the separate identity of these bones, or of multiple centres in other bones, or of the separate identities of the parasphenoid and basisphenoid were detectable in the birds examined at hatching.

The range of mean fusion times in this study was wider than the range quoted by Jollie (1957), 15 out of the 27 being outside his range, 6 below and 9 above.

The view that fusion commences around the base of the skull and spreads upward is confirmed. The first 7 mean fusion times involved basioccipital, exoccipital or prootic. Most of the next group involved these together with squamosal, supra-occipital and parasphenoid/basisphenoid. The frontal was first involved in fusion at 91 days (to pleurosphenoid). The interfrontal suture, which was the last in Jollie's series, had its mean fusion time at 102 days. The final group of fusions all involved orbitosphenoid or mesethmoid. As these were not described by Jollie, this partially accounts for the more extensive upper limit of the range in this series.

Several authors (de Beer, 1937; Bellairs & Jenkin, 1960; King & McLelland, 1975) suggest that the extensive fusion of the avian cranial bones is an adaptation to facilitate subsequent spread of pneumatization, but lack of precise detail of fusion has prevented close scrutiny of this suggestion. This study should provide useful background information for a detailed investigation of cranial pneumatization.

SUMMARY

In the neurocranium of the domestic fowl the centres of ossification present at hatch-ing and appearing subsequently have been investigated and illustrated. The controversy over centres around the orbit is reviewed and it is concluded that paired laterally placed pleurosphenoids are present by the time of hatching, while paired orbito-sphenoids situated near the midline and dorsal to the optic foramen do not appear until between 70 and 91 days after hatching. No additional 'presphenoid' centres were detected.

The neurocranial articulations were studied: 27, many of them paired, were identified. The sequence and timing of synostosis were determined.

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