DISCUSSION

"Any modification of a structure that makes it particularly suited to its role in the life of an animal may properly be called an adaptation"

CHAPTER - VIII

DISCUSSION

One of the most important facts about the phenotypic variations caused by the environment is that is adaptive. Each kind of animal or plant or a micro-organism is a complex of adaptations for performing the life functions. During the course of evolution an organism undergoes various types of changes due to alterations in the gene complex and
fixed under suitable environmental conditions. As described by Verne Grant (1967), the related species whatever studied have been found to differ in their ecological characters. It is however, safe to assume that the ecological differences are synonymous with adaptive differences in a given set of environmental conditions.

Two conditions of population environment relations provide excellent opportunities for adaptive radiation. One occurs when a species enters into a new unoccupied habitat in which diverse ecological niches are freely available. Secondly the adaptive radiation results when the organism acquires a new set of complex adaptive characters which enable it to exploit an available environment more effectively than those already present there. As in other organisms, one can surmise that in avifauna also, successful genotypes as well as favourable heterozygous variants possessing adaptive characters met the challenge of the environment resulting in the formation of new species during the course of evolution.

Birds arose from their reptilian ancestors about 130 million years ago as crude flying animals
which resembled their progenitors in many respects. With the passage of the eons of time the succeeding generations of the birds evolved into diverging kinds of forms most of which exist to this day. Flight is the characteristic attribute of the birds and has played a prominent role in their evolutionary advance. The accomplishment of the power of flight demanded considerable economy of weight with increased rigidity and strength in its general structure. Gradually, useful adaptive modifications survived under selection pressure made the bird an ideal organism fully equipped for flight and all the major systems exhibited suitable modifications as adaptations to flight. Among the very many engineering adaptations which the birds have achieved, the development and muscular control of feathers and the metabolic set up for sustained flight stand out as major adaptive keys for successful propagation.

The advent of the sustained flight enabled the birds to occupy diverging niches and habitats hitherto unoccupied by the birds and other animal forms too. This conferred many advantages to the birds and the most obvious being the availability of a variety of diet. But the absence of teeth and the modification of the forelimbs into powerful wings had already deprived
the birds some of the normal advantages for food manoeuvring. Under these conditions, the bird had to take the advantage of the vast quantity of food material so freely available in nature, it was essential that the feeding apparatus should be suitably modified to meet with the challenge of the new demand. To capture the food and ingest it, the bird has to resort to different types of operations which include tearing, biting, sucking, holding, gaping etc. During the evolutionary advance, this challenge was met by the bill by assuming a wide variety of shapes obtained during the passage of time. No wonder, today the beak is considered as the most diagnostic characteristic of the birds. It is therefore, reasonable to assume that every structural component of the feeding apparatus, including the skeletal structures, the muscles, ligaments, and the physiological set up for energy supply is adequately adapted to the supreme functional efficiency in food manoeuvring.

As stated earlier, the functional anatomy of the feeding apparatus of different birds has been studied by several investigators in the past. Restricting our observations to the chick, it would be interesting to find out how far the observations made during the present investigations lead to the better understanding of the structural adaptations.
of its feeding apparatus.

The feeding apparatus of the male chick is useful to it in some other ways too. The male uses the organ for the production of sound and in holding the female during courtship. It is but natural that, these characteristics should reflect on the sexual dimorphism as far as the feeding apparatus is concerned.

EPIDERMAL STRUCTURES OF THE BILL AND TONGUE

As described earlier, the epidermal structures of the bill and the tongue in birds exhibit wide structural modifications in response to their specific feeding habits. The birds manipulate these structures with the utmost efficiency in the capture, transport and other mechanical processes preliminary to the digestion, of the food material.

In chick, the epidermal structures covering the bill are hard and smooth. The smooth culmen of the bill makes it an efficient organ for probing. The upper bill has a slightly curved nail. Such a nail is of a great advantage to the chick in picking the food grains and seeds of grass from the ground. The curved nail also helps the bird in holding the food grains when
it is picked up, and prevent the food from falling. The maxillary tomia are sharp anteriorly whereas, they are comparatively blunt towards the commissure. It is in the anterior region of the bill that the seed is manipulated for the removal of the glumes. During this operation, the seed is held in between the sharp tomia and rotated forward and backward movements of the tongue. The obovate depression observed in the median and the lateral ridges of the buccal surface of the rhinotheca are ideally suited to lodge the massive fleshy tongue. The well developed lateral grooves present along the maxillary tomia help to lodge the mandibular tomia as the bill is closed. The sharp maxillary and the mandibular tomia are also helpful in scraping the viscous food from the ground.

The median ridges of the rhinotheca form major guide rails for the forward and backward movements of the tongue inside the buccal cavity. The epidermal covering of the tongue bears corresponding grooves on its dorsal and ventral surfaces which fit over the ridges of the rhamphotheca during the linear movements of the tongue. The palatal spines distributed along the line of the choanal slit are well developed and slightly directed inwards.
over the choanal slit. Such an arrangement of the spines prevents the food from entering into the choanal slit.

One of the functions of the tongue is to rotate the food material in the buccal cavity with the help of the lateral surface of the tongue. The posterior extremity of the tongue is provided with large horny spines which not only ensure the movements of the food material towards the gullet but also prevent the movement of the food material in the opposite direction.

Soon after the liberation from the egg, the chick starts feeding on the grains and other small sized food material. The small pointed forcep-like beak and the nail of the 1 day EX OVO chick serve as efficient organs for picking minute sized food material from the ground. By around 60 day EX OVO it starts feeding on the large sized food materials and this is facilitated by the large outgrowths of the rhamphotheca anteriorly into a well developed nail and laterally into large cutting edges. In the male bird, the nail and the maxillary tomia protrude considerably outside as irregular lateral expansions. The strong curved nail of the male bird is
of great advantage in clasping the female during mating.

OSTEOLOGY AND LIGAMENTS OF THE SKULL

BRAIN-CASE:

As a part of the feeding apparatus the brain-case plays an important role in the attachment of the muscles which bring about the movements of the lower and upper jaws. Furthermore, the brain-case forms the main spring board for the origin of the adductor muscles which arise from the upper medial surface of the lateral sides of the cranium. The surface area may be smooth or may form various depressions depending upon the mass of the muscles and the area of attachment for lodging the adductor muscles.

The orbit of the brain-case of chick is separated by a more or less complete interorbital septum which is comparatively heavily ossified. Such a structure helps in contributing extra strength and rigidity to the skull. As Zusi (1962) has pointed out, it also helps in "providing extra support for enlarged jaws and palate". Furthermore, a heavily ossified interorbital septum is of a great advantage to the skull in reducing and nullifying the force generated
B

Photographs of the adult skull of chick

1. Dorsal view
2. Lateral view
3. Ventral view
4. Ventral view (dentary removed)

F = Female skull, M = male skull
at the bill before they are transmitted to the cranium (Sims, 1955). The dorso-lateral surface of the skull is obliterated by a deep temporal fossa and a shallow rudimentary squamosal fossa. The suprametal and the lambdoidal ridges are well marked and the zygomatic process is also well developed. The upturned postorbital process of the frontal and the large zygomatic process of the squamosal provide strong support for the attachment of the thick post-orbital ligament. Furthermore the zygomatic process is broad and twisted outwards forming smooth concave surface. This flat surface and the wide depth of the temporal fossa provide a larger area for the lodging of the M. adductor mandibulae externus seresis of muscles. The well raised suprametal and the lambdoidal ridges also help in increasing the surface area for the origin of the A.M.E. medialis muscle. The frontonasal hinge is comparatively wide and well developed with a deep notch in the middle. The well developed frontonasal hinge works as an ideal pivot in the kinetic movements of the upper jaw.

The Lacrimal is short and moderately developed and contributes to the formation of a large area for the orbit. Moreover, the ventral foot of the lacrimal
Histograms showing the dimensions of the bony elements of the skull.
PLATE - XXXVIII
SKULL DIMENSIONS
DIMENSIONS OF THE BONY ELEMENTS OF THE SKULL

- CRANIAL LENGTH in mm
- CRANIAL HEIGHT in mm
- WIDTH OF THE NASAL OPENING in mm
- TEMPORAL WIDTH in mm
- WIDTH OF SUPRAORBITAL LITHIMUM in mm
- WIDTH OF FRONTONASAL HING in mm

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<th>1 DAY</th>
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extends into a stout elongation forming the main bony support for the lacrimo-jugal ligament.

UPPER JAW:

The premaxilla is long and stout with sharp cutting edges. The bone in turn is connected to the quadratojugal bar. The cutting edges of the premaxilla and the quadrato-jugal bar form an angulated commissure. The existence of a highly angulated commissure helps in giving a greater power and speed at the tip of the bill (Beecher 1962). The maxilla is highly reduced in size and as pointed out by Jollie (1957), "contributes little to the margin of the upper jaw, but forms a part of the lateral surface of the anterior end of the palatine and sends small sheet-like processes towards the middle line". The quadratojugal bar is considerably thin and pliable and slightly bent laterally outwards providing a greater area for the passage of the adductor muscles. The ball and socket joint of the quadratojugal bar with the quadrate also enhances the free movement and rotation of the upper beak during retraction.

The quadrate is articulated more or less vertically (almost 90°) with the cranium and possesses
Histograms showing the dimensions of the bony elements of the skull.
DIMENSIONS OF THE BONY ELEMENTS OF THE SKULL

- Skull Length in mm.
- Skull Height in mm.
- Skull Width in mm.

Graph showing the dimensions of the bony elements of the skull over different days and between males and females.
two well developed processes known respectively as the orbital and the otic processes. The otic process is articulated with the lateral side of the squamosal. The orbital process is comparatively large and slightly curved inwards providing a greater surface area for the origin of the pseudoternioporalis muscle. Furthermore, the ventral surface of the orbital process and the elevated anterior lateral surface of the quadrate body together provide a triangular elevated surface for the origin of the M.A.M. posterior.

LOWER JAW

The mandible appears more or less as a single piece because of the early embryonic fusion of the various skeletal components. Such a rigid structure of the mandible is best suited for seed eating habit of the animal. It requires a considerable forceful action of the jaws. The mandibular fossa is narrow and deep. The rami of the mandible are highly arched and fit tightly with those of the upper jaw in the closed bill. The low triangular depression on the surangular provides a concave surface for the insertion of the M.A.M.E. medialis muscle. Posterior most surface of the surangular is considerably depressed and smooth providing a greater area for the attachment of the M.A.M. posterior. The considerably long retroarticular
Histograms showing the dimensions of the bony elements of the skull.
SKULL DIMENSIONS
DIMENSIONS OF THE BONY ELEMENTS OF THE SKULL

- Anterior bill length in mm.
- Anterior bill height in mm.
- Upper bill length in mm.
- Posterior bill height in mm.
- Anterior bill width in mm.
- Bill width in mm.

Graph showing dimensions over different stages and sexes.
process of the dentary helps in the protraction of the upper beak as stated by Zusi (1967). The dorsal surface of the dentary is supplied with a well developed coronoid process which forms a hard bony support for the insertion of the strong tendon of the M.A.M.E. superficialis.

PALATE:

One of the main functions of the palate in birds is the transmission of the force and direction of the movements of the muscles of the upper beak. The palatine is long and supplied with a well raised palatal wing. It is slightly curved so as to form a concave bowl-like choanal field. Such a curvature of the palatine not only increases the area of attachment of the associated muscles but also provides strength to the membrane bones. The palatines are comparatively more ossified anteriorly giving more strength and rigidity to the structures and preventing disarticulation during the kinetic movements. The flat dorsoventral depression and the well raised palatal wings provide a considerably larger area for the attachment of the A.M. internus set of muscles. The petrygoid is dorsoventrally flattened and depressed anteriorly. Such a structure
Histograms showing the dimensions of the bony elements of the skull
DIMENSIONS OF THE BONY ELEMENTS OF THE SKULL

- LENGTH OF THE PALATINE IN mm.
- LENGTH OF THE PTERYGOID IN mm.
- LENGTH OF THE QUADRAT IN mm.
- LENGTH OF THE MANDIBLE IN mm.
- HEIGHT OF THE MANDIBLE IN mm.

Chart showing data for different time intervals (1 day, 10 days, 30 days, 60 days, 120 days) and different categories (male, female).
provides a comparatively large, flat surface for the anchorage of the A.M.I. dorsalis muscle. The Vomer is partly bony and partly cartilagenous and helps "to hold the palatines close together anteriorly preventing these bones from sliding upward along the lateral surfaces of the rostrum during the protrusion and from separating due to the pull of the pterygoideus muscle" (Zusi, 1962).

HYOID APPARATUS

The broad lanceolate entoglossum forms the strong bony support for the tongue. The paraglossa of both the sides are fused together leaving a narrow space in between. The basihyal is strong and stout forming the main bony support for anchorage of the M. gularis. The deep lateral grooves of the basihyal provide extra flat surface for the attachment of the M. gularis anterior. The basibranchials are considerably long and heavily ossified providing greater support to the tongue.

ARTHROLOGY OF THE QUADRAT - ARTICULAR JOINT

The arthrology of the quadrats- articular joint is of significant importance in the bird skull since it is directly connected with the dorsoventral movements of the jaws. The otic process of the quadrat
is broad and bears a flat articulating surface towards the tip which fits in a deep notch on the squamosal. Such an articulation delimits the rotation of the quadrate in a single plane and prevents the disarticulation of the former during the protractory movements of the jaw. The quadrate articulates laterally with the jugal bar and ventrally with the articular of the mandible. This articulation as described by Bock (1964) is a "complex rotatory sliding hinge" over which the mandible is moved up and down. The broad quadrate base possesses three well developed articulating condyles, together forming a triangle, which fit into the corresponding facets of the articular. The elevated "median condyle slides along well defined medial face of the broad flattened articular surface" (Zusi, 1967). This long medial face forms the main guide rail for the sliding of the quadrate while the other two condyles prevent the lower jaw from slipping backward, forward and sideward under the pressure and tension likely to occur during the gaping actions. The articular bears four articulating surfaces and three facets on its posterior surface. The dentary bares processes, the external, internal, the pseudotemporal and the retroarticular. The well
developed medial condyle of the quadrate abuts against the shallow depression situated in between the external and the retroarticular processes. Such an attachment prevents a backward movement and displacement of the mandible and at the same time delimits the forward movements of the lower jaw. The internal process also prevents sideward displacement of the mandible when the tension is applied on the latter by the post-orbital ligament.

KINESIS OF THE UPPER BEAK

Bock (1964) has described six possible functions of the cranial kinesis in birds and these have been critically reviewed by Zusi (1967). As stated by the latter author, the primary advantage of the kinesis is that it provides greater possibilities for the diversity of manipulation of the jaws. It also helps in the gaping action as well as in the maintenance of the primary axis of the bill. A correlation between the kinetic movements of the upper jaw of birds and their specific feeding habits has already been established by many investigators. Beecher (1962) examined the kinetic properties of the upper beak and noted that the seed eaters had lowest mobility of the upper jaw (13°) as the seed eating
habit required a relatively smaller gape. The observations made by Malhotra (1967) on the passerines showed that the passer, which feeds on seeds required to apply the force mainly at the bill tip and speed as such is not a major consideration, had low degree of movements of the upper beak. Dicrurus, on the other hand feeding on flying insects and required to produce a wide gape during the devouring operations, had large kinetic movements of the upper beak. (33°). Goodman and Fisher (1962) have found that the large fish eating water fowls possess a greater degree of the movement of the upper bill.

The skull chick is prokinetic with well established dorsoventral movements of the upper jaw on the frontonasal hinge. With the forward movements of the mandibular foot of the quadrate, the pterygoid pushes the palatines forward resulting in the protraction of the upper jaw. Also the forward rocking of the quadrate pushes the quadratojugal bar anteriorly which ultimately aids the raising of the upper bill. The figures obtained for kinesis of the chick are approximate and subjects to error but give a fair idea about the kinetic properties of the skull during the post-natal growth and development.
As stated earlier, the chick feeds on small sized food material soon after the liberation from the egg and a wide gaping of the bill is not required during the early periods of development. The kinetic values obtained for the skull were minimum ($3^\circ$) at 1 day \textit{EX OVO} and it showed a progressive increase during the postnatal period. At 10 day \textit{EX OVO} period the kinetic value showed a two fold increase and this can be correlated with the greater development of the jaw muscles and rapid feeding behaviour observed during the periods after the 10 day \textit{EX OVO} development. By about 60 day \textit{EX OVO} the chick appears to attain all most all the characters of the adult with a greater increase in the kinetic value ($20^\circ$). The succeeding stages revealed a by and large steady increase in the kinetic value showing stability of growth and maturation during senility. In the adult male birds the kinetic movements show greater importance in sound production and gaping actions of the beak leading to courtship plays during the mating. The comparatively high values obtained for the male ($29^\circ$) birds can be accounted for its wide gaping actions required in sound production and courtship play. Furthermore, the quadrate is comparatively more vertical in male birds and the curvature of the palatine is considerably reduced
than in the females. Such a modification helps in a complete
transmission of the force applied by the quadrate to
the bill tip resulting in a greater elevation of the
upper jaw during the protraction. In female the
quadratejugal bar is comparatively laterally
depressed whereas, it is highly arched in the male.
Such a depression of the quadratejugal bar in female
delimits the power of the kinesis to a greater extent
as pointed out by Zusi (1962). A comparatively
wide frontonasal hinge of the male bird works also
as an ideal pivot for a greater degree of kinetic
movement in the male bird.

LIGAMENTS OF THE SKULL

The ligaments of the avian skull are composed
of collagenous fibers and are flexible in nature
(Stark 1940; Barnikol 1952). The ligaments help to
maintain the tension on the bones to which they are
attached and thereby keep the bones tight together
when the jaws are closed. It holds the bones in
place firmly during the various gaping operations and
they are subjected to high tension when the bones
attached are moved. In the mobility of various bony
articulations the ligaments work as limiting factors
to the movements to the required extent and protecting
against the disarticulation of the joints etc.

The ligaments observed in the chick skull are the post-orbital ligament, the external-jugomandibular ligament, the occipitomandibular ligament, and the lacrimo-jugal ligament. All these ligaments represent more or less uniform structure except for a difference in the degrees of their development in length, thickness etc. They are directly connected with the jaw articulation and the kinetic movements of the upper beak. The post-orbital ligament is well developed and comparatively highly calcified. As observed by Bock (1964), it is flexible but inextensible and its function as a protector of the quadrate-articular joint is conspicuous. Further, as stated by the same author, when the lower jaw is depressed the post-orbital ligament becomes loaded with pressure, the quadrate swings forward to maintain the distance between the attachments of the post-orbital ligaments. The post-orbital ligament also maintains the upward tension on the articular bone and according to Zusi (1967), provides a fulcrum for the movements of the mandible. The external-jugomandibular and the occipitomandibular ligaments prevent a forward disarticulation of the mandible and provide an upward tension when the bill is
depressed. The lacrimojugal ligament is thick and well developed and is supported by a long stout bony extension from the lacrimal bone. As stated by Cracraft (1968) the ligament serves as a "protractors stop by preventing the jugals from the moving too forward during protraction".

MECHANICAL ADVANTAGE

The measurements of the length of the axis of the quadrate and the length of its orbital process have been used to determine the mechanical advantage of the skulls. The importance of the mechanical advantage of the skull during the feeding has been discussed by many investigators including Beecher (1962) and Malhotra (1967). The latter author studied the mechanical advantage of the skulls in some Indian passerines and showed that this advantage is comparatively higher in passer in confirmity with the force required to be exerted at the bill tip during the granivorous mode of feeding. On the other hand the lowest mechanical advantage in the passerines studied, is obtained in Dicrurus which requires a rapid action of the bill for catching the insects.

Attempts carried out during the present study to determine the mechanical advantage of the chick skull
during the post-natal period of growth and
development revealed by and large a steady value
throughout the periods of senility. At 10 day EX OVO
the mechanical advantage is slightly higher (.557) than
all the stages studied. The chick feeds very rapidly
soon after liberation from the egg and this feeding
behaviour can be correlated with the high mechanical
advantage during the early periods of post-natal
growth. The difference observed in the mechanical
advantage of the skull of both the sexes were however,
insignificant.

RATE OF GROWTH AND THE DIMENSIONS OF VARIOUS BONY
ELEMENTS OF THE SKULL (PLATE - XXXVII, XXXVIII,
XXXIX, XL & XLI).

The Wolff's law of transmission dealing with
the response of bone to mechanical strain has been
studied from a wide variety of viewpoints and it is
generally accepted that "the functioning of muscles
directly influences the morphology of the bones".
(Hyote and Enlow, 1966). It is believed that the
bone is responsive to extrinsic forces which
function to determine its own shape and as such forces
serve to augment any intrinsic or genetic factors
which act within the bone itself or its covering
membranes (Felts, 1959). It has been generally assumed
that the pull of a muscle acts to stimulate the disposition and the attachments of the muscles are responsible for determining the gross morphology of the whole bone.

As stated by Moore (1965) the "over all proportions and the detailed form of bones are dependent upon the mechanical strain" which the muscles produce continuously. Studies conducted by Howell (1917), Allison and Brook (1921), Gillespie (1954) have noted that a reduction of muscular activity results in the associated bones becoming smaller and less dense during development. Pratt (1943) had earlier shown that the removal of one masseter in rats of one week old created an asymmetry in the development of the mandible which grows towards the operated side. Experimental evidences reported by Dockladal (1964) revealed that a bilateral removal of the masseter and temporal muscles from newly born rats led to a decrease in the length of the face and the braincase and the width of the cranium.

Measurements of various bony elements taken during the postnatal period of the chick throw some light on the rate of growth of various components and their response to the mechanical strain applied by the
muscles. The highest rate of growth is observed in the skull length which increased considerably (from 37 mm. to 73 mm.) during this period. The cranial length and the mandibular length also showed comparatively a high rate of growth. A high rate of growth observed in the skull length and the mandibular length could be attributed to an adaptation for great mechanical stress of various muscles which these bones are subjected to. On the other hand, the rate of growth observed for the width of the supraorbital isthmus, width of the frontonasal hinge and the temporal width are almost slow and uniform. It may be interesting to note that these structures are not directly connected with the operation of the jaw muscles and the growth rate observed is steady and uniform. The rate of growth observed for the upper bill length is higher in comparison to other dimensions obtained for the bill viz., the anterior bill height, the upper bill length, anterior bill width, posterior bill width etc. A high rate of the upper bill shows a comparatively higher development of the bill during the post-natal period.

Of all the dimensions of the various individual bones of the skull studied, length of the palatine shows a very high rate of growth. In chick
the retraction of the upper beak involves the mobility of a series of bony elements and the M.A.M. Internus exerts the mechanical force for the operation. The M.A.M.I. dorsalis which is attached to the pterygoid is comparatively reduced in size whereas, the M.A.M.I. ventralis is broad and highly massive. The palatine provides the main bony surface for the origin of M.A.M.I. ventralis. The rate of growth observed for the pterygoid is considerably slow and can be attributed to a comparatively low rate of growth of the muscle. M.A.M.I. Ventralis grows into massive structures during the post-natal period and the rate of growth obtained for the palatine is considerably higher.

The dimensions of the various bony elements obtained separately for the male and female birds reveal the presence of sexual dimorphism. The skull length and the skull width evince a greater degree of growth and development of the male skull which is a great advantage in using the bill as an efficient organ in offense and defense. As is well known, the cock is famous for its fighting habit, a comparatively higher palatine length in the male, provides considerably large bony surface for the attachment of the massive M.A.M.I. ventralis muscle,
the contraction of which brings about the retraction of the upper jaw which is so essential in biting.

The width of the supraborbitallisthmus and the frontonasal hinge is also considerably higher in male birds. A wide frontonasal hinge contributes extra rigidity to the bill (Richardson, 1942) and also works as an ideal pivot in the kinetic movements of comparatively greater degrees. A large kinetic ability confers an advantage to the male bird both during fighting and the production of sound.

SALIENT FEATURES OF THE MYOLOGY OF THE FEEDING APPARATUS

The unparalleled versatility of the avian bill as an efficient tool largely depends on its mobility in various planes and directions. The bird manipulates the bill in a great variety of ways to seize the prey with utmost efficiency. A fish eater for instance is known for its alertness and as soon as the prey is cited the bird opens the mouth with the least possible delay and traps the prey. Besides catching the fish, they also have to be careful in preventing the struggling catch from escaping. This necessitates the need of exercising a strong grip on the prey. A seed eater on the other hand picks the tiny seeds from the ground, since the food is quite secured, a hurried operation of picking the
food is not very essential. Some of birds are also known to remove the glume from the seed and this may mean a sustained operation of the beak before the food is finally ingested. As stated earlier, several authors who worked on the myology of the feeding apparatus have observed striking correlations existing between the structure and disposition of various muscles and specific feeding habits.

In chick the jaw muscles which are associated with the seizure of the prey and its transport towards the gullet may be divided into three major categories based on its primary functions.

I. MUSCLES OPERATING THE BEAK

A. ADDUCTORS OF THE LOWER JAW
   1. M.A.M.E. superficialis
   2. M.A.M.E. medialis
   3. M.A.M.E. profundus

B. ADDUCTORS OF THE LOWER JAW AND RETRACTORS OF THE UPPER JAW
   1. M.Pseudotemporalis
   2. M.A.M. Posterior
3. M.A.M.I. Dorsalis
4. M.A.M.I. V. Anterior
5. M.A.M.I. V. Posterior

C. ABDUCTORS OF THE LOWER JAW
1. M. Depressor mandibulae

D. PROTRACTORS OF THE UPPER JAW

II. MUSCLES WHICH RAISE THE BUCCAL FLOOR
1. M. Intermandibularis
2. M. Gularis anterior.

III. MUSCLES OPERATING THE TONGUE

A. DEPRESSORS.
1. M. Interkeratoideus
2. M. Hyoglossus
3. M. Hypoglossus anterior
4. M. Hypoglossus posterior

B. LEVATORS:
1. M. Gularis anterior
2. Gularis posterior

C. EXTENORS
1. M. Branchiomandibularis
D. RETRACTORS

1. M. Gularis anterior
2. M. Sternohyoideus
3. M. Cricohyoideus
4. M. Thyrohyoideus
5. M. Tracheohyoideus

It may be mentioned here that a muscle can function in more than one way. For instance, some retractors of the upper jaw, like the M. Pseudotemporalis and M. A. M. Internus, secondarily also serve as adductors of the lower jaw. The depressor mandibulae muscle is also known to serve in protraction of the upper beak. The functions attributed here refer to main functions performed by various muscles.

1. MUSCLES OPERATING THE BEAK
2. ADDUCTORS OF THE LOWER JAW
3. M.A.M. Externus superficialis

This muscle plays an important role in the adduction of the lower jaw. It is a well developed, fan-shaped, pinnate muscle lodged in the deep temporal fossa of the cranium. The muscle is massive and broad towards the origin and supplied with a stout, tendinous ribbon towards the insertion. The tendinous
ribbon provides the extra area for the attachment of the fibers and this strong tendinous ribbon is best suited to lift the mandible with a greater force and helps to maintain a tight grip on the food material.

2. M.M. Enternus medialis

This is a highly developed muscle which spreads as a massive fleshy bundle towards the floor of the orbit. It arises in a narrow aponeurotic sheath and extends below the quadrate-jugal bar filling the space left between the zygomatic process and the surangular. The muscle is mostly fleshy and supplied with a well developed median raphe which runs downwards towards the mandible, and terminates in a broad tendinous sheath which is situated superficially over the belly. The insertion is partly fleshy and partly tendinous over the surangular. The triangular depression on the lateral surface of the surangular offers the bony surface for the anchorage of the deeper fibers while the superficial fibers get attached to the tendinous sheath. Such a broad insertion ensures a greater grip over the food material as the jaws are pulled upwards.
3. **M.A.M.E. Externus profundus**

The muscle is comparatively less developed and runs along the lateroventral extremity of the M.A.M.E. Medialis. The muscle is spindle-shaped, lodged in the narrow and elongated squamosal fossa. The fibers show a highly pinnate arrangement and the median raphe is considerably thick and stout. The muscle gains insertion mainly on the broad tendon of the M.A.M.E. medialis, and partly on the surangular immediately behind the insertion of the former muscle. Such an extensive insertion shows a co-ordinating action of both the muscles together resulting in applying a considerably strong grip over the food materials when the beak is closed.

4. **M.A.M. Medius**

The muscle is represented by a single unit. It is partly fleshy and partly tendinous and originating from the posterior wall of the orbit. The muscle is supplied with a broad and long tendon which becomes narrow and strap-like as it runs downward towards the dentary, where it gets embedded in the main muscle mass. The tendinous structure provides considerably extra area for the origin of the
fibers. The insertion is fleshy broad and massive along the entire inner surface of the articular. Such an insertion facilitates the bird in applying a considerably strong pull over the mandible by creating a greater pressure on the articular in the vertical direction and partly by increasing the length of the effort arm.

**ADDUCTORS OF THE LOWER JAW AND RETRACTORS OF THE UPPER JAW.**

As stated earlier, the M.Pseudotemporalis and M.A.M. Posterior perform the dual functions, primarily as adductors of the lower jaw and secondarily as retractors of the upper jaw.

1. **M. Pseudotemporalis.**

This is a highly developed muscle with a considerably broad origin which covers the entire dorsal surface of the orbital process of the quadrate. The muscle runs almost vertically downwards as a broad fleshy sheet to get inserted on the inner surface of the surangular. A small aponeurotic sheath is present towards the tip of the orbital process of the quadrate and adds extra surface area for the origin of the fibers. The vertically running fibers help in applying a considerably greater pull on the surangular
in the upward direction. The contraction of the muscle also rocks the quadrato orbital process of the quadrato downward resulting in the retraction of the upper beak.

2. M.A.M. Posterior.

This is a small but massive muscle which envelopes the entire ventral surface of the quadrato body towards the posterior extremity of the orbital process. The origin as well as the insertion are mostly fleshy and broad. The muscle is provided with a small tendon towards the origin the the fibers exhibit mostly parallel arrangement. Because of the fleshy and parallel nature, the muscle is ideally suited for quick actions for short durations.

RETRACTORS OF THE UPPER JAW AND ADDUCTORS OF THE LOWER JAW

As already stated the M.A.M. Internus performs two functions viz. retractions of the upper beak and adduction of the lower beak. Nonetheless, the main function of the muscle is the retraction of the upper beak.
The **M.A.M. Internus** is a well developed muscle which forms the massive fleshy floor of the orbit. The muscle is divisible into two parts, the dorsalis and the ventralis. The dorsalis part is comparatively reduced in size and occupies the dorsal extremity of the pterygoid. The ventralis is further divided into an anterior and a posterior parts. All the parts are highly tendinous in nature supplied with broad aponeurotic sheaths spreading over the entire ventral surface of the belly. The highly tendinous nature of the muscle helps in creating a considerably strong pull for a long duration on the palatine and the pterygoid resulting in a forceful retraction of the upper beak.

**ABDUCTOR OF THE LOWER JAW**

The **M. depressor mandibulae** is the sole abductor of the lower jaw and brings about its depression by pulling the mandible from behind the quadrato-articular joint. The muscle also helps simultaneously to certain extent in the protraction of the upper arm of the bill.
M. depressor mandibulae is broad and highly developed with a broad massive origin and a narrow compact insertion. The muscle is supplied with a deeply situated aponeurotic sheath towards the origin and a narrow tendinous sheath at the insertion. Except for this, the muscle is mostly fleshy and parallel in nature facilitating the quick and repetitive opening of the beak.

PROTRACTION OF THE UPPER BEAK

As stated earlier, the M. depressor mandibulae also working as the protractor of the upper jaw, the M. sphenopterygo-quadratus serves as the main protractor of the upper beak. This is a highly tendinous muscle compact in nature. It spreads along the inner lateral surface of the laterosphenoid bone. The tendinous material present towards the insertion spreads considerably dorsally over the belly as a stout strap along its anterior end. The highly tendinous nature of this muscle helps the bird in applying a sustained pull of the quadrate towards the cranium.

The main adductors and abductors of the lower jaw are highly fleshy and comparatively less tendinous than the protractors and retractors of the
upper jaw. The protractors and retractors on the other hand are more tendinous and comparatively less fleshy in nature. This structural heterogeneity of the jaw muscles enforces that the adduction and abduction in the chick are quick and repetitive whereas the protration and retraction are slow and sustained. A quick opening of the bill is of great advantage to the chick's germinivorous feeding habits. The protration and the retraction of the upper beak involve the mobility of a series of interconnected bony elements and require a strong sustained pull for a considerably longer duration in creating alterations in the natural position of the bony components. The presence of the well developed tendinous structures in the adductor and abductor muscles on the other hand ensures a great advantage to the bird in maintaining a strong upward tension which is useful in narrowing the gape. The longer work arms are known to reduce the effective force of adduction considerably towards the bill tip and in chicks this deficiency is compensated to a greater extent by the presence of the tendinous materials in the adductors muscles which help it in maintaining strong upward tensions.
MUSCLES OPERATING THE BUCCAL FLOOR

The raising of the buccal floor is brought about by two sets of muscles, the M.intermandibularis and M. gularis posterior. The depression of the buccal floor on the other hand is accomplished by the adduction of the lower jaw.

The M. intermandibularis and M.gularis are well developed in chick. The origin of the M. intermandibularis is quite extensive and covers most of the surface of the groove present on the inner lateral surface of the dentary. The M.gularis posterior arises partly and partly tendinously from the surface of the crest present above on the dorsal side of the cranium and partly from the occipital bone. The insertions of both the muscles are also considerably broad. Both the muscles exhibit a parallel arrangement of fibers and facilitate a quick raising of the buccal floor and make the gulping easier.

MUSCLES OPERATING THE TONGUE

The main function of the tongue in birds involves adjustment of food in a proper direction
and its transport towards the gullet. In male chick it also helps to certain extent in the production of sound. Various movement of the tongue during the feeding operations are the levation, depression, extension and retraction.

LEVATORS OF THE TONGUE

As stated by Goodman and Fisher (1962), the muscles which are responsible for the raising of the buccal floor also simultaneously bring about the levation of the tongue. The M. intermandibularis and M. gularis posterior described earlier also serve in the levation of the tongue.

The raising of the tongue is also brought about by the M. gularis anterior. It is a well developed long strap-like muscle which gains a broad insertion on the lateral surface of the basihyal. The muscle exhibits a parallel arrangement of the fibers and the high degree of development of the muscle reflects its adaptive ability for a more effective raising of the tongue.

DEPRESSORS OF THE TONGUE

The depression of the tongue is brought about by the M. interkratoideus, M. hyoglossus, M. hypoglossus
anterior and M. hypoglossus posterior. The M. Interkeratoideus is broad and massive towards the origin but becomes considerably narrow and compact towards its hypobranchial insertion. It shows a parallel arrangement of the fibers. The M. hyoglossus is very well developed, massive and compact with partly fleshy and partly tendinous origin and insertion. The tendons are well developed and strap-like and the fibers show a pinnate arrangement. The muscle also helps in the lateral movements of the tongue to a certain extent. The M. hypoglossus anterior which is situated on the ventral surface of the tongue also is pinnate in structure. The origin is fleshy and broad whereas the insertion is narrow and tendinous at the tip of the tongue. This muscle is best suited to bring about the depression of the tongue anteriorly. The hypoglossus posterior is broad and well developed and extends considerably downwards in the buccal cavity. This muscle brings out the depression of the posterior part of the tongue.

EXTENSORS OF THE TONGUE

The forward movement of the tongue is brought about by a single muscle, the M. branchiomandibularis. This is a massive band of
parallel muscle fibers which arise in a broad fleshy origin from the groove present on the inner surface of the dentary. The insertion is also fleshy and massive and envelopes the entire surface of the ceratobranchial.

RETRACTORS OF THE TONGUE

The retraction of the tongue results by the combined action of several muscles viz., M.gularis anterior, M.sternohyoideus, M.cricoideus and M.thyroglossus. These muscles bring about the adduction of the gongue along with its retraction. The M.sternohyoideus is well developed and spreads as a thick band of parallel fibers. The broad fleshy insertion covers the entire inner surface of the hypobranchial. The M.cricoideus and the M. thyroglossus are in the form of thick elongated ribbons. All these muscles are well suited for the quick handling of the food and its transportation towards the gullet.

All the jaw and tongue muscles studied are comparatively highly developed and more massive in the male birds. This difference in the degree of development of muscles can be explained on the specific behaviour of the male birds. The muscles are comparatively more massive and the tendinous material is more thick and stout. The high
development of the tendinous material in the adductors is of great advantage to the male bird in the prolonged opening and closing the mouth for producing long and extended call notes and the highly tendinous nature of the protractors and retractor ensures the cock in the sustained protraction and retraction of the upper beak in holding the female during the sex play respectively.

POSTNATAL GROWTH OF THE JAW MUSCLES

Muscles are known to undergo pronounced morphological alterations which are progressive with age and yet various muscles preserve their structural identity throughout their adult life. As stated by Bourne (1960), the major changes in the muscle are the "increase in the fibrous connective tissue and fat and modification of water and electrolytic contents".

The functional capacity of avian bill is limited by the speed of contraction of the muscles on one hand and the force exerted by them on the other. As a muscle approaches its maximum force the velocity of contraction fails. For instance, the tearing of the flesh of the prey means a forceful action and is determined by the number and state of
development of the active fibers which in turn are
affected by the training to which the muscles have
been subjected during growth. On the other hand an
instant snapping of the beak is essential to catch
insects on wings. The balance is thus struck between
the speed and the force of muscular contraction
in order to accomplish the task with utmost
functional efficiency.

As described earlier in chicks both the
adduction and abduction are quick and repetitive
processes than the protraction and retraction of
the upper jaw. The latter functions are slow and
sustained. A muscle which is highly fleshy in
structure is best suited for quick and repetitive
contractions. It has been already noted that the
adductors and abductors of the lower jaw are
comparatively less tendinous and more fleshy than
the protractors and retractors of the upper jaw.

The chick is known to consume its food very
rapidly soon after liberation from the egg, all the
jaw muscles are generally involved in quick and
repetitive contractions during the early post natal
period. It is interesting to note that all those jaw
muscles viz., adductors, abductors, protractors and
retractors are highly fleshy and the tendinous structures appear as thin transparent linings over the muscle belly. The tendinous material grows quicker in the protractors and retractors and by about 10 day EX OVO, these structures have already become broad, stout and considerably long. On the other hand, the tendinous material assumes a stout and broad appearance only by about 40th day EX OVO in the adductors and the abductors.

The chick acquires almost all the characters of the adult by about 60 day EX OVO and this is well reflected in the development of the muscles. By 60 day EX OVO the origin as well as the insertion of all the muscles become considerably extensive and the tendinous structures assume the appearance of the adult animal. During the succeeding stages the muscles acquire more fleshy material and become considerably massive. Similar observations have also been made by other workers in the field. According to Scott (1954) an increase in the fibrous tissue and tendon substance separating and giving attachments to the muscle bundles, but is caused largely by an increase in size of the individual muscle fibers. There is also a remarkable increase in bulk of the fibrous connective
tissue between and around the muscle bundles.

Lorrian Smith (1932) also describes a similar increase in bulk of the muscle as a function of its activity. His observations also revealed that when a muscle has less work it atrophies. But when it has more work it hypertrophies. Thus, the "size of a muscle is a register of the work it has to do".

A consistent increase in the size of all the muscles during the postnatal period of the chick can be attributed to an increase in size of the muscle ingredients in relation to the various functional demands during growth and development. Further, the present studies have also revealed that during the post-natal growth period the origins and insertions of all the muscles become extensive and spread considerably over large areas of the associated bones. As stated by Scott (1954), "the increase in area of the attachments of the origin and insertion can be attributed to the growth in the width of the muscle substance".

QUANTITATIVE ANALYSIS OF THE JAW MUSCLES

The effective force exerted by the bill of the bird during its feeding operations depends upon several factors. Since, the feeding behaviour of birds shows immense variations among the different groups,
the feeding mechanism is suitably modified for the purpose. The various structural components of the lever system and the muscle which supplies the power for their operation are structurally and physiologically equipped to play specific roles. As stated earlier, several investigators (Goodman and Fisher, 1962, Malhotra, 1968, Mansuri, 1969, etc.) have described the structural variations which are observed in the lever systems in relation to the specific feeding behaviour of the birds or the bird group concerned.

The potential strength of the force exerted at the tip of the bill varies inversely as the length of the work arm. On the other hand, the torque varies directly with the length of the moment arm. This explains why generally the seed eating birds have a shorter bill with a larger moment arm. Conversely, the fish eaters possess a longer beak. The fish eating birds generally use the anterior and the middle part of the bill to hold the prey and hardly require to exert any force towards the bill tip. Kinesis of the upper beak is another significant factor responsible for the efficient functioning of the feeding apparatus and its
significance is already described earlier.

The force of adduction, abduction, protraction and retraction is also highly dependant on the morphological and physiological set up of the individual muscle fiber. However, for general consideration and relative study of the dependant muscle, the total mass of the muscle may be taken approximately as a general index of the muscle power. Equally important is the angle of the muscle which it makes with the force arm. Since, wider the angle higher the value of its sine. Adductors and abductors generally play an important role in the feeding operations and it is interesting to note that the most of the birds examined here and by the earlier workers show a high value of the sine $\angleFd$ for their insertions are close to the pivot. However, birds such as D. autunnalis, B. nigricans, etc., studied by Goodman and Fisher (1962) feeding mainly on seeds and small invertebrates, have low values of sine $\angleFd$ (D. autunnalis = 0.484, B. nigricans = 0.475). The values obtained for the total effective force of all the muscles at 1 day EX OVO period are obviously very low (Table - 43). But by 10 day EX OVO period the effective force for adduction and abduction increases more than twice (Table - 43). By 60 day EX OVO these
force almost increases by about five times between the 10 day and 60 day EX OVO period. The increase in the effective force of adduction between the 1 day EX OVO and the adult male ranges almost about twenty seven times and that of the female is about nineteen times. On the other hand the difference observed for abduction is about forty seven times more in the case of the adult male than the 1 day EX OVO whereas, about fortyone times in the case of the adult female. This could be appreciated in view of the fact that the bird depends largely on adduction and abduction for packing.

TABLE - 43: COMBINED EFFECTIVE FORCE OF THE JAW MUSCLES

<table>
<thead>
<tr>
<th>AGE</th>
<th>ADDUCTION</th>
<th>ABDUCTION</th>
<th>RETRACTION</th>
<th>PROTRACTION</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 DAY</td>
<td>0.00173</td>
<td>0.00026</td>
<td>0.00320</td>
<td>0.00091</td>
</tr>
<tr>
<td>10 DAY</td>
<td>0.00352</td>
<td>0.00067</td>
<td>0.00568</td>
<td>0.00101</td>
</tr>
<tr>
<td>60 DAY</td>
<td>0.01725</td>
<td>0.00518</td>
<td>0.01731</td>
<td>0.00259</td>
</tr>
<tr>
<td>ADULT MALE</td>
<td>0.04692</td>
<td>0.01233</td>
<td>0.04714</td>
<td>0.00537</td>
</tr>
<tr>
<td>ADULT FEMALE</td>
<td>0.03329</td>
<td>0.01069</td>
<td>0.04071</td>
<td>0.00333</td>
</tr>
</tbody>
</table>

Unlike in most of the other birds, the protraction and retraction do not seem to play a very significant role in the feeding operations.
In birds such as a hoopoe which thrusts its beak into the soil and then makes the gape wider, the animal has to use a greater force in the protraction of the upper beak because the bill has to operate against the resistance exerted by the soil. The retraction of the upper beak is made on the other hand easier by the resistance of the soil. However, opposite is the case in the flesh eaters in general. Since, they thrust their beak into the flesh of the prey, the resistance exerted by the food enhances the protraction of the upper bill. But they are apparent to exert higher force in bringing back the retraction of the beak. No such forces interplay in the feeding operations in the chicks and it is interesting to note that the increase in the effective force of retraction and protraction between the 1 day EX UO and the adult bird is considerably less. In chick the increase in the effective force of retraction is fourteen and twelve times in the male and the female birds respectively. The protractor muscle shows a lowest increase and the figures obtained for the male and the female birds are 5.9 and 3.6 times respectively. Comparatively higher values of retraction may be attributed to the fact that these muscles also serve as adductors of the lower jaw. Moreover, both the adductors and the retractors are involved in the
prevention of the food from escaping.

The figures also show that effective forces obtained for the males are comparatively higher in the various movements of the bill. This adaptation could be explained on the fact that these movements are highly significant in the production of sound and the typical sex play of the male bird which needs a wider opening of the beak.

HISTOCHEMICAL ORGANIZATION OF THE JAW MUSCLES (PLATE – XLII)

The application of histochemical techniques to the study of avian skeletal muscles has revealed the existence of discrete fiber types which can be differentiated by localization of various metabolites and enzymes. Normally various fiber types are observed intermingling in a mosaic pattern when viewed in cross sections.

The histochemical studies have shown that the fibers described as the Type I are generally narrow in diameter, rich in succinate dehydrogenase, alkaline phosphatase, and lipase. Furthermore, they are usually red in color and copious in blood supply. The cytoplasm of the Type I fiber is granular and
considerably large mitochondrial distribution. Similarly, the Type I fibers show a comparatively high concentration of glycogen, phosphorylase, aldolase, etc. These fibers are known for their slow and sustained activity. On the other hand, the Type II fibers are broad in diameter, white in color with comparatively low blood supply. The concentrations to glycogen, phosphorylase, aldolase, etc, are considerably higher in the Type II fibers. The cytoplasm is agranular and the mitochondrial distribution is generally sparse. These fibers in turn show low concentrations of fat, myoglobin, succinate dehydrogenase, lipase, and other oxidative enzymes. These fibers are rapid in action and comparatively fast in contraction. Attempts have been carried out by various investigators to unravel the correlations existing between the functional requirements of the muscle and its histochemical organisation. An ideal example can be drawn from the work of Salt, (1963) who studied the histochemical organisation of the pectoral muscles of some passerine birds. The flight mechanism of the birds
consists of a series of rapid wing beats usually followed by a long glide. The pectoralis major is called upon to work for strong propulsion stroke and is composed entirely of dark-fat loaded (Type I) fibers. The pectoralis minor on the other hand plays the major role in the wing upstrokes and besides it helps in holding the base of the wing in position during both upward and downward movements while gliding. This muscle is composed of two types of fibers, the fat loaded as well as glycogen loaded types (Type I and Type II). The upward power stroke is performed by the fat loaded fibers (Type I) whereas, the holding of the wings in particular position is performed by the glycogen loaded fibers. The studies conducted by Nene & George (1965) have thrown some more light on the functional aspects and they have shown that the wing muscles of pigeon which is a powerful flier, are better adapted for sustained tonic contraction, having more number of fat loaded fibers than the chick which is obviously a passive flier having muscles with large number of Type II fibers.

Earlier histochemical observations conducted in the leg and breast muscles of chicks have revealed
that the breast muscles are composed predominantly of white fibers (Nene and George, 1963; Cosmos, 1966) whereas, the leg muscles are composed of mixed fiber patterns viz., red (Type I), white (Type II) and intermediate fiber types (Cosmos, 1966). The various jaw muscles of chick studied during the present investigation have shown the apparent existence of two discrete fiber types in all the jaw muscles viz., Type I and Type II. This distinct heterogeneity of the fiber types was clearly discernable as early as the 10 day EX OVO period.

The existence of two discrete fiber types in the jaw muscles of chick elucidates the apparent existence of two well distinct metabolic entities in the muscles. The occurrence of the large and densely packed mitochondria and a comparatively higher storage of fat and succinate dehydrogenase within the Type I fibers show the accomplishment for the predominant aerobic metabolism which is best suited for slow and sustained muscular contraction. The Type II fibers on the other hand are enriched with their high storage of glycogen and other glycolytic enzymes and are best suited for the release of considerable energy for quick and short contractions.
The histochemical profile of the 19 day IN OVO and 1 day EX OVO jaw muscles show no apparent difference in the Type I and Type II fibers. During this period virtually all the fibers are normal in size, uniform in diameter and architecture. They appear to be predominant in fat and SDH store but moderately stained for glycogen. The predominance of fat and SDH in both the fiber types of 10 day IN OVO and 1 day EX OVO period evinces the predominance of fat metabolism in all the muscles. During this period the embryo is about to come out of the egg and the jaw muscles in them indulge in the slow and sustained operation of breaking the egg shell. The occurrence of fat and SDH in all the muscle fibers can be attributed to its accomplishment for such a slow operation.

At 10 day EX OVO period all the fibers differentiate into two well distinct types with a greater increase in the diameter in the Type II fibers. At 10 day EX OVO period the Type II fibers appear rich in glycogen store and considerably larger in diameter. Such a postnatal differentiation in the skeletal muscles between seven to ten days in rat has been reported by Dubowitz (1963).
According to Cosmos (1966) some of the muscle fibers upon maturation differentiate into specialised types for specific function while others grow with little alteration in their enzyme contents. Goldspink (1962) has reported identical results in M. biceps brachii of the mouse where the formation of the new fibers found to result from the conversion of the small fibers without any increase in their total number. Thus, apparently the newly formed large fibers are differentiated from the first formed smaller fibers according to the specific functional demand of the muscle. The Type II fibers of the jaw muscles are specialised for predominant glycolytic metabolism in view of the fact that these fibers have rich glycogen store and greater diameter than the other fibers. Moreover, the considerably greater percent distribution of the Type II fibers can also be taken as a fair index. As described earlier, the chick starts feeding rapidly soon after liberation from the egg and the jaw muscles indulge in quick and repetitive contractions during earlier periods of postnatal development. This specialisation of the Type II fibers with their considerable increase in their diameter and glycogen store with a prominent decline in the SDH concentration could be correlated with the above said specific feeding behaviour which
requires a constant release of high energy.

The apparent increase in the diameter and percent
distribution of the Type I fibers observed at 50 day
*EX OVO* period could be accounted for the senile
accomplishment of the metabolism of the Type I fibers,
since, by around 60 day *EX OVO* the chick assumes almost
all the characters of the adult. The steady increase in
the diameter, percent distribution and identical
histochemical profile of staining reactions of all the
fibers observed during the succeeding stages of the
senility, reveal the stabilisation of the metabolic
patterns at maturity. As already seen in the foregoing
description, the growth of the muscle has resulted by
an increase in the fiberous connective tissue and
largely by an increase in the size of the individual
muscle fiber. As described by Goldspink (1969) the
growth of the muscle fibers may exist in two different
levels of development. The increase in size of the
muscle during growth has been due to the number of Type I
fibers which undergo further growth into large specialised
Type II fibers. This further growth of the fibers is
the result of a "disproportionately large increase in
the myofibrillar material within the fibers"
As described earlier in chicks, the adduction and abduction involve quick and repetitive movements. The protraction and retraction of the upper jaw on the other hand are slow and sustained. The adduction of the lower jaw is mainly brought about by the contraction of the *M.A.M.* Externus and *M.A.M.* Medius and depression of the lower jaw is mainly resulted by the contraction of the *M.* depressor mandibulae. All these muscles are filled mainly by glycogen. The assemblage of the comparatively large Type II fibers and their percent distribution in the adductor and abductor muscles ensures the accomplishment of predominant anaerobic metabolism utilising glycogen as the chief reserve fuel for quick and repetitive contractions of the former set of muscles. As far the retraction of the upper jaw is concerned, it is effected mainly by the contraction of the *M.A.M.* Internus and *M.* Pseudotemporalis. The presence of the comparatively large Type I fibers and their considerably higher percent distribution in these two muscles reveal the apparent existence of a predominant fat metabolism in the retractor muscles which are best suited for the constant availability of energy for slow and sustained contraction. These observations are in conformity with the findings of the earlier workers that the muscles indulged in quick and repetitive contractions are mainly
glycogen loaded and anaerobic in metabolism whereas, those responsible for slow and sustained activity are mainly fat loaded and aerobic in metabolism (Padykula, 1952; Dubowitz and Pearse, 1960; Cosmos, 1966; George and Berger, 1966; etc.).

QUANTITATIVE BIOCHEMICAL ANALYSIS OF THE JAW MUSCLES (PLATE - XLIII, XLIV, & XLV).

In performance of muscular activity and muscle tone, the energy is expended. The energy is liberated from a continuous chain of complex chemical reactions supported by a constant burning of the reserve fuel. The level of existence of a particular reserve fuel serves as fair index for physiological activity and functional capacity of the muscles. For instance muscles which indulge in sustained activity requires a continuous generation of high energy for a comparatively longer duration. On the other hand, a muscle intended for fast contractions for short periods needs the generation of high energy compounds for a short period. In such cases, glycogen serves as the chief source for the supply of energy in the muscles and is made available through rapid glycolytic reactions. For the sustained operations, however, fat is the ideal fuel since it yields comparatively more energy per unit weight of the
Histograms showing the amount of glygogen (%) in relation to the dry weight of the muscles.
QUANTITATIVE ESTIMATION OF GLYCOGEN IN RELATION TO DRY WEIGHT OF THE MUSCLES (%)
reserve fuel.

A quantitative assessment of the abdominal muscles of chicken and pigeon carried out by Ghinoy and George (1964) illustrates metabolic identity of the muscle fibers with the function. According to these authors the M. obliqueus abdominis and M. transverse abdominis of the pigeon consist of fibers which are narrower and contain comparatively a high level of fat and SDH than those of M. obliqueus abdominis internus and rectus abdominis and also M. obliqueus abdominis externus and transverse of the chick.

A quantitative assessment of the glycogen in the jaw muscles of chick has revealed that of all the jaw muscles, the M. A. M. medius contains the highest level of glycogen. The M. A. M. externus also shows a considerably high glycogen store in its fibers. As already stated, these serve as powerful adductors of the lower jaw and possess and reveal the existence of a comparatively broader Type II fibers. Further, the percent distribution of these fibers were also higher in these muscles (Table - 44). The presence of a considerably high load of glycogen and a greater:
Histograms showing the amount and rate of catalase activity in relation to the fresh weight of the muscles:
PLATE - XLIV

CATALASE
QUANTITATIVE ESTIMATION OF CATALASE IN RELATION TO FRESH WEIGHT OF THE MUSCLE.

A = amount of the enzyme.
B = rate of the enzyme activity.
percent distribution of these fibers in these muscles indicate that these fibers are physiologically better equipped for an adequate energy release essential for quick and repetitive opening of the beak. A quantitative level of glycogen obtained for M. pseudotemporalis and M. spheno-pterygo-quadratus on the other hand is considerably low. These muscles work respectively as the major retractors and protractors of the upper jaw. As stated previously protraction and retraction of the upper beak involves slow and sustained contractions requiring a constant release of high energy for an extended activity for longer duration. It is therefore, noteworthy that these muscles contain more amount of fat and SDH. In the M.A.M. internus which serves primarily as a retractor and secondarily as an adductor of the beak, the distribution of the Type I and Type II fibers is more or less similar (Table - 45) and the Type II fibers are comparatively narrower in size than those observed in M.A.M. medius and M.A.M. externus. Thus these muscles are moderately equipped both for quick and repetitive as well as slow and sustained activities.

The results obtained for the quantitative analysis of the catalase showed that all the muscles which are better equipped for fat and SDH metabolism contain higher
### TABLE - 44.

**BIOCHEMICAL ORGANISATION OF THE ADULT JAW MUSCLES OF CHICK**

Quantitative amount of % Glycogen present in relation to the Type II fibers in the jaw muscles.

<table>
<thead>
<tr>
<th>NAME OF THE MUSCLE</th>
<th>% GLYCOGEN PER GM.FR.</th>
<th>AVERAGE DIAMETER OF THE TYPE II FIBERS IN U</th>
<th>AVERAGE % DISTRIBUTION OF THE TYPE II FIBERS</th>
</tr>
</thead>
<tbody>
<tr>
<td>M.A.M. EXTERNUS</td>
<td>0.3305</td>
<td>52.40</td>
<td>60.00</td>
</tr>
<tr>
<td>M.A.M. MEDIUS</td>
<td>0.6350</td>
<td>49.30</td>
<td>48.89</td>
</tr>
<tr>
<td>M.PSEUDOTEMPORALIS</td>
<td>0.1245</td>
<td>52.10</td>
<td>33.33</td>
</tr>
<tr>
<td>M.A.M. INTERNUS</td>
<td>0.2436</td>
<td>49.60</td>
<td>54.43</td>
</tr>
<tr>
<td>M.DEPRESSOR MANIDIBULAE</td>
<td>0.7105</td>
<td>51.00</td>
<td>48.09</td>
</tr>
</tbody>
</table>

### TABLE - 45.

**BIOCHEMICAL ORGANISATION OF THE ADULT JAW MUSCLES OF CHICK**

Quantitative amount of catalase and ascorbic acid in relation to the Type I fibers.

<table>
<thead>
<tr>
<th>NAME OF MUSCLE</th>
<th>CATALASE ACTIVITY PER.GM. TISSUE</th>
<th>RATE OF AMOUNT OF CATALASE ACTIVITY</th>
<th>AMOUNT OF AA PER.GM. TISSUE</th>
<th>AVERAGE DIAMETER OF THE TYPE I FIBERS</th>
<th>AVERAGE DIAMETER OF THE TYPE II FIBERS</th>
</tr>
</thead>
<tbody>
<tr>
<td>M.A.M.EXTERNUS</td>
<td>09.29</td>
<td>10.66</td>
<td>0.4219</td>
<td>31.70</td>
<td>40.00</td>
</tr>
<tr>
<td>M.PSEUDOTEMPORALIS</td>
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<td>33.63</td>
<td>0.9330</td>
<td>32.70</td>
<td>66.66</td>
</tr>
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<td>M.A.M.INTERNUS</td>
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<td>32.09</td>
<td>0.4880</td>
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<td>35.01</td>
</tr>
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<td>M.DEPRESSOR MANIDIBULAE</td>
<td>09.31</td>
<td>17.09</td>
<td>0.3250</td>
<td>35.60</td>
<td>47.46</td>
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</table>
amount of catalase and comparatively a higher rate of enzymatic activity (Table -45). The adductor and abductor muscles on the other hand show a low catalase content and considerably a low rate of activity.

The physiological significance of ascorbic acid and its free radical in the oxidative, lipid and protein metabolism of avian flight muscles has been carried out by several investigators. The results available from these investigations suggest the possibility of a close correlation between the content of the ascorbic acid and a higher physiological activity (Burns, 1960; Davidson and Passmore, 1963; Harper, 1967; Chinoy, 1969 etc.). Recent observations of Chinoy (1969) in the pigeon pectoralis muscles have shown that the Type I fibers have comparatively greater concentration of ascorbic acid and the higher ascorbic acid concentration of the Type I fibers has been correlated with the higher level of metabolic activity of the fibers. Furthermore, the ascorbic acid also indulges in the energy transfer mechanism through its peroxidative transformation into its free radical monodehydroascorbic acid which is a much more powerful electron donor on account of its active unpaired electron. Studies conducted by Kolomitsene et al. (1967) have also thrown considerable light on
the functional significance of the ascorbic acid in animal tissues. The observations recorded by this author show that the concentration of lipid free radical increases considerably with further addition of ascorbic acid in irradiated liver. This finding also suggests the possibility of the significant physiological role played by the ascorbic acid in increasing the lipid synthesis and thereby enhance the fat metabolism.

In the chick, the highest level of free form of ascorbic acid (AA) is observed in M.pseudotemporalis and M.sphenopterygo-quadratus (Table -45) in comparison to the other muscles studied here. Furthermore, the bound form of ascorbic acid (ASG) and its utilization (AAU) is considerably higher in M.sphenopterygo-quadratus. On the contrary, though the bound form of ascorbic acid (ASG) is considerably low in M.pseudotemporalis, the free form (AA) and its utilization (AAU) is significantly higher (Table -45). These muscles respectively serve as protractors and retractors of the beak and better equipped for fat metabolism. The higher level of free ascorbic acid (AA) together with its higher utilization confirms the possibility of a seemingly higher fat metabolism.
PLATE - XLV
ASCORBIC ACID
QUANTITATIVE ESTIMATION OF AA, ASG, & AAU. IN RELATION TO FRESH WEIGHT OF THE MUSCLE.
adductor and abductor muscles studied reveal the existence of considerably a low level of free and a bound form of ascorbic acid as well as low utilization in comparison to the protractors and retractors of the upper jaw. As they consist of glycogen loaded fibers they are poorly equipped for SDH and fat metabolism. The presence of an intermediate level of ascorbic acid (AA) ascorbigen (ASG) and ascorbic acid utilization (AAU) in the M.A.M.internus further confirms that these muscles show moderate physiological activity both for fat and glycogen metabolism.

Thus, a study of the quantitative biochemical analysis of the jaw muscles showed that correlations exist between the metabolic load of the muscle and the specific role it plays in the operation of the jaws. The adductors and abductors of the lower jaw are quick and repetitive in contraction and are observed to be rich in glycogen store. They show considerably low levels of catalase and ascorbic acid. Conversely, the muscles which serve as protractors and retractors of the upper jaw exhibit a slow and sustained activity and evince high levels of catalase and ascorbic acid. They are apparently poor in glycogen store. The former set of muscles are adapted for a
predominant glycolytic metabolism whereas the latter are best suited for the fat metabolism.

The evolutionary success of an organism depends upon the successful establishment of new mutants and fixation of well established ones. The successful establishment of an organism essentially depends upon the adaptive value of the specific characters. Selection tends to preserve those characters which have some adaptive value and eliminate those which may not be of any use as well as those which may be harmful to the organism. In view of the genetic drift the establishment of characters in a set of population shows a lot of successful variants with the passage of time. This is essentially true of birds also. As stated earlier, the origin and evolution of the avifauna have extended over long periods of geological era and have permitted them to occupy various niches by various structural adaptation culminating in the origin and evolution of the present day avifauna into several groups. As a bird the chick has become a passive flier during the course of evolution and today makes very little use of its wings. However, it gradually associated itself
with human habitats and adapted to feed on the food material available from the vicinity of the human surroundings. A close study of the feeding apparatus of this bird has shown that both structurally and physiologically the various components of the feeding apparatus are efficiently equipped to play the role they are called upon to do.

The various bony elements of the feeding apparatus of the chick are suitably modified for this purpose and their set up confers to the functional demand best suitable for its feeding operations. The various movements of the feeding apparatus are effectively directed and controlled by a set of muscles and the studies have revealed the presence of excellent structural and physiological adaptations to pull and push the lever systems of the jaw with required magnitude of momentum. The epidermal structures on their part ensure a firm grip over the food until it is finally passed on to the gullet. Thus, every part of the feeding apparatus, right from the epidermal envelope to the ligaments and muscles, is well adapted to its specific feeding behaviour.