Scanning electron microscopic studies of gill arches and rakers in relation to feeding habits of some fresh water fishes

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Abstract The surface ultrastructure of the gill arches and the gill rakers of the three concerned species Oreochromis niloticus, Chrysichthys auratus and Clarias gariepinus was investigated by scanning electron microscopy. These structures show significant adaptive modifications associated with the food and feeding habits of these fishes. Short and tuberous type gill-rakers in O. niloticus, are a well interesting filter of food. In C. auratus gill rakers were short with broad base, they serve to strain water which was to bathe the gills and prevent any solid particles from passing over it. Gill rakers in C. gariepinus were long, cylindrical in shape and arising at acute angles to the arch, they help to strain food and other materials, thus protect gill filaments from damage. Prominent epithelial protuberances on the gill rakers and gill arches enable the taste buds, located at their summit, to project well above the surface of the epithelium. This could increase the efficiency of the taste buds in selective sorting of palatable food. Co-occurrence of teeth and taste buds on the epi- and hypopharyngeal bones (Types I–III) denotes that food processing and gestation occur simultaneously in the pharynx. Caniform, villiform and papilliform teeth on the epi- and hypopharyngeal bones of the three studied species respectively in O. niloticus, C. auratus and C. gariepinus were associated with a complex food-processing cycle. Mucous secretions, oozing through mucous cell openings, provide lubrication facilitating smooth passage of food through the pharynx.

Introduction

Oreochromis niloticus, Chrysichthys auratus and Clarias gariepinus are three of the most important fresh water fishes in the River Nile in Egypt. O. niloticus lives almost in inshore water and feeds mainly on periphytes and algae while C. auratus lives in middle water, feeds on insects, crustacean, mollusks, nematodes, fish plants and bottom deposits were of minor importance. C. gariepinus was completely omnivorous, feeding on fish, insect larvae, mollusks, planktonic organisms, water weeds and bottom deposits.
Gills were the main sites of gas exchange in almost all fishes (Moyle and Cech, 1996). In addition to their respiratory function, the gills play an important role in the excretion of certain waste products and in the maintenance of the fish salt balance (Norman, 1963). The gill dimensions and organization of gill arches and rakers reflect the feeding habits of the fish (Magnuson and Heitz, 1971; Hughes, 1980, 1984; Fernandes and Rantin, 1986; Fernandes et al., 1995; Fernandes, 1996).

Among fishes, diversity of the food resources leads to the evolution of various adaptive characters in the pharynx, which plays an indispensable role in the retention, maneuvering and transport of food for swallowing. The pharynx, in teleost, was characterized by the presence of gill arches. These were located at the boundary between the pharyngeal cavity and the opercular chamber on either side of the head. The gill arches in general were equipped with gill rakers toward their pharyngeal side and were considered to play an important role in feeding. A review of literature revealed that, the surface ultrastructure of gill arches and gill rakers was derived from studies on fish species having different feeding habits that include plankton feeders Rhinomugil corsula (Munshi et al., 1984), and Gadus chapa (Ghosh et al., 1988); filter feeder Brevoortia tyrannus (Friedland, 1985); ilyoophagous (periphyton feeder) Hypostomus commersonii (Eiras-Stofella and Charvet-Almeida, 1997), Prochilodus scorf (Eiras-Stofella and Charvet-Almeida, 1998), Mugil curena, Mugil liza and Mugil platans (Eiras-Stofella et al., 2001); omnivorous Fundulus heteroclitus and (Hossler et al., 1985), Cyprinus carpio (Sibbing and Uribe, 1985; Sibbing, 1988), and carnivorous fishes Anabas testudineus (Munshi et al., 1984), Notopierous chitula (Ghosh et al., 1988), Eugerres brasiliun (Eiras-Stofella and Charvet-Almeida, 2000), and Cthorops sirigosa (Fernandes et al., 2003). Kumari et al. (2005) described surface ultrastructure of gill arches and gill rakers in relation to the feeding ecology of a carnivorous catfish Rota rita. Vigliano et al. (2006) described the ultrastructural characterization of gills in Juveniles of the argentinian silverside Odontesthes bonariensis. Also Pichugin and Sidorov (2006) explained the number and form of gill rakers in Sakhalin trout Parahucho perryi. Mir and Channa (2009) used the SEM study to explain the gills of the snow Trout Schizothorax carvifrons Heckel. Kumari et al. (2009) described surface ultrastructure of gill arches and gill rakers in relation to feeding in a herbivorous bottom feeder fish of an Indian major carp Cirrhinus mirgala. Also Kumari et al. (2011) described the surface ultrastructure of the gill filaments and the secondary lamellae of the carp C. mirgala. The present study aimed to give more scanning electron microscopical information about the gill system of three species of fresh water fishes with different feeding habits which inhabit the River Nile; O. niloticus, C. auratus and C. gariepinus.

Material and methods

This study was carried out on fishes of O. niloticus, C. auratus and C. gariepinus. The length of fishes is 2, 7 and 5 cm, respectively. Five fishes from each species were used to demonstrate the gross morphological features. The opercular cavity was opened; the specimens were washed very carefully in physiological saline (Breipohl et al., 1973a,b) to remove the mucus on the surface and then fixed in 10% formalin, examined grossly and photographed. For scanning electron microscopy, three fishes from each species were used. Pieces of the gill arches and gill rakers were taken, fixed in 10% formalin. This procedure was followed by a second fixation in 1% osmium tetroxide (Delton, 1955) for at least 6 h, washing and dehydration in increasing concentrations of ethanol. The dehydration samples were dried with the critical point drier Tousimis Audosamdr-815. The dried material was coated by gold sputter coater (SPI-Module) and samples examined by JEOL-JSM-5500 LV reflection scanning electron microscopy. The material was stored over silica gel, so that it remained in perfect condition for many weeks.

Results

The gill system in the three species, O. niloticus, C. auratus and C. gariepinus had the form of a triangular mass with a caudally directed base. The gill system consisted of four pairs of gills, which were termed from lateral to medial as first (I), second (II), third (III) and fourth (IV) as shown in Figs. 1–3. In addition, C. gariepinus had a rudimentary fifth gill.

Each gill was semilunar in shape consisting of a gill arch that carried gill rakers on its concave aspect and gill filaments on its convex aspect. The gill arch had two extremities; rostral and caudal. The rostral extremity of each gill arch joined that of the opposite side in a transverse median bridge. The bridges of the gill arches united together forming an inter-branchial septum between the contra-lateral gills. This septum was flattened dorso-ventrally. The gills of both sides diverged caudally leaving a triangular shaped area which was bounded rostro-laterally, by the fourth pair of gills and was occupied by the floor of the pharynx. This floor was modified into two distinct structures; hypo-pharyngeal bone (an anterior post-lingual organ) and lower pharyngeal jaw (a posterior edentulous epithelium). The roof of the pharynx, opposite to the lower pharyngeal jaw, was modified into an oval-shaped structure, the epi-pharyngeal bone (the chewing pad) covering the basiocipital region of the skull. The caudal extremities of the four gill arches curved dorsally, rostrally and slightly

![Figure 1](image-url)
ventrally where they are connected with each other. These arches were attached to the medial aspect of the operculum and the dorsolateral wall of the pharynx. In the three species, the gaps between the gill arches were generally wider in *C. gariepinus* than in *O. niloticus* and *C. auratus*, while in *C. auratus* these gaps were wider than in *O. niloticus* (Figs. 1–3).

It was found that, the epithelium covering the gill arches of the three studied species demonstrated a mosaic of variable dimensions. The exposed surfaces of the epithelial cells were covered by microridges. These, in general, appear uniform in width and have a smooth surface, sinuous, or at times straight and compactly arranged (as in *O. niloticus* as shown in Fig. 4), lying parallel to each other or irregularly interwoven to form web like patterns (as in *C. auratus* and *C. gariepinus* as shown in Figs. 5 and 6). The boundaries between adjacent epithelial cells were demarcated by a well-defined double row of microridges (Figs. 4–6). The adjoining microridges on each epithelial cell were often interconnected with fine transverse connections, Viz., the microbridges (Figs. 4–6). In addition, mucous cells were scattered in between the arch epithelial cells, these cells were more numerous in *C. auratus* and *C. gariepinus* than in *O. niloticus*. These mucous cells were often filled with blobs of mucous secretion as shown in Figs. 4–6.

In the investigated fish species the gill rakers differed in form, arrangement and length. In *O. niloticus*, they were arranged in two rows, medial and lateral. The rakers of the medial row were directed dorso-medially while those of the lateral row were directed dorso-laterally (Fig. 7). The rakers of...
the adjacent gills were interdigitated (Fig. 1). The gaps between the rakers of the same gill decreased to the epibranchial part. The rakers appeared as relatively short, and wide-based processed with tuberous ends (Fig. 7).

It has been noted that the gill rakers in *C. auratus*, were arranged in two rows, medial and lateral (Fig. 3). The rakers of the medial row were directed ventro-medially, while those of the lateral row were directed ventro-laterally. The rakers of the adjacent gills were interdigitated (Fig. 2). The gaps between the rakers of the same gill were equal in length. The rakers appeared as relatively short and broad-based processed with segmented tuberous ends (Fig. 8).

In *C. gariepinus*, they were arranged in three rows; medial, intermediate and lateral (Figs. 3 and 9). The rakers of the medial and lateral rows were numerous with long processes arising from both sides of the gill arch, while those of the intermediate row were few and short (Figs. 3 and 9). The rakers of the lateral row were present in all gills including the fifth one, while those of the medial row were found only in the third and fourth gills, being longer in the third one. The rakers of the intermediate row were found in the four main gills; they were best developed in the third gill and were the weakest in the first one. The rakers of the third, fourth and fifth gills were interdigitated (Fig. 3). The gaps between the rakers of the same gill decreased to the epibranchial part. The rakers appeared as cylindrical in shape arising at acute angles to the arch. Their free ends were curved rostrolaterally as shown in Figs. 3 and 9.

The epipharyngeal bone (chewing pad) was divided into two rounded or oval structures as shown in Figs. 10–12 in the three concerned species. Each lobe appeared like half of a chewing pad with its surface bearing teeth amid epithelial protuberances.
It has been noted that, in *O. niloticus*, the teeth were caniform (Fig. 10). The taste buds were of Type III, which do not project above the normal level of the neighboring epithelial cells as epithelial pores (Fig. 10).

Whereas, in *C. auratus* and *C. gariepinus*, the pharyngeal teeth were villiform and papilliform respectively. Moreover, in the previous two species the taste buds were of Types I and II (Figs. 11 and 12).

The hypopharyngeal bone (post-lingual organ and lower pharyngeal jaw) was distinguished into an anterior and a posterior region. The anterior region of the post-lingual organ was elongated and narrow. It widened gradually toward the posterior region, which appeared somewhat triangular in outline (Figs. 13–15). The surfaces of the post-lingual organ were studied with teeth and a large number of taste buds, interspersed among the teeth.

In *O. niloticus*, the teeth were caniform and the taste buds were of Type III (Figs. 13 and 16).

In *C. auratus*, the teeth were villiform (Figs. 14 and 17). They were elongated, stout and conical with sharp pointed ends. The taste buds were of Types I and II (Figs. 18 and 19), respectively.

In *C. gariepinus*, the teeth were papilliform (Figs. 15 and 20). They were elongated, with sharp pointed ends. The taste buds were of Types I and II (Fig. 20), respectively.

The posterior region of the hypopharyngeal bone was known as the lower pharyngeal jaw. It was a narrow zone of edentulous epithelium as shown in the three species studied (Figs. 13–15).
Discussion

In the present investigation, the gill arches and gill rakers show significant adaptive modifications, associated with the food and feeding ecology of the studied fishes.

As most bony fishes, the three studied species possess four pair of gills. Although *C. gariepinus* has a rudimentary fifth gill, without gill filaments. Each gill is formed of a curved gill arch carrying gill rakers on its concave aspect and gill filaments on its convex surface.

In *O. niloticus*, the gill rakers were generally short and widely spaced. The gill rakers could be considered to constitute the branchial sieve as an adaptation for the efficient filtering of small food particles in the water gulped by the fish. Hyatt (1979), Hoogenboezem et al. (1991) and Kumari et al. (2009) in herbivorous filter feeding, reported that the branchial sieve is made of short gill rakers, while those of zooplanktivorous fishes were long. Ojha et al. (1987) in plankton feeder mullet *R. corsula* and *Sicamugil cascasia*; Guinea and Fernandez (1992) in filter-feeders (four species of mullet), *Liza aurata*, *Liza saliens*, *Liza ramada* and *Chelon labrosus* and Eiras-Stofella et al. (2001) in periphyton feeder *M. curema*, *M. liza* and *M. platanus*, reported gill rakers with secondary and tertiary structures to increase the efficiency of filtering mechanism and the position and morphology of gill rakers in these fishes act as a selective screen preventing the entrance of large and undesirable organisms.

The middle feeder *C. auratus* is able to expand its pharyngeal cavity, thus accommodating large quantities of food or large size food items including mollusks, small fishes, crustaceans, and insects. The arrangement of relatively short and

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Figure 14 Scanning electron photomicrograph of *Chrysichthys auratus*; showing hypopharyngeal bones bearing villiform teeth (arrow) and taste buds of Types I and II (thick arrow) on the pharyngeal surfaces. Note a narrow zone of edentulous epithelium (white arrow) between the bones.

Figure 15 Scanning electron photomicrograph of *Clarias gariepinus*; showing hypopharyngeal bones bearing papilliform teeth (arrow) and taste buds of Types I and II (thick arrow) on the pharyngeal surfaces. Note a narrow zone of edentulous epithelium (white arrow) between the bones.

Figure 16 Scanning electron photomicrograph of *Oreochromis niloticus*; showing hypopharyngeal bones bearing caniform teeth (arrow) and taste buds of Type III (thick arrow) on the pharyngeal surfaces. Also showing the lower pharyngeal jaw or the edentulous epithelium (white arrow).

Figure 17 Scanning electron photomicrograph of *Chrysichthys auratus*; showing a higher magnification of the hypopharyngeal bones bearing villiform teeth (arrow) and taste buds of Types I and II (thick arrow).
broad base gill-rakers, serves to strain water which is to bathe the gills and prevent any solid particles from passing over it.

Magnuson and Heitz (1971), Durbin (1979) and White and Bruton (1983) postulated that the number and shape as well as spacing of rakers reflect the feeding habits of different fish species. In this respect, C. gariepinus gill rakers were long, narrow spaced and cylindrical in shape, arising at acute angles to the arch that helps to strain food and other materials as well as protect gill filaments from damage. The gill rakers were arranged in three rows; medial, intermediate and lateral. The structures of the intermediate gill rakers show significant adaptive modifications associated with the food and feeding ecology of the fish, which serve as taste buds. This could increase the efficiency of the fish in selective, sorting of palatable food. Furthermore, Drenner et al. (1978) have assumed that gill rakers operate as passive sieves, retaining only those particles larger than a given inter-raker spacing. However, Sanderson et al. (1991), in an experimental study, noticed that the rakers act as a barrier to water flow rather than as a sieve. They change the direction of the water toward the roof of the oral cavity where food particles were trapped by its mucous covering before being ingested. It is suggested that the gill rakers perform a dual function; they change the direction of the water as a first step and act as a sieve in a second step.

The characteristic surface feature of the epithelial cells covering the gill arch and gill rakers in the three studied species is the presence of the microridges forming intricate patterns. These surface structures have also been reported in epithelia of gill arches and gill rakers in several fish species (Hossler et al., 1985; Ojha et al., 1987; Eiras-Stofella, 1994; Eiras-Stofella and Charvet-Almeida, 1998; Eiras-Stofella et al., 2001; Evans et al., 2005; Kumari et al., 2005, 2009, 2011). More recently, these microridges have been suggested to enhance mechanical flexibility and protection (Olson, 1995) and to impart a firm consistency to the free surface of the epithelial cells (Mittal et al., 2004). Microbridges were often interconnecting together, that may enhance their consistency or rigidity as suggested by Mittal et al., (2004) in their description of the opercular epidermis of Lepidocephalichthys guntea.

In the present investigation, taste buds were present in a great number on the pharyngeal side of the gill arches and on the gill rakers as well as on the epi and hypopharyngeal bones may be associated with their involvement in gestation in the pharynx. These structures show significant adaptive modifications associated with the food and feeding ecology of the fishes. Prominent epithelial protuberances on the gill rakers and the gill arches enable the taste buds, located at their summit, to project well above the surface of the epithelium. This could increase the efficiency of the taste buds in selective sorting of palatable food. Surface specializations of the post-lingual organ were recognized with adaptive modifications for selecting, trapping or holding food particles. Taste buds have also been reported on the pharyngeal side of the gill rakers and the gill arches in the carnivore Brachydano rario (Karlsson, 1983) and in F. heteroclitus (Hossler et al., 1985), mainly on the gill arches rather than the gill rakers in the car-
nivore N. chitala, on the gill rakers in the plankton feeder G. chapra and in the herbivore Labeo rohita (Ghosh et al., 1988) and on the periphyton feeder M. curema, M. liza, and M. plat anus (Eiras-Stofella et al., 2001), and the carnivorous Rhinolepis stri gosa (Fernandes et al., 2003). More recently, Eiras-Stofella and Charvet-Almeida (2000) and Eiras-Stofella and Fank-de-Carvalho (2002) observed taste buds on the gill rakers and the pharyngeal side of gill arches of ilyophagous P. scrofa and the omnivorous E. brasili annus and Cathorops spixii, respectively. They suggested that the chemical receptors might be used to help in food selection at swallowing. Kumari et al., 2005 in carnivorous fish R. rita, recorded the presence of a great number of taste buds on the pharyngeal side of the gill arches, on the gill rakers and on the epi and hypopharyngeal bones. While, Kumari et al., 2009 in a herbivorous fish C. mrigala the presence of a great number of taste buds on the gill rakers, median ridges, and transverse flap-like septa between the gill as well as on the postlingual organ and chewing pad insure their role in food selection.

Occurrence of a great number of taste buds together with teeth on the epi-and hypopharyngeal bones in the three studied species suggests that food processing and gestation work simultaneously in the pharynx and this may serve in the final determination of the suitability of potential food items prior to swallowing, as proposed by Linser et al. (1998) in Micropterus salmoides. Co-occurrences of teeth and taste buds within the pharyngeal cavity have also been reported in a variety of fish species (Reutter et al., 1974; Ezeasor, 1982; Sibbing, 1982; Hossler and Merchant, 1983; Hossler et al., 1986; Northcott and Beveridge, 1988; Kumari et al., 2005, 2009).

Slightly curved caniform, villiform and stout papilliform teeth on the epi and hypopharyngeal bones in the three studied species respectively (O. niloticus, C. auratus, and C. gariepinus), can be associated with a complex food processing cycle. Liem (1986) and Drucker and Jensen (1991) showed that during the process of mastication or winnowing, surface debris is stripped from food particles and unpalatable material is fully dislodged as the food passes into the esophagus. Lauder (1983) reported that the pharyngeal jaw in Lepomis micropholus and Lepomis gibbosus, is equipped with molariform teeth as an adaptation to crush the snails which they feed on. Linser et al., 1998 reported the presence of straight and curved caniform pharyngeal teeth in piscivorous M. salmoides, and suggested that those were more suitable for piercing flesh and removing scales than for crushing very hard objects such as snails. Tibbetts and Carseldine, 2003, while describing the anatomy of the pharyngeal mill in the herbivorous Arrhanthus sclerolepis kreffitti, suggested a model of pharyngeal jaw apparatus activity to tentatively explain the sequence of treatment of food. This included shredding, grinding of food, and rupturing cells of the tissues to release their contents. A high degree of maceration derived from the activity of the pharyngeal jaw apparatus in different fish species was also reported by Kumari et al., 2005 in R. rita, they found villiform and caniform teeth in the epi-and hypopharyngeal bones. Recently, Kumari et al., 2009 concluded the molariform teeth bone on the lower pharyngeal jaw of C. mrigala and a series of extensive regularly spaced ridges on the free surface of the chewing pad act as an efficient pharyngeal mill in crushing, grinding and mastication of food.

Mucus elaborated by mucous cells in the epithelium covering the gill arches and the gill rakers of the three concerned species may be involved in lubrication, assisting the smooth passage of food items through the pharynx, thus protecting the epithelium from mechanical injury. The role of mucous secretions in the lubrication of food during its passage in the gut in different fish species is widely accepted (Ezeasor and Stokoe, 1980; Martin and Blaber, 1984; Anderson, 1986; Sinha and Chakrabarti, 1985; Park and Kim, 2001; Podkowa and Goniakowska-Witalinska, 2003; Yashpal et al., 2006; Kumari et al., 2005, 2009). Mucus in different fish species has also been considered to play an important role in various food-processing activities. These include absorption (Ezeasor and Stokoe, 1980; Grau et al., 1992), lubrication of occluding tooth surfaces of the pharyngeal mill (Tibbetts, 1992), pregastric digestion (Mur ray et al., 1994), extraction of nutrients from plant material digested by fish (Tibbetts, 1997), reduction of adhesion, thereby ensuring their continued effectiveness (Tibbetts and Carseldine, 2003).

The present work ascertains the mucous nature of the gill surface epithelium. The presence of more mucous cells in the epithelium of C. auratus, and C. gariepinus than in O. niloticus, indicates a high mucous secreting character of the gills in these species. This mucous nature is important not only as a protective barrier, but also has an ion regulatory function. This fact explains why C. auratus, and C. gariepinus survive longer outside water.

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References


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