CHAPTER - IV

FUNCTIONAL MORPHOLOGY OF CRANIUM
(An analysis)
A detailed description of the different skeletal elements (bones, muscles, and ligaments) of the head has been provided in the previous chapters (vide Chapters I, II, and III). Attempts have also been made to find out the asymmetry present therein and to correlate the asymmetry with the adaptation of the fish. But the aim of the present work is not only to study the discrete skeletal elements of the head and the associated asymmetry but also to have a better understanding of the feeding biology of the fishes from the study of the disposition of different anatomical features. Of course, no experiment could be done, and hence deduction method has been utilised to explain the functional morphology of the cranium.

Research in morphology has developed a recent trend to establish a relationship between function and form of living organisms. According to Russell (1916), form is dependent on function. Romer (1949) commented that 'the almost complete separation of form and function prevalent in instruction today is both unnatural and unfortunate. It is doubtful if there is such a thing as a non-functioning structure, although mention of function is often taboo in morphologic works'.

For the purpose of better presentation as well as for making it more meaningful, the form of different functional elements have been first analysed in relation to their surrounding associates. Subsequently, an attempt has been made to visualise the involvement of different functional elements and their associates to carry out the process of feeding.

At the onset, the form of the suspensorial elements should be considered because of their great functional importance. Functionally suspensorium is not a single structural element but composed of closely related elements like bones, ligaments, muscles, and tissues performing one or more functions together as mentioned by Liem.
These functional units are closely connected to form couplings (Liem, 1967a,b) which perform the desired function.

The structure of the suspensorial elements are modified to carry out different functions efficiently. The contraction of m. levator arcus palatini, m. protractor hyomandibularis and m. adductor arcus palatini causes movement of the hyomandibular and pterygopalatine arch during the process of feeding and respiration. For this ball and socket joint between the neurocranium and hyomandibular is necessary so as to allow the latter some degree of flexibility. This is very explicit in the fishes studied.

The symplectic end of hyomandibular plays a significant role in the suspensorium as from it hangs the rest of the bones of the suspensorium and interhyal linking in series the various bones of the jaws and branchial apparatus. In the presently studied group of fishes as the feeding is carried out on the blind side so more force is likely to be exerted on the symplectic end of hyomandibular of that side. Eventually to meet the functional need the symplectic end of hyomandibular on the blind side has enlarged so as to provide more area for a firmer attachment with the other bones of the suspensorium.

Quadrate also plays an important role in the suspensorium. The fan-shaped structure of quadrate is well designed for the transmission of forces from hyomandibular to lower jaw. Large area of the articular facet of quadrate of the blind side allows more rotation to the angular (vide Chapter I - Osteology part) as a result during the opening of mouth, the lower jaw moves more towards the blind side so as to help the fish to pick up the bottom living prey.

The type of saddle joint i.e. the articulation between convex surface of one bone fits into concavity of the adjoining bone (Duvalls, 1959), between the quadrate and angular permits flexion, extension, abduction, adduction and circumduction (Wells, 1951).
The metapterygoid remains separated from the hyomandibular and quadrate by a strip of cartilage which perhaps increases the flexibility among them. Moreover, the metapterygoid provides suitable surface area for attachment of \( m. \) levator arcus palatini and \( m. \) adductor arcus palatini.

In order to meet the functional need of the blind side, the suspensorium of that side has firmer ligamentous attachment with the neurocranium. This is explicit from the presence of pterygoid-lateral ethmoid ligament (in \( C. \) bilineatus and \( C. \) lingua) and pterygoid-prevomer ligament only on the blind side as well as relatively well-developed pterygoid-first infraorbital ligament on the same side.

\( M. \) levator arcus palatini and \( m. \) adductor arcus palatini which are inserted on the suspensorium help in the movement of the latter. The contraction of \( m. \) protractor hyomandibularis and \( m. \) levator arcus palatini elevates or abducts the hyomandibular as well as the pterygopalatine arch and thereby causes the expansion of the orobranchial chamber. On the other hand, the contraction of \( m. \) adductor arcus palatini adducts the hyomandibular and the pterygopalatine arch and thereby decreases the volume of the orobranchial cavity. Such increase and decrease of orobranchial cavity is an indispensable functional requirement for both respiration and feeding.

The interhyal is attached to the symplectic end of the hyomandibular by a cartilaginous bridge and to the metapterygoid by the interhyal-metapterygoid ligament. This type of attachment also suggests that the interhyal acts as an additional suspensorium.

To carry out feeding and to forebear the stress which is a consequence of feeding activity, the premaxilla of the blind side not only possesses dentition but also it is stouter and has ligamentous attachment with the mandible. The functional modification of the lower jaw is also worth mentioning. Not only it is provided
with dentition but also its articulation with the quadrate is quite remarkable. The area of the articulating facet of the angular on the blind side is more than twice than that of the ocular side. This allows a greater mechanical advantage and mobility between the angular and quadrate and thus provides sufficient freedom for outward rotation of the lower jaw. Such type of arrangement is highly advantageous for the fish for picking up the bottom living organisms.

Like the bones of the jaws and suspensorium, the bones of the opercular apparatus are also mobile and therefore its structural disposition along with joints and ligaments needs special attention from functional standpoint.

Preopercle has a remarkable functional importance. It binds the different elements of the suspensorium like the hyomandibular and the quadrate and thus strengthens the suspensorium. In addition, the preopercle also provides area for attachment of adductor mandibulae muscles. Presence of a relatively wide preopercle on the blind side provides more strength to the suspensorium on that side.

The ball and socket articulation or 'saddle joint' between the hyomandibular and the opercle permits the versatile movement of the latter. However, the movement of the opercle depends upon its associated muscles and ligaments. In the presently studied fishes the associated muscles and ligaments are moderately developed.

M. levator operculi is responsible for the levation of the opercle. When the opercle is levated, the motion is transmitted to the interopercle via the subopercle and the opercle-interopercle ligament, eventually pulls the caudoventral end of the lower jaw via interopercle-retroarticulart and interopercle-dentary ligament resulting in the depression of the lower jaw. Thus both the opercle and interopercle actively take part in operculi-opercular apparatus-mandible coupling. In the presently studied fishes the presence
of relatively well developed opercle-interopercle ligament, interopercle-retroarticular ligament and interopercle-dentary ligament on the blind side probably helps to pull the lower jaw more effectively. The dorsal border of the opercle is rigid and thereby provides a strong foothold for the insertion of m. levator operculi and m. adductor operculi. While the contraction of the former, levation, the contraction of the latter causes adduction of the opercle.

It is noteworthy to mention here that the subopercle of the present group of fishes does not have strong attachment either with opercle or interopercle and thus seems that it is functionally less important. According to Liem (1970) the size reduction of the subopercle is correlated with the increased efficiency of the levator operculi-opercular apparatus - mandible coupling, which is accomplished by a vertical alignment of the coupling and the elimination of the subopercle from the coupling. This enhances the speed and the degree of jaw opening and protrusion essential for predatory habit.

The hyoid and branchial apparatus have great functional role as they have link with other movable elements of the skull. Dorsally the interhyal is movably connected to the symplectic process of the hyomandibular. Ventrally the hyoid has ligamentous connection with the urohyal. Since all these connections are movable, the hyoid apparatus is very potent from functional standpoint. The design of os pharyngeus superior and os pharyngeus inferior is best suited for mastication of the food material.

The form of different morphological elements of the skull has been dealt with from the functional point of view. Now an attempt will be made to explain the result of interaction among the different structural elements for carrying out the process of feeding and respiration. Feeding and respiration though distinctly separate processes from physiological standpoint yet they have got common
basis from functional morphological standpoint. This is because the basic structures like the jaws, suspensorium and other associates act conjointly both during feeding and respiration. The opening and closing of the mouth, increase and decrease in the volume of the orobranchial cavity are also the common features of the respiratory as well as feeding mechanism. Besides the above mentioned common features, the water current which enters the mouth, serves as a food current as well as a respiratory current, and are thus interdependent processes and should be considered jointly.

According to Liem (1970) the feeding process is accomplished by the following three steps: gnathous, ganthoparyngeal and pharyngeal.

For procurement of prey the first action to be performed is the opening of the mouth. The mouth is opened by the lowering of the lower jaws. The lowering of the jaws is caused by the action of a group of synergistic muscles and ligaments rather than by a single one. However, the main role is played by m. cleithrohyoideus, m. protractor hyoidei and m. levator operculi. The pull created by the contraction of m. cleithrohyoideus is transmitted to the lower jaw via urohyal-hypohyal ligament and thus resulting in the slight lowering of the lower jaw. Simultaneously the contraction pull of m. levator operculi is transmitted to the lower jaw via opercle-interopercle ligament, angular-interopercle ligament and retro-articular-interopercle ligament and also causes the lowering of the lower jaw. The contraction of protractor hyoidei group of muscles also causes slight lowering of the lower jaw as their contraction brings both the hyoid bar and the lower jaw close to each other. With the opening of the mouth the lower jaw of the blind side also projects towards the blind side (vide Chapter I - Osteology part) and this helps the fish to pick up the bottom living organisms.

However, once the food is captured - it is retained there by the strong adduction of the jaws. This is achieved by the contraction of the adductor mandibulae group of muscles. It is noteworthy to
mention here that a strong adduction is possible on the blind side due to the presence of better developed mandibular group of muscles on that side.

During the gnathopharyngeal phase the captured food material moves posteriorly from the anterior buccal cavity. Further advancement of the food into the orobranchial region is assisted by the inspiratory movement of the respiration. For fulfilling this phase of deglutition m. levator arcus palatini and m. protractor hyomandibularis undergo contraction with the consequent enlargement of the orobranchial chamber. Enlargement of orobranchial chamber also results through the action of posteroventral movement of hypobranchial apparatus with the help of ventral branchial muscles.

The gnathopharyngeal phase is followed by the pharyngeal phase of deglutition during which the food organism is brought into the space between the os pharyngeus superior and os pharyngeus inferior for mastication. This phase is very much complicated owing to the participation of a large number of branchial muscles, specially the masticatory ones.

Contraction of m. retractor os pharyngeus superioris retracts the os pharyngeus superior upward and backward. The m. protractor os pharyngeus superioris on contraction protracts the os pharyngeus superior. Contraction of m. levator externus, m. levator internus and m. obliquus dorsalis causes the elevation of the os pharyngeus superior. The contraction of m. transversus os pharyngeus superioris causes the approximation of os pharyngeus superior of either side.

The movement of os pharyngeus inferior is also complicated. It is elevated by m. levator os pharyngeus inferioris. The retraction and depression of the same is caused by the contraction of m. retractor os pharyngeus inferioris and m. depressor os pharyngeus inferioris, respectively. The m. protractor os pharyngeus inferioris on the other hand protracts os pharyngeus inferior of either side.
and transversus os pharyngeus inferioris helps in their approximation. So the various muscles connected with the os pharyngeus superior and os pharyngeus inferior work in such a coordinated manner that the mastication is performed effectively. After mastication both the os pharyngeus bones retract and allow the masticated food to pass into the oesophagus.

It has already been stated that feeding and respiration have common functional basis. However, as the mechanism of opening and closing of mouth has been dealt previously so needs no repetition. The subsequent respiratory movements start after the water reaches the orobranchial chamber.

According to Saunders (1961) the constant flow of respiratory current is possible due to a differential pressure in the orobranchial and opercular chambers. For allowing entrance of water into the orobranchial chamber the concomitant enlargement of the same is required. The expansion of the orobranchial chamber is brought about by the simultaneous contraction of m. levator arcus palatini and m. protractor hyomandibularis. The increase in the volume of the orobranchial cavity causes decrease of the hydrostatic pressure therein and readily ensures the entry of water into it.

The expansion of the orobranchial chamber is immediately followed by its reduction. This is caused by the relaxation of m. levator arcus palatini, m. protractor hyomandibularis and contraction of m. adductor arcus palatini. A reduction in the volume of orobranchial chambers is also achieved by the contraction of m. adductor mandibularis, I, II, III. The decrease in the volume of the orobranchial cavity causes increase of hydrostatic pressure within it, which ultimately forces water into the opercular chamber, where there is already a diminution of pressure due to previous expiration of water. The reduction in the volume of the orobranchial cavity is immediately followed by the expansion of the opercular chamber.
The dorsolateral and ventrolateral expansion of the opercular chamber is caused mainly by the contraction of m. dilator operculi and m. abductor branchiostegalis. The expansion of the opercular chamber with the resultant decrease of hydrostatic pressure within it readily acts as a suction pump to draw water from the orobranchial chamber. It is noteworthy to mention here the view of Saunders (1961) that during suction phase water cannot enter the opercular cavity from the posterior aspect due to presence of flexible opercular flap which firmly affix itself as a valve. The expansion of the opercular chamber is immediately followed by its reduction.

Reduction in the volume of the opercular chamber is achieved mainly by the contraction of m. adductor operculi. However, the contraction of m. constrictor branchiostegalis and m. adductor branchiostegalis also helps in reducing the volume of opercular chamber. Such reduction causes increase of hydrostatic pressure within opercular chamber which finally forces the water out through the opercular opening.

Thus a continuous flow of water is maintained by the repetition of the above mentioned process for carrying out respiration effectively.

In conclusions it may be stated that many structural elements are there in the head, but they never act independently. Synergistic i.e. interdependence is the rule of nature and the role of separate functional unit is insignificant. This illustrates very explicitly the concept of wholism.