CHAPTER 1

DEVELOPMENTAL, STRUCTURAL AND FUNCTIONAL INTEGRATION OF GIZZARDS WITH DIET VARIATIONS IN CERTAIN AVIAN MEMBERS

According to the structural modifications - organizationally speaking at cellular, tissue or organ levels - statutory changes in functions occur almost invariably. These variations in structure and function of both external and internal organs of animals are in conjunction with the urgency in their struggle for survival in a changing or changed environment. One major environmental factor that constantly induces such modifications is the food. The structural peculiarities exhibited by animals to procure and consume various types of food are innumerable. Not only feeding apparatus and its mechanisms undergo modification according to types of food but entire digestive tract also gets geared and committed as per the specific type of the ingested food. However, finer may be the mechanisms of digestion, absorption and assimilation of food, they follow the predetermined infalliable methods tried and improved during the course of evolution. Though the chordate alimentary canal is built on a basic ingenious architectural prototype, multitude of variations exhibited by individual species are accountable to the type of diet they consume. While the variations in the structure of beaks and feet of birds are believed to be due to the influence of the food on them, the alimentary canal also equally demonstrates variations under such influences.

Though the avian alimentary canal as a whole has been the subject of intensive research, a detailed and comparative account on gizzards with reference to diet occupies a relatively small space in the literature compared to the other part of the digestive system. Studies on different aspects of avian gizzard include those of Kuo (1932), Kuo & Shen (1936), Shklyar (1938), Sjörgren (1941), Hibbard (1942), Joos (1952), Calhoun (1954), Romanoff (1960), Farner (1960), Grillo (1969), Bennett (1969a, b, c), Bennett & Cobb (1969) and Cobb & Bennett (1969a, b).

Stomach of birds consists of two distinct parts viz., proventriculus which is glandular and gizzard which is heavily muscular. Not only the anatomical features distinguish them from each other but physiological activities of these two parts are distinctly different. The proventriculus secretes digestive enzymes and mucous whereas, though, gizzard has a glandular lining, its secretion does not contain digestive enzymes but keratin which forms hard lamellated rough coat over its inner surface. The chief function of the gizzard is a mechanical one of grinding. Its heavy muscular wall, in conjunction with the hard covering of keratin, serves the masticatory act, which in mammals, is carried out by teeth.

The muscular gizzards of granivores being the most complex and highly developed, a good understanding of its development would be profitable while discussing the functional adaptations of the organ. Since the ontogeny is a repetition of phylogeny, the earlier stages of development of highly evolved gizzard may reflect the adaptations of earlier models. Studies on the development of gizzard in ovo have been carried out by several workers and their reports are cited by Romanoff (1960). However, very little is known about the post-hatching development of gizzard in pigeon. During the post-hatching period gradual changes in the diet of the developing pigeon from more or less liquid like "pigeon milk" to hard grains are noted. Changes in the diet and its consistency would demand corresponding morphophysiological changes of the organ. To understand the correlation of the structure and function of the gizzard during post-hatching development, the present study was deemed worthwhile.

Large variations in size and muscularity of gizzard are found in birds which are known to differ in their diets. Heavily muscular and large sized gizzards are seen in those birds which feed on grains and seeds, while those of birds of prey are relatively less muscular. Intermediate forms of gizzards for their degree of muscularity and size are seen in birds who feed on mixed diet and in all frugivores.

The morphological variations obvious in the gizzards of birds with different diets logically should present variations in their physiological activities too. However, the physiological variations need not be strictly in conformity with the morphological changes. The chief function of the avian gizzard is a mechanical one of grinding. Varied force for grinding would be required to treat the food of different consistency. With the demand of varied force, the muscular activities of the gizzard would vary and the physiological variations in the activities of the smooth muscles could be the natural consequence. In order to get a comparative knowledge of the physiological activities of the gizzards in birds with different diets, number of birds as listed below were selected for the studies.

In order to understand the physiological variations in the gizzards of these birds, it was thought desirable to get a comparative morphological knowledge of their gizzards. Thus the anatomical considerations of gizzards of representative birds having variability in diet dealt in the present chapter are also deemed to become a prelude to the later chapters of the thesis that record the histophysiological differences in gizzards with reference to structural and functional adaptations.

MATERIALS AND METHODS

Post-hatched developing as well as adult pigeons reared in a well maintained aviary and adult representative birds shot by means of an air rifle from the University campus in the early morning hours were used for the present study. The young pigeons used were of 1, 5, 10, 15, 20, 25 and 30 days age of post-hatched development. The adult birds were grouped as under after carefully examining their gizzard contents, the groupings thus made tallied with those made by Salim Ali (1968).

GRANIVORE:

Blue Rock Pigeon (*Columba livia*)

CARNIVORE:

Rufousbacked Shrike (*Lanius schach*)
Pariah Kite (*Milvus migrans*)

OMNIVORE:

Brahminy Myna (*Sturnus pagodarum*)
Jungle Crow (*Corvus macrorhynchus*)
Domestic Fowl (*Gallus domesticus*)

INSECTIVORE:

Indian Robin (*Saxicoloides fulicata*)
Green Bee-eater (*Merops orientalis*)
Drongo (*Dicrurus adsimilis*)
Crow Pheasant (*Centropus sinensis*)
Jungle Babbler (*Turdoides striatus*)
Redvented Bulbul (*Pycnonotus cafer*)
Koel (*Eudynamus scolopacea*)
Common Myna (*Acridotheres tristis*)
House Sparrow (*Passer domesticus*)

FRUGIVORE:

Rose-ringed Parakeet (*Psittacula krameri*)

NECTAR FEEDER:

Purple Sunbird (*Necterina asiatica*)

For the anatomical study, after recording the body weight and the gizzard weight, a piece of gizzard was fixed on a chuck of a cryostat microtome maintained at -20°C. Fresh frozen sections of 12 µ thickness were used for measuring the thicknesses of keratin, mucosal, connective tissue and muscular layers.

RESULTS AND DISCUSSION

From the observations made on the gizzards of pigeon during different days of its post-hatching development, it becomes evident that there is a parallel increase in all the parts of the gizzard. As the body weight shows an increase from the day of hatching till the adulthood is reached, a corresponding increase in the gizzard weight is also noted (Table I). A progressive increase in the thickness of keratin, mucosal, connective tissue and muscular layers is the characteristic feature during the course of development culminating ultimately in the highest values observed in the adult (Table II). This increase, when viewed with the functional aspect of the organ, indicates the amount of muscular activity the organ has to perform during different periods of early (post-hatching) development. Studies by Kuo & Shen (1936) on developing chick gizzard (*in ovo*) have conclusively proved that the peristaltic contraction of that organ starts from the day 9th or 10th of incubation. Studies of Bennett & Cobb (1969), also on chick, indicated that the morphological changes observed in the gizzard after hatching are associated with a tremendous increase in the muscular layer of that organ.

As the development progresses, gradual changes in the consistency of the food that is ingested by the young

TABLE I SHOWING THE BODY WEIGHT, GIZZARD WEIGHT AND THEIR RATIO OF THE DEVELOPING PIGEON*

Age in days	Body weight	Gizzard weight	Gizzard:Body weight ratio
1	13.5	0.408	3.037
5	85	4.155	4.888
10	135	4.568	3.235
15	181	4.513	2.548
20	203	4.731	2.449
25	212	4.984	2.209
30	245	5.174	2.111
Adult	310	5.581	1.800

*Average of 5 birds

TABLE II SHOWING THE THICKNESS (IN MICRONS) OF THE KERATIN, MUCOSAL, SUBMUCOSAL AND MUSCULAR LAYERS IN THE GIZZARD OF DEVELOPING PIGEON*

Age in days	Keratin layer	Mucosal layer	Submucosal layer	Muscular layer
1	210	330	150	3900
5	225	435	180	6900
10	300	450	210	7050
15	360	465	220	7500
20	375	480	260	8250
25	390	480	280	8550
30	420	480	300	9000
Adult	525	600	340	9600

*Average of 5 birds

one are known. To start with, as said before, the food is more or less in the liquid form ("Pigeon milk"); next it consists of semidigested fragments of grains, then the broken but undigested grains and finally the whole grains. Correlating with the changes in the consistency of the food, corresponding changes in the thickness of the four components of the gizzard are noticed which are for meeting the necessary functional (mechanical) requirements of the organ. Thus the allometric growth of the gizzard, during development, is in response to its functional adaptations at different periods of early (post-hatching) development. The increase in muscularity and concomitant increase in the connective tissue are in good correlation with the resultant mechanical action the gizzard has to put in, being of a low order during the initial days, of a moderate thereafter and of a high order during the final periods of development and ultimately in the adult. Concomitant increase in the connective tissue in the interfascicular region and muscle fibres is quite understandable as the former provides anchorage for the increasing number of smooth muscle fibres. Changes in the thickness of the keratin covering of mucosa also vouche for the differential treatment needed in mechanical digestion of food during different stages of post-natal development.

A more pronounced mucosal layer could be well for active synthesis and secretion of keratin which is of utmost necessity for the mechanical break down of the grains.

From the data collected from the comparative studies on the gizzards of adult birds with different dietary preference, it becomes evident that gizzard weight or size do not fall into linearly accountable categories with respect to different consistencies of food. Generally it is said that the size of a particular organ is due to the physiological demand imposed on it, e.g., as we find that the skeletal muscles increase in size when much exercised. However, there is also another belief which contends that the growth and size of an organ are genetically predetermined. A conscientious approach that emerges out of recent influx of informations on the problem of regulation of growth is echoed by Goss (1972). According to him "..... the allometric growth of each organ is, of course, adapted to the needs of the organisms. These genetic adaptations have been shaped by natural selection and are independent of the short-term vicissitudes of the environment. Physiological adaptations on the other hand are responsible for the fluctuations in organ weights that reflect increases or decreases in functional demands. These two adaptations work together like the coarse and fine adjustments in focussing a microscope." It is quite certain that work load of gizzard varies according to the consistency of the food. Thus, in the birds consuming grains, the gizzard has to perform a vigorous muscular action, whereas in those eating comparatively soft food like flesh and insects, the gizzard does not have to perform such vigorous actions. It is understandable that in the latter group the gizzard acts as a store bag besides churning the food, whereas in the former group the gizzard is an active masticatory organ. Irrespective of differences in the type and consistency of food in different birds, their body weight to gizzard weight ratio remains little affected (Table III). This means that the growth and size of the gizzard are genetically predtermined and do not fluctuate in accordance with the functional demands. Since the structural peculiarities of gizzard are under the influence of genes, the birds with inherent habits of prefering specific type of food cannot change their diet or feeding habits. Nevertheless, large number of birds consume mixed diet consisting of insects and grains or fruits in which case the structural details of their gizzards (Figs. 4-12; 14-16) resemble more or less those of granivores (Fig. 1). Perhaps most of the birds listed as insectivores, frugivores, omnivores and nectar feeder are primarily adapted for grains and seeds but have secondarily taken to insects or other types

TABLE III SHOWING THE BODY WEIGHT, GIZZARD WEIGHT AND THEIR RATIO OF THE ADULT REPRESENTATIVE BIRDS*

Birds	Body weight	Gizzard weight	Gizzard:Body weight ratio
Blue rock pigeon	310	5.581	1.800
Shrike	40	1.163	2.907
Pariah kite	980	4.900	0.500
Brahminy myna	31	0.971	2.757
Jungle crow	407	5.225	1.650
Domestic fowl	1105	11.78	1.066
Indian robin	18	0.60	3.333
Green bee-eater	16	0.382	2.387
Brongo	45	1.483	3.295
Crow pheasent	215	3.873	1.801
Jungle babbler	48	1.152	2.401
Redvented bulbul	40	1.273	3.1825
Koel	220	3.991	1.814
Common myna	100	1.366	1.366
House sparrow	16	0.264	1.650
Parakeet	118	2.387	2.023
Purple sunbird	07	0.193	2.7575

*Average of 5 birds

TABLE IV SHOWING THE THICKNESS (IN MICRONS) OF THE KERATIN, MUCOSAL, SUBMUCOSAL, AND MUSCULAR LAYERS IN THE GIZZARDS OF ADULT REPRESENTATIVE BIRDS*

Birds	Keratin layer	Mucosal layer	Submucosal layer	Muscular layer
Blue rock pigeon	525	600	340	9600
Shrike	300	225	90	2400
Pariah kite	225	270	120	2850
Brahminy myna	195	120	45	3000
Jungle crow	180	570	105	5700
Domestic fowl	410	750	210	9000
Indian robin	240	240	105	2100
Green bee-eater	270	75	30	1950
Drongo	300	450	30	3000
Crow pheasent	345	570	45	4500
Jungle babbler	180	120	30	4050
Redvented bulbul	195	240	150	2250
Koel	225	150	150	4200
Common myna	210	225	135	3000
House sparrow	180	60	30	1650
Parakeet	135	180	30	2400
Purple sunbird	45	90	30	750

*Average of 5 birds

Figures 1 to 17 present semidiagrammatic illustrations of gizzards of representative birds chosen for the present investigations, All the figures are drawn to the actual size of gizzards.

In each figure, (a) represents external view of the gizzard along with proventriculus and beginning portion of duodenum, while (b) represents its sectional view to show its inside and thickness of the gizzard wall.

Figure 1. Gizzard of pigeon (Granivore).

In this figure the inset shown in (b) is presented as (c) which gives a magnified view of the gizzard wall. The inset given in (c) is presented as microphotograph (d) wherein the keratin layer is not shown.

K - Keratinized lining
MT - Mucosal tubules
SMCT - Submucosal connective tissue
IFCT - Inter fascicular connective tissue
SM - Smooth muscle fasciculus

Figure 2. Gizzard of Shrike (Carnivore)

Figure 3. Gizzard of Kite (Carnivore)

Figure 4. Gizzard of Brahminy myna (Omnivore)

Figure 5. Gizzard of Crow (Omnivore)

Figure 6. Gizzard of Fowl (Omnivore)

Figure 7. Gizzard of Indian robin (Insectivore)

Figure 8. Gizzard of Green bee-eater (Insectivore)

Figure 9. Gizzard of Drongo (Insectivore)

Figure 10. Gizzard of Crow pheasent (Insectivore)

Figure 11. Gizzard of Jungle babbler (Insectivore)

Figure 12. Gizzard of Redvented bulbul (Insectivore)

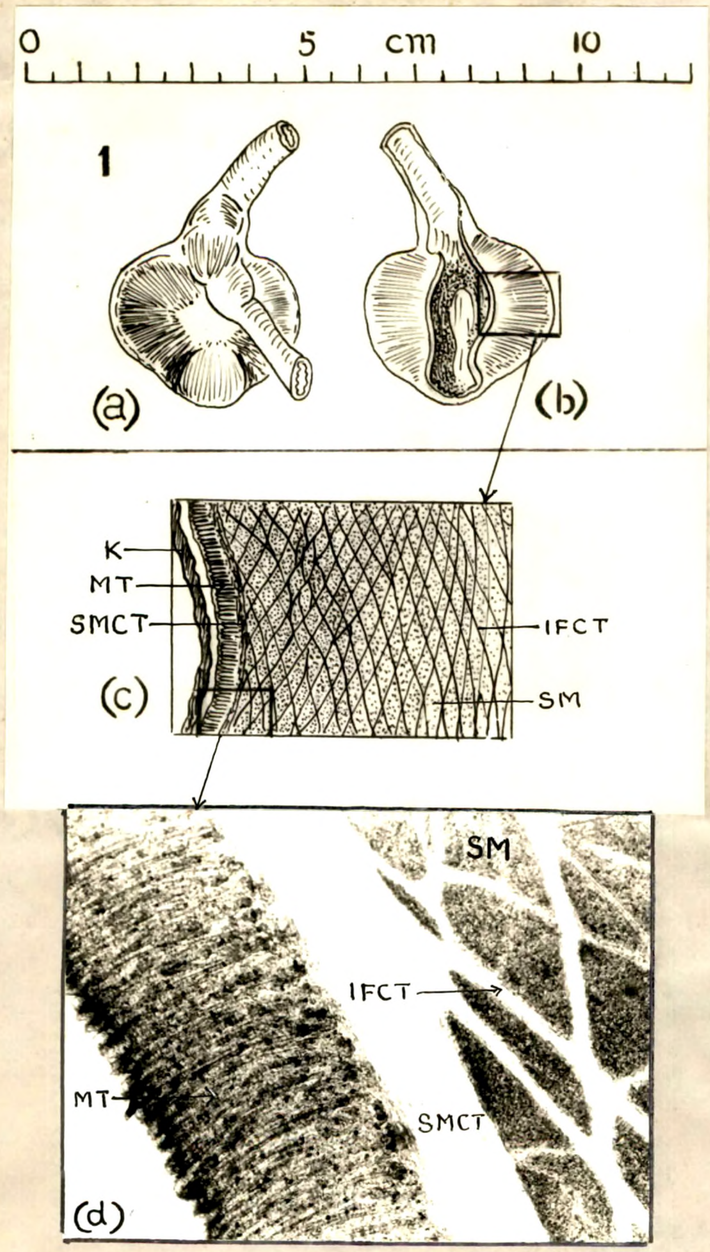
Figure 13. Gizzard of Koel (Insectivore)

Figure 14. Gizzard of Common myna (Insectivore)

Figure 15. Gizzard of House sparrow (Insectivore)

Figure 16. Gizzard of Parakeet (Frugivore)

Figure 17. Gizzard of Sunbird (Nectar feeder)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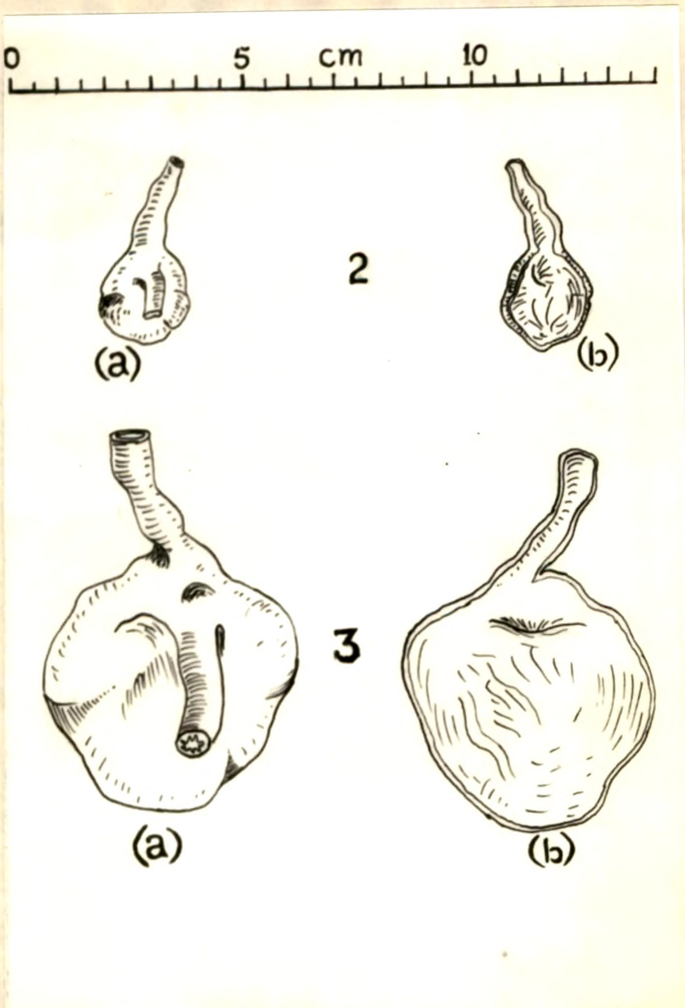
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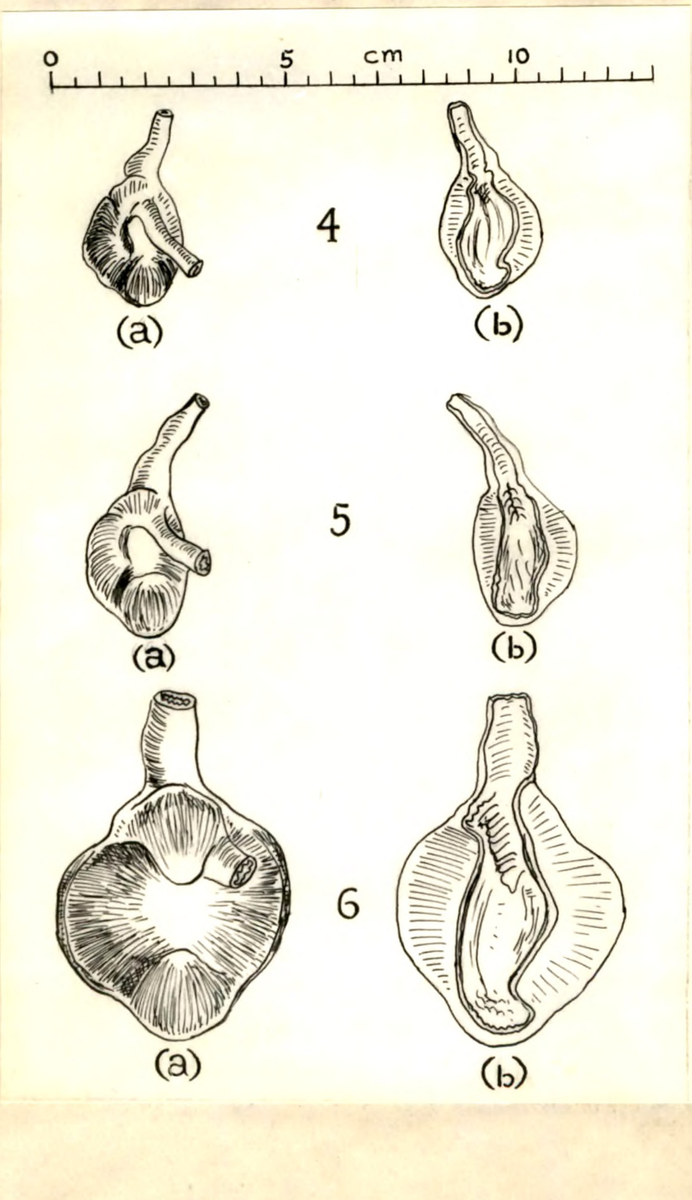
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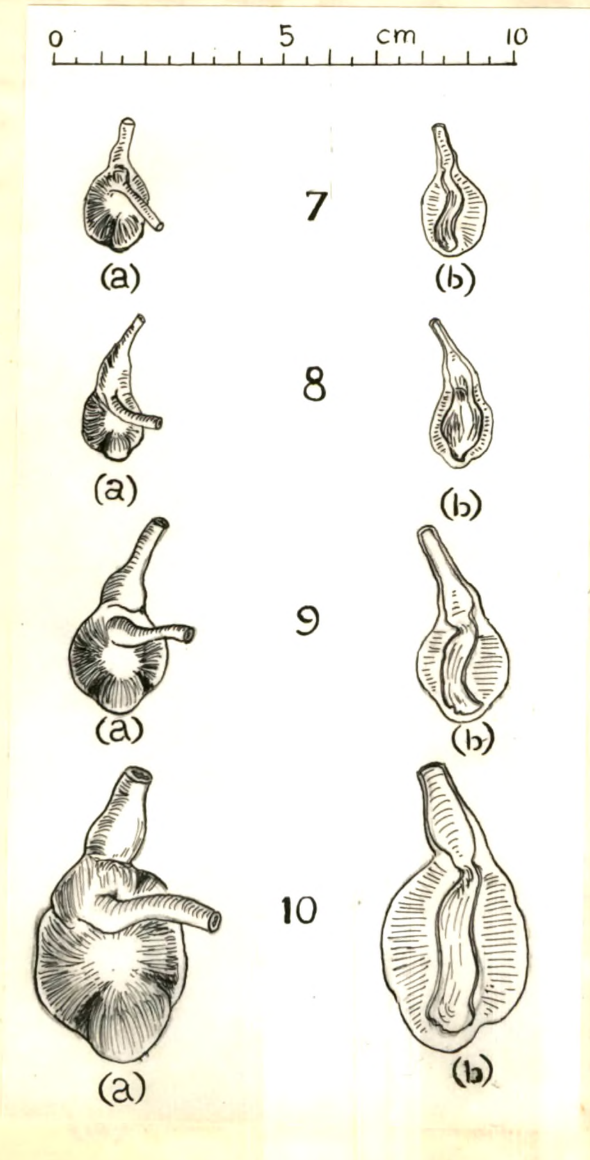
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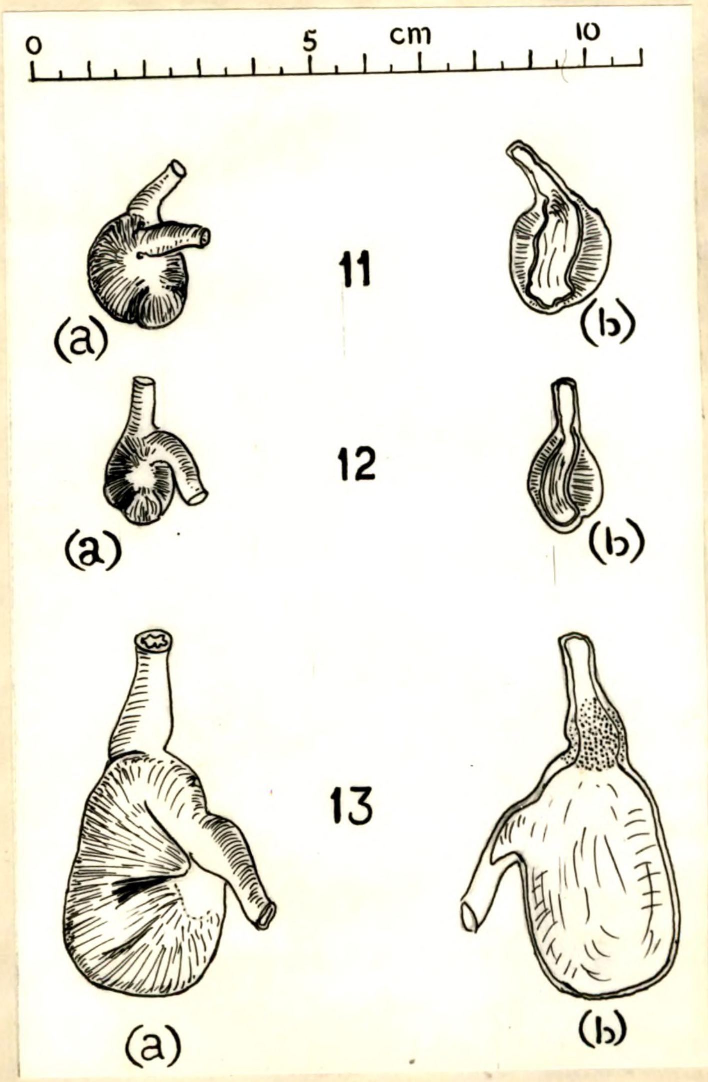
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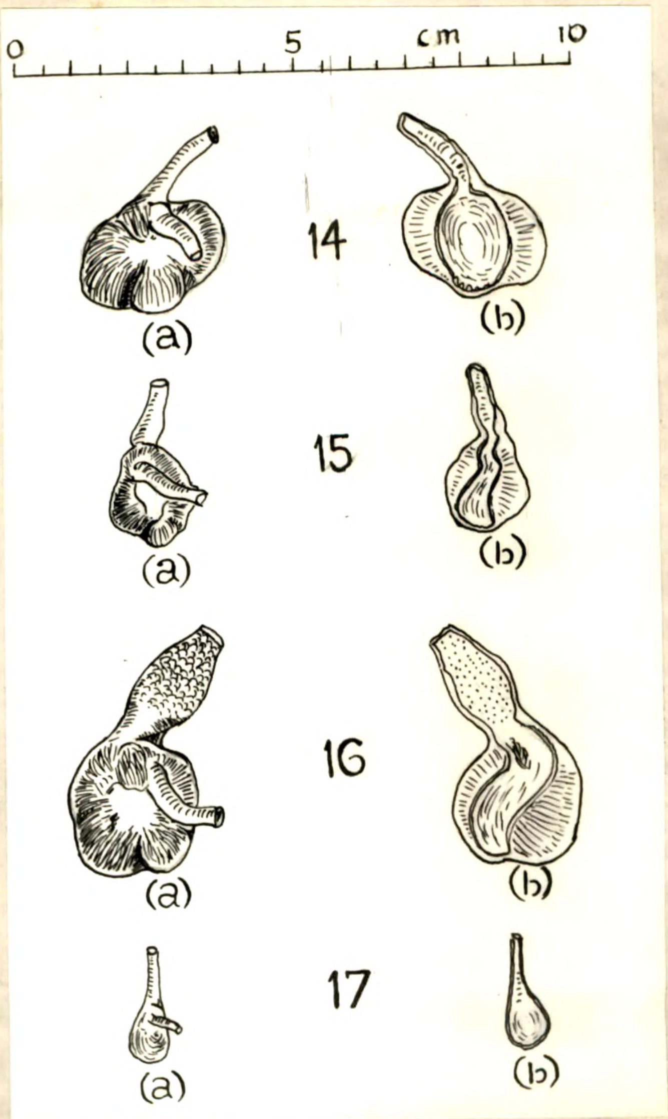
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of food. With the exception of a few viz., Shrike, Kite, Koel and to a certain extent Sunbird (Figs. 2, 3, 13, 17), all the other birds studied possess a well developed muscular gizzard. However, they differ each other in the thickness of its component parts viz., the keratin, mucosal, submucosal and muscular layers (Table IV). These differences are undoubtedly based on the type and consistency of food.

The granivore, represented by pigeon, is found to have a thick keratin layer. Keratin layer becomes stratified as newer ones are secreted by the mucosal tubules and added to the existing ones. Since the demand for the formation of keratin layer is higher in birds consuming harder food materials as in granivores and omnivores, the mucosal layer consisting of secretory tubules responsible for keratin secretion, is also well developed in such birds.

In general, the structural variations are very striking in only one factor that is, either the gizzard is highly muscular or sac like. Amongst gizzards with highly developed muscular layer, very little, if any, variations are noticed in their structural components. Perhaps the difference lies in the physiological and/or biochemical aspects. In some birds gizzard may have to perform continuous or sustained activity especially in those with crop (pigeon); while in others, it may function only spasmodically as and when food is ingested. Such differences in activity calls for metabolic adaptations. Reports and discussions on such metabolic adaptations have been recorded in the subsequent chapters of the thesis.