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The distribution of pneumatisation in the skeleton of the adult domestic fowl

D. A. HOGG
Department of Veterinary Anatomy, University of Nairobi, P.O. Box 30197, *Nairobi, Kenya*

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INTRODUCTION

Widespread pneumatisation of the skeleton has long been recognised as an outstanding characteristic of birds. While there is general agreement that the process varies widely in different species there are few detailed anatomical accounts of the involvement of the skeleton in particular species. The major exception to this is the skull where pneumatisation is used extensively in ornithology as an index of age and maturity. The method involved is transillumination of the skull but its accuracy as an index for actual pneumatisation is questionable (Hogg, 1980).

Despite the importance of pneumatisation in the spread of infection from respiratory system to skeleton in domestic poultry, remarkably little attention has been paid to the anatomical details of the process. The few and markedly contradictory accounts concerning the domestic fowl were reviewed by King (1957) who reinvestigated the subject, largely confirming Campana's (1875) findings. Both studies excluded the skull and the numbers involved were small, although subsequently King & Kelly (1956) examined the third thoracic vertebra and sternal ribs in a larger number of specimens. Campana (1875) believed that in the adult, or by the breeding age, the boundary between the medullary and pneumatic parts of the bones is already established and is fixed for each species independently of its mode of life, though he admitted that under unspecified physiological or pathological conditions the proportions may vary a little. King (1957), on the other hand, finds considerable variations in the six birds in his main series which were of differing age and sex.

Pneumatisation of the skull of the domestic fowl has not been the subject of detailed study although the excellent account of skull development by Jollie (1957) makes several references to the occurrence of pneumatisation in particular elements. The work of Bremer (1940) is an interesting description of the process of development of pneumatisation in the skull and raises many questions which have not since been pursued. The anatomical distribution of pneumatisation is, however, described only in general terms.

The aims of this study have been to investigate the distribution of pneumatisation in the skull of the fowl, to ascertain its extent in the postcranial skeleton in a larger number of birds than investigated previously, and to attempt to gain some information on the degree of variation which occurs in a group of birds similar in age, breed, sex and environment.

Nomenclature is in accordance with the *Nomina Anatomica Avium* (Baumel *et al.* 1979).

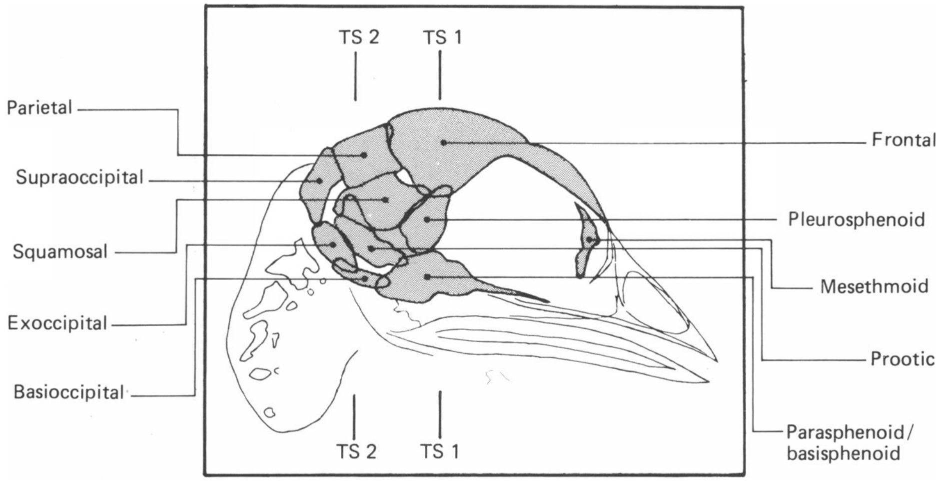

Fig. 1. Diagram of lateral radiograph of mid-sagittally sectioned skull from chick at hatching. ×3 (Hogg, 1978.)

MATERIALS AND METHODS

Group I

Five adult hens and three adult cockerels, of unknown age and of the White Leghorn variety, were killed with pentobarbitone sodium. The heads were removed, skinned, frozen and sectioned mid-sagittally with a fine bandsaw. The elements of the neurocranium revealed by this section were the frontal, parietal, supraoccipital, basioccipital, parasphenoid/basisphenoid and the orbitosphenoid bones but as complete fusion of these bones had occurred, only their approximate areas could be delineated by reference to immature specimens. Two transverse (coronal) sections (Fig. 1) were then cut in each half, the first (TS 1) just caudal to the orbit and the second (TS 2) just caudal to the external acoustic meatus. Approximate areas of the individual bony elements were again estimated by reference to immature specimens, as indicated in Figure 1. TS 1 therefore included the frontal, pleurosphenoid and parasphenoid/basisphenoid and TS 2 included the parietal, squamosal, prootic, exoccipital and basioccipital bones. If the mesethmoid bone had been missed by the mid-sagittal section this was now separately sectioned. Of the remainder of the skull, the two half mandibles, pterygoids, quadrates and the facial skeleton, i.e. the premaxilla, maxilla, prefrontal, jugal, quadratojugal, palatine and nasal bones, were all separately recognisable and were removed and sectioned. All sectioned surfaces were examined with the aid of a Zeiss operating microscope at magnifications up to ×40. Portions of facial bones, mesethmoid, quadrate, pterygoid, mandible and columella were removed from four birds and prepared for histological examination with staining by haematoxylin and eosin.

Group II

Fifty one Golden Comet birds, forty eight hens and three cockerels aged 2½ years, were examined. These were breeding stock from the same hatch and had always been kept under the same conditions of management. They were similarly killed and the bones to be examined stripped of flesh and frozen. The skulls were sectioned mid-sagittally and examined under the operating microscope as previously described. The

Table 1. *Occurrence and extent of pneumatisation in hen cranial bones*

	Extent of pneumatisation (%)					
Bone	100	75	50	25	0	Total no.
Frontal	4	42	2	0	0	48
Parietal	46	0	1	1	0	48
Supraoccipital	47	0	1	0	0	48
Basioccipital	0	1	16	31	0	48
Parasphenoid/ Basisphenoid	48	0	0	0	0	48
Quadrate	44	3	1	0	0	48
Pterygoid	41	0	0	1	6	48

Table 2. *Occurrence of pneumatisation in* 3 *cranial bones in the hens*

	Pneumatisation		
Bone	+	−	Total
Orbitosphenoid	48	0	48
Mesethmoid	48	0	48
Left mandible (articular region)	22	26	48

+, pneumatisation present; −, pneumatisation absent.

Table 3. *Numerical variation in cervical vertebrae*

No. of cervical vertebrae	Frequency
15	1 (2·0%)
16	48 (94·1%)
17	2 (3·9%)

occurrence and extent of pneumatisation in the frontal, parietal, supraoccipital, basioccipital and parasphenoid/basisphenoid bones were recorded. Extent of pneumatisation referred to the *distance* which pneumatisation had spread through the bone rather than *completeness* of pneumatisation within the bone. Due to their smaller size, the orbitosphenoid and mesethmoid bones were simply recorded as being pneumatised or not. The pterygoid and quadrate bones were removed, sectioned and the occurrence and extent of pneumatisation recorded. The articular region of the mandible was examined for the presence of pneumatisation.

When frozen, the whole vertebral column could readily be sawn mid-sagittally, enabling the individual vertebrae to be counted and identified. The occurrence and extent of pneumatisation in cervical and thoracic vertebrae were recorded. The synsacral vertebrae were counted by reference to ridges along the roof of the vertebral canal or to the intervertebral foramina. The synsacrum was considered to consist of the last thoracic and the lumbosacral vertebrae as there was no obvious indication of any coccygeal vertebrae. The lumbosacral vertebrae, being smaller, were recorded simply as pneumatised or not.

Table 4. *Occurrence and extent of pneumatisation in the cervical vertebrae of three cockerels, C_1, C_2, C_3*

Cervical vertebrae	C_1	C_2	C_3
1	–	–	–
2	–	–	–
3	++	–	++++
4	++++	–	++++
5	++++	++++	++++
6	++++	++++	++++
7	++++	++++	++++
8	++++	++++	++++
9	++++	++++	++++
10	++++	++++	++++
11	++++	++++	++++
12	++++	++++	++++
13	++++	++++	++++
14	++++	++++	++++
15	++++	++++	++++
16	++++	0	++++

++++, 100%; +++, 75%; ++, 50%; +, 25% pneumatisation present; –, pneumatisation absent; 0, bone absent.

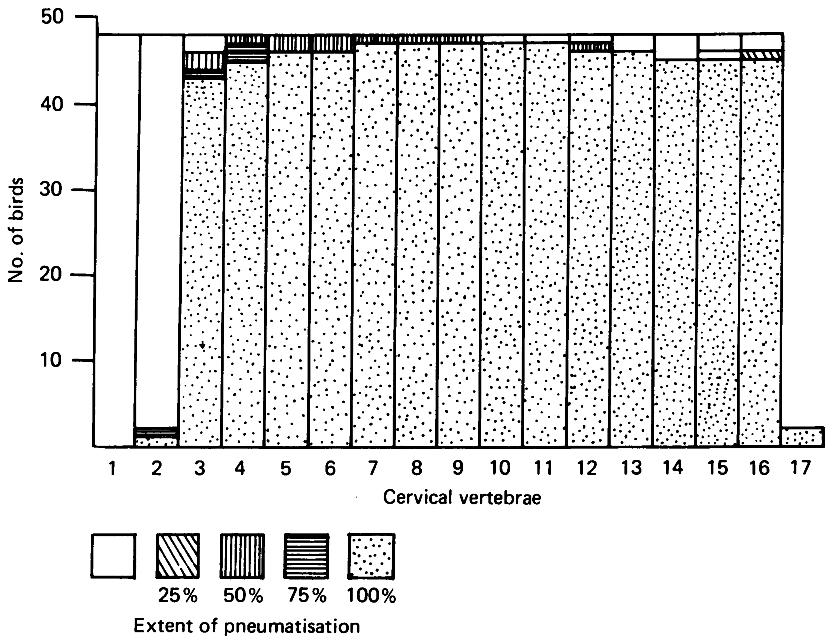

Fig. 2. Occurrence and variation in extent of pneumatisation in hen cervical vertebrae.

Table 5. *Occurrence and extent of pneumatisation of the thoracic vertebrae of three cockerels, C_1, C_2, C_3*

Thoracic vertebrae	C_1	C_2	C_3
1	++++	++++	++++
2	++++	–	–
3	++++	–	–
4	++++	++++	++++
5	++++	++++	++++

++++, 100% pneumatisation present; –, pneumatisation absent.

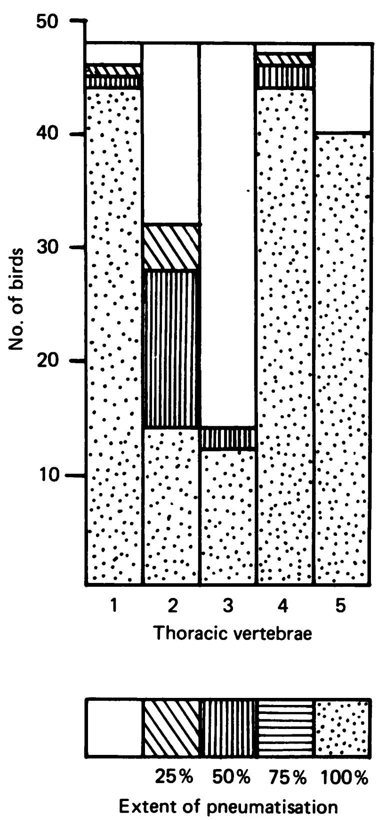

Fig. 3. Occurrence and variation in extent of pneumatisation in hen thoracic vertebrae.

The sternum was sawn mid-sagittally through body and keel and the pneumatised length expressed as a percentage of the ossified length. The sternal processes were sectioned with forceps.

The two halves of the pelvic girdle were sectioned longitudinally through ilium and ischium, and the pubis sectioned with forceps. Evidence of pneumatisation was recorded.

The coracoids, humeri and femora were sawn longitudinally and pneumatised length, when present, expressed as a percentage of total length measured to the

Table 6. *Numerical variation in lumbosacral vertebrae*

No. of lumbosacral vertebrae	No. of birds	%
15	45	88·2
14	6	11·8

Table 7. *Numerical variation in free coccygeal vertebrae*

No. of free coccygeal vertebrae	No. of birds	%
5	37	72·5
4	14	27·5

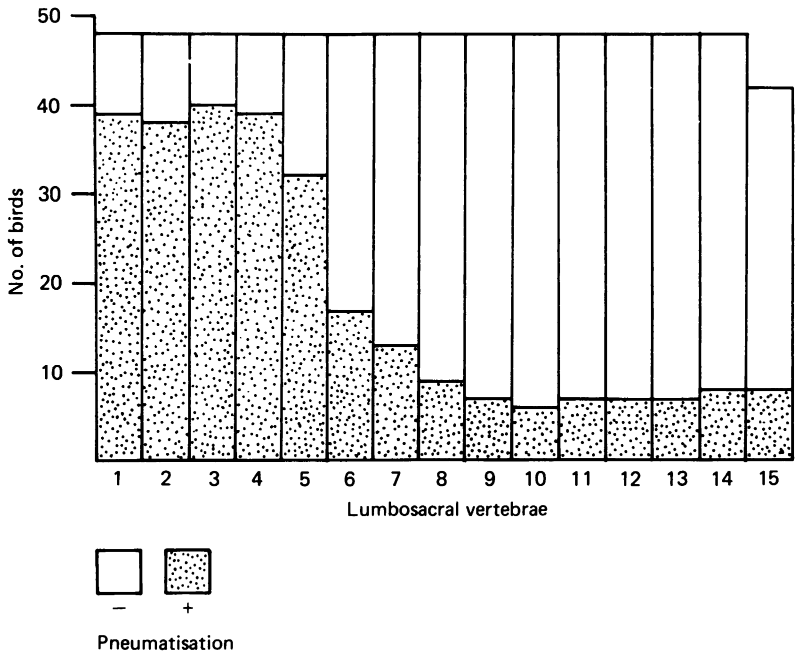

Fig. 4. Occurrence of pneumatisation in hen lumbosacral vertebrae.

surfaces of articular cartilages. The remaining, more distal, limb bones were not examined as it was felt that these were no longer controversial.

Pneumatisation when present was readily recognisable both grossly and histologically, as described by Hogg (1980).

RESULTS

Group I

Gross examination of the skull bones in all eight birds revealed pneumatisation in the mesethmoid, frontal, parietal, supraoccipital, basioccipital, exoccipital, para-

Table 8. *Occurrence of pneumatisation in hen vertebral ribs*

Vertebral rib no.	Pneumatisation present			Pneumatisation absent	Total
	Unilateral	Bilateral	Total		
1	8	25	33	15	48
2	8	5	13	35	48
3	1	0	1	47	48
4	0	0	0	48	48
5	0	0	0	48	48
6	0	0	0	48	48
7	0	0	0	48	48

Table 9. *Numerical variation in sternal ribs*

No. of pairs of sternal ribs	No. of birds	%
5	49	96·1
4	2	3·9

Table 10. *Occurrence of pneumatisation in the hen sternum*

Sternum	Pneumatised	Non-pneumatised	Total no.
Body and keel	20	28	48
Craniolateral process	0	48	48
Caudolateral process	0	48	48

Table 11. *Occurrence of pneumatisation in the sternum of three cockerels, C_1, C_2 and C_3*

Sternum	C_1	C_2	C_3
Body and keel	+	+	+
Craniolateral process	+ (bilateral)	+ (bilateral)	−
Caudolateral process	+ (unilateral)	−	−

+, pneumatisation present; −, pneumatisation absent.

sphenoid/basisphenoid, prootic, squamosal, orbitosphenoid, pleurosphenoid, quadrate and pterygoid bones. The mandible was pneumatised in three birds. In the bones examined histologically the findings confirmed those of gross examination with the exception of one prefrontal bone in which pneumatisation was only detectable histologically. The columella was not pneumatised.

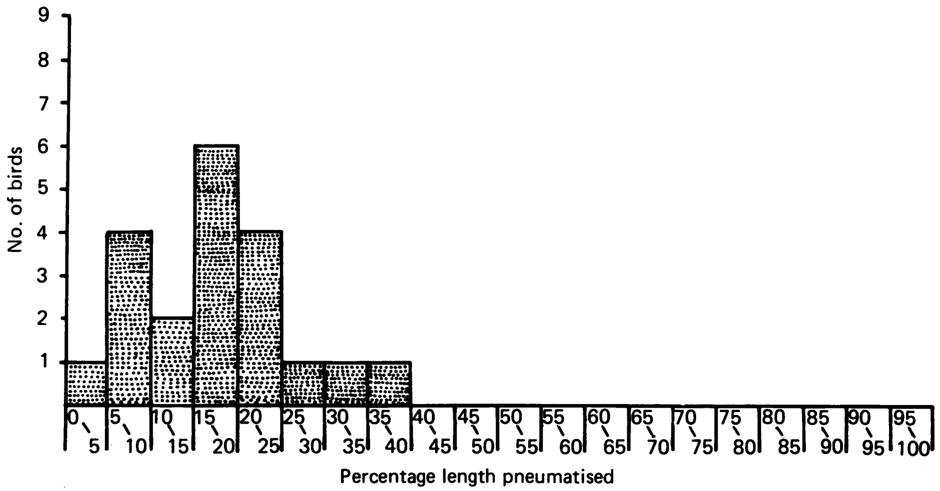

Fig. 5. Variation in extent of pneumatisation in body and keel of hen sterna.

Table 12. *Occurrence of pneumatisation in the hen os coxae*

Bone	Pneumatised	Non-pneumatised	Total
Ilium	2 (bilateral) 2 (unilateral)	44	48
Ischium	0	48	48
Pubis	0	48	48

Group II

(i) *Skull*

The occurrence and extent of pneumatisation in the skull bones examined in the hens in this group are shown in Tables 1 and 2.

In all three cockerels, pneumatisation occurred in the orbitosphenoid, mesethmoid and mandible and extended throughout the whole of the frontal, parietal, supra-occipital, basioccipital, parasphenoid/basisphenoid, quadrate and pterygoid bones.

(ii) *Vertebrae*

Cervical: The number of vertebrae in the birds examined is shown in Table 3. The occurrence and variation in the extent of pneumatisation are shown for the hens in Figure 2 and the data for the three cockerels are shown in Table 4.

Thoracic: All birds had five vertebrae. The occurrence and variation of pneumatisation in the hens are shown in Figure 3 and the data for the three cockerels in Table 5.

Lumbosacral: The number of vertebrae in the birds examined is shown in Table 6. The occurrence of pneumatisation is shown for the hens in Figure 4.

In one cockerel pneumatisation was detected in all lumbosacral vertebrae while in the other two male birds it was found only in lumbosacral vertebrae 1–7.

Coccygeal: The number of vertebrae in the birds examined is shown in Table 7. No pneumatisation was detected.

Table 13. *Occurrence of pneumatisation in the hen humerus*

Pneumatisation present			Pneumatisation absent	Total
Unilateral	Bilateral	Total		
14 (6 left) (8 right)	23	37	11	48

Table 14. *Percentage extent of pneumatisation in the humerus of three cockerels*, C_1, C_2, C_3

Humerus	C_1	C_2	C_3
Left	98	80	53
Right	98	87	78

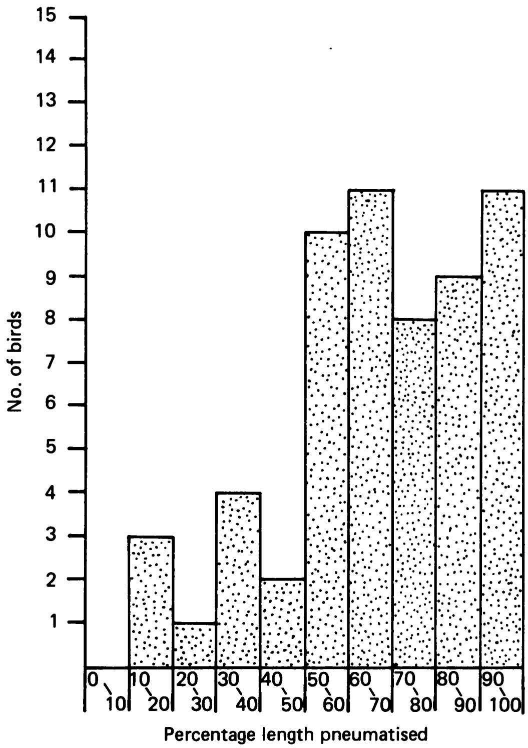

Fig. 6. Variation in extent of pneumatisation in hen humeri.

(iii) *Ribs*

Vertebral: No numerical variation was found. The occurrence of pneumatisation in the hens is shown in Table 8. In all three cockerels the first rib was bilaterally pneumatised.

Sternal: The number of sternal ribs in the birds examined is shown in Table 9. No pneumatisation was detected.

Table 15. *Occurrence of pneumatisation in the hen coracoid*

Pneumatisation present			Pneumatisation absent	Total
Unilateral	Bilateral	Total		
5 (2 left) (3 right)	5	10	38	48

Table 16. *Percentage extent of pneumatisation in the coracoid of three cockerels, C_1, C_2, C_3*

Coracoid	C_1	C_2	C_3
Left	85	55	0
Right	94	82	0

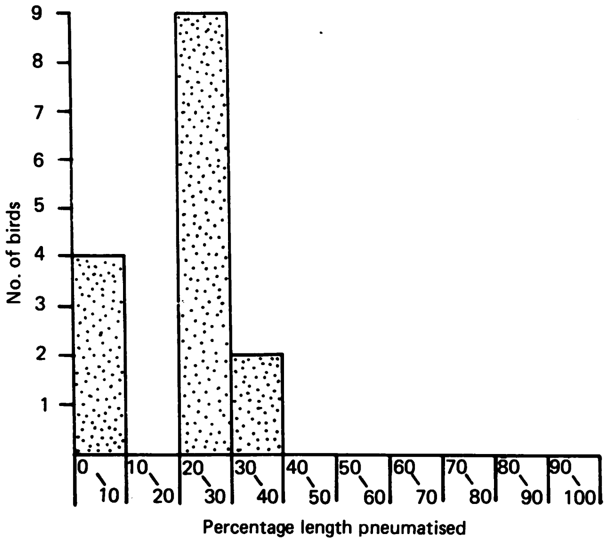

Fig. 7. Variation in extent of pneumatisation in hen coracoids.

(iv) *Sternum*

The occurrence of pneumatisation is shown for the hens in Table 10 and for the cockerels in Table 11. The variation in extent in the body and keel of the sternum in the hens is shown in Figure 5.

(v) *Os coxae*

The occurrence of pneumatisation in the hens is shown in Table 12; it did not occur in the cockerels.

(vi) *Humerus*

The occurrence of pneumatisation in the hens is shown in Table 13 and the variation in its extent in Figure 6. The data for the cockerels are shown in Table 14.

(vii) *Coracoid*

The occurrence of pneumatisation in the hens is shown in Table 15 and the pattern of variation in extent in Figure 7. The data for the three cockerels are shown in Table 16.

(viii) *Femur*

Pneumatisation was not detected.

DISCUSSION

All bones of the neurocranium are constantly pneumatised though some variation in extent is detectable, especially in the basioccipital and the frontal. The facial skeleton other than the mandible is virtually unpneumatised, in apparent contradiction to Bremer (1940) who describes the process as spreading eventually to involve various unnamed elements in the facial skeleton. The pterygoid and the mandible, on the other hand, are variably pneumatised. Bremer (1940) describes an extension from the tympanic cavity as growing forward and reaching, but failing to penetrate, the developing mandible. It would seem, therefore, that in some cases penetration may in fact occur. This raises interesting questions concerning the process involved which demand further investigation. Possibly a period of 'receptivity' of the bone to the invading air sac may exist.

Altogether the skull exhibits rather less variability in the occurrence and extent of pneumatisation than does the postcranial skeleton. Here the only bones which are constantly pneumatised are the cervical vertebrae 5–9, whereas King (1957) and King & Kelly (1956) find pneumatisation to be constant in all cervical vertebrae (other than the atlas and axis), in thoracic vertebrae 4 and 5, in the cranial third of the lumbosacral mass and in the humerus and coracoid. The bones found to be variably pneumatised in the present study, therefore, are more numerous. This group also contains several bones which were not found to be pneumatised at all by King (1957), particularly the axis and vertebral rib 3. However, sternal ribs 2 and 3, found to be pneumatised by King & Kelly (1956) in a few instances, are not pneumatised in any birds in the present study.

King (1957) commented that although his list of constantly pneumatised bones agrees closely with the findings of Campana (1875) it contains rather fewer bones than suggested by most textbooks of the day. The results of the present study show still fewer regularly pneumatised bones, for which there may be two reasons. The first is that in a process like pneumatisation where considerable variation occurs between individuals, examination of a large number of specimens will inevitably reveal more variation than will a small sample, up to a limiting number in the population where all variation is revealed. It should not be assumed that this limit has been achieved in this study. Further variation might well have been revealed had more, similar, birds been available and could yet have involved those bones which were regularly pneumatised in the birds of this study. The second possible explanation would be that the birds in this study were relatively lightly pneumatised. The absence of constant pneumatisation in the humerus is probably the most surprising result in the whole of the present study, in view of the previous widespread agreement on its pneumatisation. The coracoid and os coxae show a much lower incidence than implied by Campana (1875) and King (1957). All sternal ribs in this study are negative compared with the 10% incidence in the similar number of birds examined by King & Kelly (1956).

Examination of the extent of pneumatisation within individual bones demonstrates that, even in cases of full involvement of the basis cranii, humerus or vertebrae, traces of red marrow always persist as described by Campana (1875).

The cervical air sac pneumatises the cervical vertebrae, thoracic vertebrae 1-3 and the vertebral ribs (King, 1975). It appears that this air sac grows cranially and caudally to involve these bones and generally reaches the 3rd cervical at the cranial limit. It would seem, therefore, that if the sac reaches the axis it can give rise to pneumatisation within it. The structure of the axis is similar to that of the succeeding cervical vertebrae in containing cancellous bone, unlike the atlas which is all compact bone. As only two instances of pneumatisation of the axis have been found in this study, it is not surprising that this has not been reported previously where smaller numbers have been examined. The theory of the extent of air sac growth determining the extent of pneumatisation is also supported by the finding that the 3rd cervical vertebra has a slightly lower incidence of pneumatisation than the succeeding members of the series. Similarly the ossa coxarum are the most caudal bones pneumatised by the abdominal air sacs and have the lowest incidence of pneumatisation in that group. In the femur pneumatisation is not found and this again may be an indication of the failure of the air sac to grow as far caudally in the fowl as in other species which have pneumatised femora.

The marked asymmetry of pneumatisation in some individuals is a very striking feature. The high incidence of unilateral pneumatisation of the humerus is an example. It is also noteworthy that in many of the instances where it does occur, the pneumatisation of the humerus is extensive. This might be explained by the existence of a critical period for air sac penetration of the bone. Failure to do so at the critical time would mean that no subsequent development of pneumatisation would be possible. If penetration should occur during the critical period, however, then presumably the final extent achieved could be considerable and would be governed by other factors entirely.

Altogether the level of variability of pneumatisation in this similar group of birds is remarkably high and raises many questions relevant to the pneumatisation of bone in general.

Only three cockerels were included in the survey as it was not the main intention to investigate sex differences. However, even with such a limited number there is a strong suggestion of greater pneumatisation in the male bird. Only in two birds, both cockerels, were the sternal processes pneumatised and the basioccipital was fully pneumatised, including its condylar part, only in the cockerels. In the bones where it has been possible to estimate the extent of pneumatisation there is a fairly consistent high level in the cockerels.

SUMMARY

The occurrence of pneumatisation in the skull of the adult domestic fowl was investigated in eight birds by gross and histological examination. It was found to occur regularly throughout the neurocranium and in the quadrate and variably in the mandible, but to be absent in the facial skeleton. Close agreement was found between gross and histological examination.

The entire skeletons of fifty one adult birds all from the same hatch and kept under the same conditions were examined grossly for evidence of the occurrence and extent

of pneumatisation. Previous findings for the skull were confirmed with the additional information that pneumatisation in the pterygoid was variable. Variation in the extent of skull pneumatisation was less than in the postcranial skeleton, where only cervical vertebrae 5–9 were found to be regularly pneumatised. The humerus and coracoid were variably pneumatised, often unilaterally. The os coxae and sternum had a very low incidence of pneumatisation. The three cockerels in the group appeared to be relatively well pneumatised.

Some possible factors governing the occurrence and extent of pneumatisation in the skeleton are discussed.

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