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Surface architecture of the mouth cavity of a carnivorous fish *Rita rita* (Hamilton, 1822) (Siluriformes, Bagridae)

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ABSTRACT. The topological characteristics of the mouth cavity of the carnivorous fish *Rita rita* were explored by means of scanning electron microscopy. The mouth cavity lining of *R. rita* may be distinguished into the roof and the floor. Papilliform teeth present on the premaxillae and the anterior regions of the dentaries are associated with seizing, grasping and holding of prey. The molariform teeth on the palatine regions and the dentaries are used for crushing and grinding of food items. The taste buds in the mouth cavity are of three types (types I, II, and III). The different types of taste buds are elevated from the epithelium at different levels, which may be useful for ensuring full utilization of the gustatory ability of the fish, detection and analysing of taste substances, as well as for assessing the quality and palatability of food, during its retention in the mouth cavity. A firm consistency or rigidity of the free surface of the epithelial cells may be attributed to compactly arranged microridges. These structures protect against physical abrasions potentially caused during food manoeuvring and swallowing. Furthermore, protection of the epithelium from abrasion is enhanced with mucous cell secretions, which lubricate ingested food items. Observations of the surface architecture of the mouth cavity of *R. rita* are discussed within the context of feeding and habitat preferences as well as ecomorphological adaptation of the species.

KEY WORDS : *Rita rita,* mouth cavity, surface architecture, SEM.

INTRODUCTION

The mouth cavity is an important component of the alimentary canal. It may be involved in the seizure, the selection of food, rejection of undesirable items ingested by fish and pre-digestion preparation of food. Among species, the mouth cavity shows great plasticity and structural adaptability for the exploitation of different food items (Kapoor et al., 1975; Kapoor & Khanna, 1994; Horn, 1998).

Literature on the surface ultra-structure of the mouth cavity in fish is scanty. Surface organisation of the mouth cavity, using scanning electron microscope, was studied for the carnivorous fishes *Gadus morhua* Linnaeus, 1758 (Bishop & Odense, 1966); *Sparus aurata* Linnaeus, 1758 (Cataldi et al., 1987) and the surface plankton feeder, *Catla catla* Hamilton, 1822 (Sinha & Chakrabarti 1985). Meyer-Rochow (1981) described the distribution and surface morphology of taste buds on the tongue of a variety of fishes having different food habits and inhabiting a variety of habitats. Ezeasor (1982) described taste buds in the oropharyngeal cavity of an active predator *Salmo gairdneri* Richardson, 1836. Hansen et al. (2002) reported the development of taste buds at different locations including the oropharyngeal cavity of *Danio rerio* Hamilton, 1822. More recently, Fishelson & Delarea (2004) and Fishelson et al. (2004) described the form and distribution of taste buds and dentition in the oropharyngeal cavity of several blenniid, gobiid and cardinal fish species.

The mouth cavity has been described using light microscopy in catfishes e.g. *Rita rita* Hamilton, 1822 (Islam, 1951; Khanna, 1962), *Heteropneustes fossilis* Bloch, 1794 (Chitray & Saxena, 1962), *Mystus* (= *Sperata*) *aor* Hamilton, 1822 and *Silonia silondia* Hamilton, 1822 (Khanna, 1962), *Mystus gulio* Hamilton, 1822 (Pasha, 1964), and *Clarias batrachus* Linnaeus, 1758 (Sastry, 1973; Sinha & Moitra, 1978). Sinha & Chakrabarti (1986) and Chakrabarti & Sinha (1987), using scanning electron microscopy, described the surface architecture of the mouth cavity of *Mystus* (= *Sperata*) *aor* Hamilton, 1822 and *Mystus vittatus* Bloch, 1794 respectively. Atema (1971) and Caprio et al. (1993) described the structure, function and distribution of taste buds in the mouth cavity of the channel catfish *Ictalurus (=Ameiurus) natalis* Lesueur, 1819. More recently, Golubtsov et al. (2004) studied the dentition in African catfish *Andersonia leptura* Boulenger, 1900 and *Siluranodon auritus* Geoffroy Saint-Hilaire, 1809.

Rita rita Hamilton, 1822 (Bagridae, Siluriformes) is a sluggish, bottom dwelling, carnivorous catfish and the bulk of its food primarily consists of molluscs. In addition, it feeds on small fishes, crustaceans, insects, as well as on decaying organic matter.

The objective of this study was to examine the surface architecture of the mouth cavity of *R. rita* to better understand its role in relation to the species' food and habitat preferences.

MATERIALS AND METHODS

Live specimens of *R. rita* (mean ± SD standard length, SL, 105 ± 6 mm; n = 10) were collected from the river Ganges at Varanasi, Uttar Pradesh. The fishes were maintained in a laboratory aquarium with a layer of sand at the bottom for 24 – 48 h at 25 ± 2 ºC and were fed with minced goat liver. The fishes were cold anaesthetised following Mittal & Whitear (1978), to excise the roof and the floor of the mouth cavity. The excised tissues were treated and prepared for scanning electron microscopy following Pinky et al. (2002). Critical point dried tissues were attached to stubs with the roof or floor facing upwards, were coated with gold and were then examined with a scanning electron microscope (Leo, 435 VP, England). The results were recorded on a Pentium IV computer (Vintron).

OBSERVATIONS

In *R. rita* the mouth cavity is spacious and opens anteriorly through a wide transverse mouth, which is bordered by the upper and the lower lips. The mouth cavity lining was, for convenience, divided into two regions – the dorsal roof and the ventral floor.

The roof of the mouth cavity comprised antero-posteriorly an upper jaw consisting of the premaxillae and the maxillae; the velum – a thin fold at the inner boundary of the upper jaw; the palatine regions bilaterally supported by the palatine bones; and the palate extending up to the pharynx (Fig. 1a). The upper jaw displayed two ovoid areas borne on the premaxillae that appeared fused in the middle of the jaw. The palatine regions, in general, were ovoid, separated from each other by a part of the palate; they converged or even merged anteriorly (Fig. 1a).

The floor of the mouth cavity comprised antero-posteriorly a lower jaw consisting of the dentaries and the angulars; the velum - a thin fold at the inner boundary of the lower jaw; and the tongue extending up to the pharynx (Fig. 1b). In the lower jaw, an elongated ridge-like structure occurred between the dentaries (Figs 1b, c, d). The ridge was narrow at the anterior side and gradually widened towards the posterior side of the jaw (Fig. 1c). The tongue consisted of an anterior region and the major posterior region extending up to the pharynx. The middle part of the posterior region was differentiated into an elongated ridge-like structure similar to that between the dentaries (Figs 1b, e).

The palatine regions, the dentaries and the oval areas on the premaxillae were characterized by the presence of teeth (Figs 1a, b). In contrast, the palate, the tongue, the velum, the maxillae and the angulars, were edentulous. In addition, the teeth were papilliform on the premaxillary regions (Figs 1a, f), molariform on the palatine regions (Fig. 1a) or both on the dentaries (Figs 1b, c).

The papilliform teeth were short, conical shaped, relatively widely spaced and irregularly distributed on the entire surface of the oval area of each premaxilla (Figs 1a, f). They were, however, restricted to the outer regions of the anterior areas of the dentaries (Fig. 1b). The papilliform teeth pierced through the epithelium, thus only the distal part of each tooth was exposed. The tooth tips appeared fragile and often showed wear and breakages. The proximal part of the tooth remained covered under the epithelium (Fig. 1g).

The molariform teeth in the palatine region and on the dentaries were arranged in several rows. They were round and small in diameter at the anterior and outer areas with their diameter gradually increasing towards the posterior and inner areas (Figs 1a, b). The rows of these teeth on the dentaries and palatine regions were generally oriented parallel to their outer margins. The small molariform teeth, probably in developing stage and on their way of eruption, remained covered by the epithelium, which at times was seen ruptured at one or several places (Figs 1h, i). In contrast, the large molariform teeth pushed their way through the epithelium and their free surfaces were thus exposed (Fig. 1i).

The epithelial surface of the mouth cavity appeared smooth. In the anterior region of the tongue, however, it was folded into extensive horizontal ridges separated by shallow grooves (Fig. 1j). Further, the surface of the epithelium covering the lateral sides of the molariform teeth was uneven or indented like a honeycomb as the epithelial cells showed characteristic depressions or invaginations (Fig. 1h).

The epithelium of the mouth cavity consisted of a mosaic pavement of irregular polygonal epithelial cells of varied dimensions (Figs 2a - d). The free surface of each epithelial cell was characterised by the presence of a series of microridges. The microridges of the cells appeared smooth, uniform in width and sinuous. They were compactly arranged, extensive and often form maze-like patterns (Figs 2a, b) or extensively branched and interwoven to form web-like patterns (Figs 2c, d).

On the epithelium, rounded or somewhat triangular crypts were evident between 2-3 epithelial cells at irregular intervals. These crypts represented the mucous cell openings (Figs 2a, c, d) as well as the taste pores of the taste buds, which were either slightly sunken or at the level of the epithelium. The taste buds were characterised by the presence of several microvilli, each representing a taste hair, projected at the surface through the taste pore (Fig. 2 d). The mucous cell openings and the taste buds, however, could not be observed in the epithelium covering the surface of the molariform teeth (Fig. 2b).

Furthermore, the epithelium was characterised by the presence of a large number of prominent, irregularly distributed conical or papillate epithelial protrusions (Figs 1a, b, c), which were either isolated or in small groups of 2-5 (Figs 1d, i, j; Figs 2e, f, g). The protrusions on the palate, the tongue, the velum and in between the papilliform teeth on the jaws were small in dimensions and low in height. In contrast, protrusions in the vicinity of the molariform teeth on the palatine region and dentaries, were often relatively large in dimensions (Fig. 1i; Fig. 2g), concentrated and projected well above the surface of the epithelium.

The characteristic ridge-like structures between the dentaries (Figs 1b, c, d), in the lower jaw, and on the posterior region of the tongue (Figs 1b, e) were formed by clusters of large, conspicuous, irregularly polyhedral, mound-like epithelial elevations, which were separated from each other by deep clefts. On the surface of each such elevation, several prominent papillate or conical epithelial protrusions were evident (Fig. 1e).

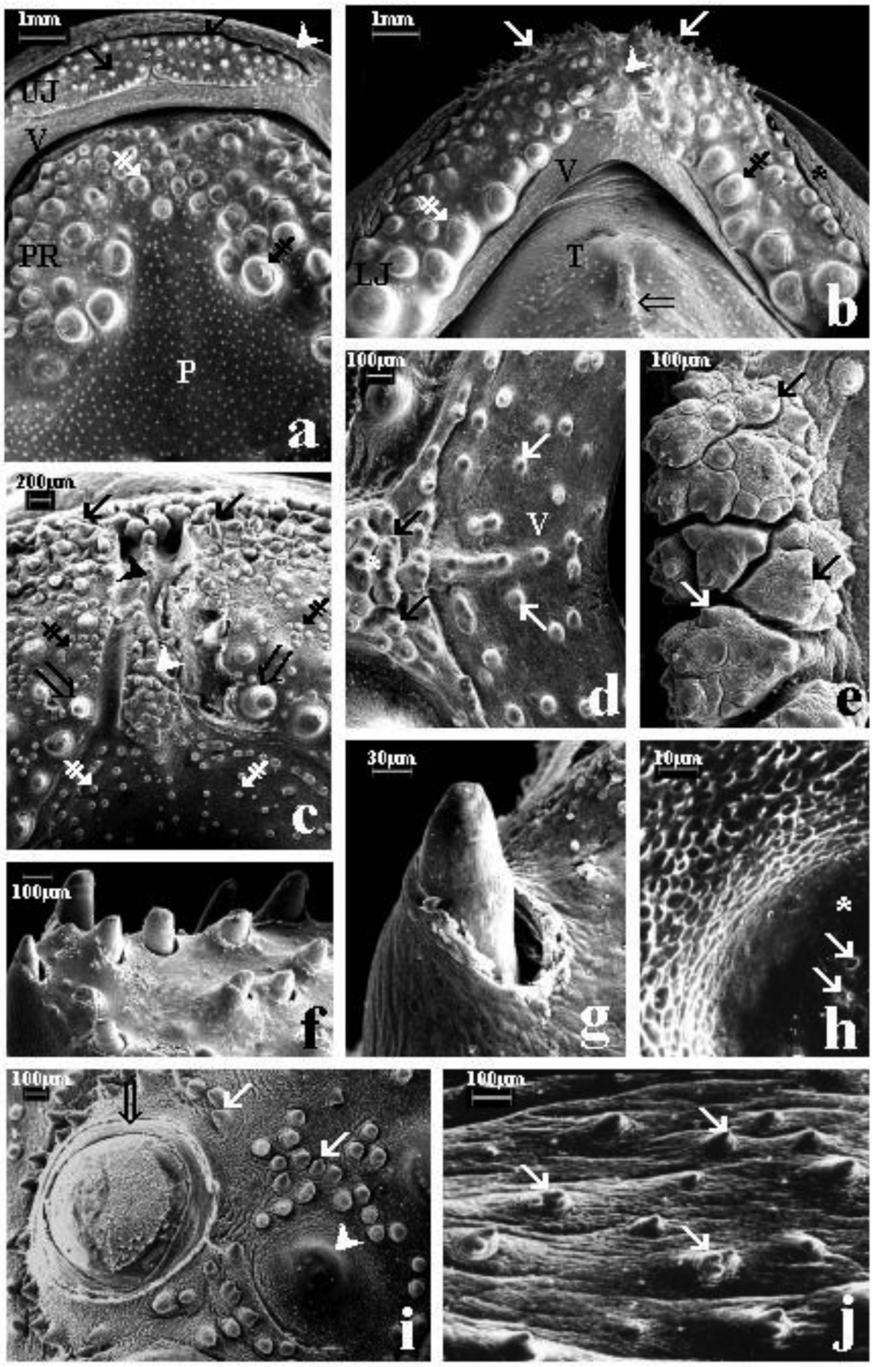

Fig. 1. – Scanning electron photomicrographs of the surface architecture of (a, f-i) the roof and (b-e, j) the floor of the mouth cavity of *Rita rita*. In figures anterior is to the top except in (d) where anterior is to the left. **(a)** UJ : Upper Jaw; V : Velum; PR : Palatine Regions; and P : Palate. Upper lip : arrowhead; Papilliform teeth on UJ : arrows; Molariform teeth on PR : barred arrows; and dots like epithelial protrusions on P, V and in between the teeth. (Scale bar = 1mm). **(b)** LJ : Lower Jaw; V : velum and T : Tongue. Lower lip : asterisk; Papilliform (arrows), and molariform teeth (barred arrows) on dentaries, ridge-like structure (arrowhead) between the dentaries and on T (open arrow); and dots like epithelial protrusions on T, V and in between the teeth. (Scale bar = 1mm). **(c)** Ridge-like structure (arrowheads) between the dentaries. Papilliform (arrows) and molariform teeth (open arrows) on the dentaries. Epithelial protrusions (barred arrows) on V and in between the teeth. (Scale bar = 200µm). **(d)** V and ridge-like structure between dentaries : asterisk. Taste buds : arrows (Scale bar = 100 µm). **(e)** Ridge-like structure on T with clusters of mound-like epithelial elevations separated by deep clefts. Taste buds : arrows. (Scale bar = 100 µm). **(f)** UJ with papilliform teeth. (Scale bar = 100µm). **(g)** Papilliform tooth piercing through the epithelium. (Scale bar = 30µm). **(h)** PR with a part of small molariform tooth (asterisk), which in lower magnification (i) is indicated by arrowhead. Ruptures of epithelium : arrows. Epithelial cells at the lateral side of the tooth were invaginated. (Scale bar = 10µm). **(i)** PR with a small tooth (arrowhead) covered with epithelium and a large tooth (open arrow) with exposed surface. Conical epithelial protrusions : arrows. (Scale bar = 100µm). **(j)** Anterior region of T with ridges separated by shallow grooves. Conical or papillated epithelial protrusions : arrows. (Scale bar = 100µm)

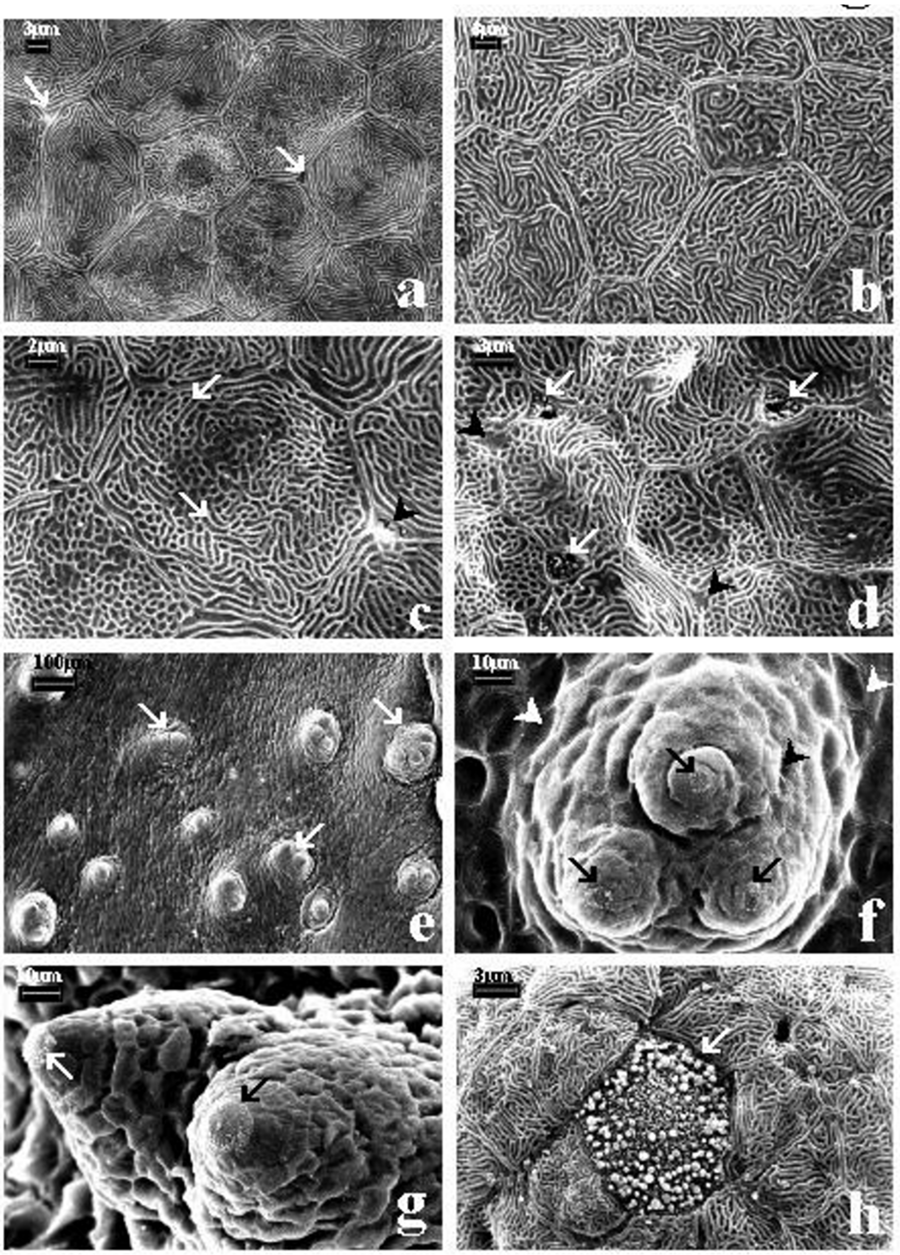

Fig. 2. – Scanning electron photomicrographs of the surface architecture of the epithelium of : (a, f, h) the palate (P); (b) the molariform tooth; (c, d, g) the palatine region (PR) and (e) the tongue (T). **(a-d)** Mosaic pavement of epithelial cells with distinct boundaries and compactly arranged microridges. **(a)** Micro-ridges on P, in parallel formation. Mucous cell apertures : arrows. (Scale bar = 3µm). **(b)** Micro-ridges on the surface of the tooth in parallel formation. (Scale bar = 2µm). **(c)** Micro-ridges on PR in web-like formations. Fine micro-bridges : arrows; Mucous cell aperture : arrowhead. (Scale bar = 2µm). **(d)** Type III taste buds with taste hairs : arrows. Mucous cell apertures : arrowheads. (Scale bar = 3µm). **(e)** Conical/papillate epithelial protrusions on T : arrows. (Scale bar = 100µm). **(f)** Papillate epithelial protrusions with taste buds : arrows. Epithelial cells are concentrically arranged with characteristic invaginations : arrowheads. (Scale bar = 10µm). **(g)** Epithelium in the vicinity of a molariform tooth. Conical epithelial protrusions with taste buds and microvilli : arrows. (Scale bar = 10µm). **(h)** Summit of epithelial protrusion with taste bud : arrow. Small microvilli are concentrated in the centre, whereas large ones are found in the periphery. (Scale bar = 3µm)

The epithelial protrusions were covered with concentrically arranged epithelial cells (Figs 2f, g). The latter often showed shallow depressions or invaginations. At the peak of each protrusion, a taste bud was located, with closely packed microvilli serving as taste hairs, which protrude to the surface through a rounded taste pore (Figs 2f, g). The microvilli, as viewed from the top, could be divided into two types : (a) those small in diameter, short and papillate, in the centre of the taste pore (Fig. 2h); and (b) those relatively large in diameter, elongated in the peripheral region of the taste pore (Fig. 2h).

The taste buds, on the basis of the degree of elevation and external surface morphology, were grouped into three categories (i.e., Type I, Type II and Type III) following Reutter et al. (1974) and Ezeasor (1982). The type I taste buds were prominently elevated being located on epithelial protrusions (Fig. 2g), projected well above the surface, often in the vicinity of molariform teeth (Fig. 1i) and on the ridge like structures between the dentaries and on the tongue (Figs 1c, e). The type II taste buds were slightly elevated being located on small, low-height epithelial protrusions, on the palate, the tongue and the velum (Fig. 1d; Figs 2e, f). The taste pores of these taste buds appear in slight depressions at the apices of the epithelial protrusions. The type III taste buds were located either slightly sunken or at the level of the general epithelium throughout the mouth cavity (Fig. 2d). Furthermore, REUTTER et al. (1974) postulated that the taste bud Type I and II are mostly mechanoreceptors and Type III are essentially chemoreceptors.

DISCUSSION

Differences described for the dentition, the distribution of taste buds and mucous cells and the patterns of microridges on the epithelial cells at different regions of the roof and the floor of the mouth cavity of *R. rita* could be considered as adaptations to various food preferences and feeding behaviour of the fish.

The presence of papilliform teeth on the premaxillae and the outer regions of the dentaries may be associated with seizing, grasping, holding and preventing the escape of small prey, occurring in the diet of *R. rita*. Notwithstanding, ISLAM (1951) failed to mention the presence of teeth in the mouth cavity of several teleost fishes, including *R. rita*, whereas KHANNA (1962), using light microscopy, reported their presence on the premaxillae but not on the dentaries. Nonetheless, recent scanning electron microscope studies have shown the presence of similar elongated conical and spine-shaped teeth on the jaws of *Denticeps clupeoides* Clausen, 1959 (SIRE et al., 1998), *Atherion elymus* Jordan & Starks, 1901 (SIRE & ALLIZARD, 2001) and several cardinal fish species (FISHELSON et al., 2004). These fishes feed also on small prey. Teeth on jaws, similar to the papilliform teeth of *R. rita*, have also been described light microscopically in several other catfishes [e.g. *Mystus* (= *Sperata*) *aor* Hamilton, 1822 and *Silonia silondia* Hamilton, 1822; KHANNA, 1962; *Clarias batrachus* Linnaeus, 1758; SASTRY, 1973; *Mystus gulio* Hamilton, 1822; PASHA, 1964; *Heteropneustes fossilis* Bloch, 1794; CHITRAY & SAXENA, 1962; *Andersonia leptura* and *Siluranodon auritus*; GOLUBTSOV et al., 2004]. Most of these fishes are bottom-dwelling species and their food primarily consists of small fish and invertebrates. KHANNA (1962) reported pronounced, large, curved teeth on the jaws as well as on vomers and palatines of piscivores *Muraenesox* (= *Congresox*) *talabon* Cuvier, 1829, *Harpadon nehereus* Hamilton, 1822, *Notopterus* (= *Chitala*) *chitala* Hamilton, 1822, and *Channa marulius* Hamilton, 1822. He suggested that such teeth are intended to hold securely the prey in the mouth. BISHOP & ODENSE (1966) also reported simple, pointed curved teeth in the mouth cavity of the carnivorous *Gadus morhua* Linnaeus, 1758 and suggested that they help impale prey. In herbivorous fishes however (e.g. *Labeo horie* Heckel, 1846-49; GIRGIS, 1952; *Cirrhinus mrigala* Hamilton, 1822; KHANNA, 1962; SASTRY, 1973; *Labeo* (= *Sinilabeo*) *dero* Hamilton, 1822; SAXENA, 1980; *Hilsa* (= *Tenualosa*) *ilisha* Hamilton, 1822 and *Mugil* (= *Rhinomugil*) *corsula* Hamilton, 1822; SASTRY, 1973), where holding or grasping of food is not required, the jaws are edentulous.

The presence of molariform teeth with rounded and blunt surfaces have also been reported for *R. rita* in the past (KHANNA, 1962). These structures may be associated with the crushing and grinding of hard bodied prey (e.g., molluscs, crustaceans). BOND, 1979 suggested that in *Anarrhichthys ocellatus* Ayres, 1855, which feed on shelled animals, molariform teeth on the jaws are used to crush the shells. Molar-like or plated teeth have also been reported in adult *Sparus aurata* Linnaeus, 1758, which feed mainly on molluscs, polycheates, and crustaceans (CATALDI et al., 1987). Molariform teeth may also be used to compress food into a manageable lump, prevent its escape and ensure its progress towards the throat (WHITEHEAD, 1977).

Sense of taste is an important property in fish for distinguishing from a variety of food available to them in an aquatic environment (HARA, 1994). In *R. rita*, the presence of taste buds could be considered as an adaptation to its bottom dwelling and sluggish feeding behaviour compensating for the restricted visibility in the foul turbid water it inhabits. KHANNA (1968) studied the distribution of taste buds in the mouth cavity of a variety of fishes. He showed that taste buds were rare or absent from highly predaceous carnivores – *Muraenesox* (=*Congresox*) *telabon* Cuvier, 1829 and *Harpadon nehereus* Hamilton, 1822), which rely more on their eyesight for detecting prey. *Channa striata* Bloch, 1793, a carnivorous fish, which feed both by sight and taste, has a better gustatory sense; and *Tor tor* Hamilton, 1822, a hill stream carnivorous fish, which selects its food from among the mud, has the best developed gustatory faculty with numerous taste buds in the buccal cavity. Further, KHANNA (1968) reported that in the plankton feeder *Ilisha filigera* Valenciennes, 1847 taste buds are present but in much less number than in *Tor tor*. In addition, MEYER- ROCHOW (1981) also reported few taste buds on the tongue of *Carapus mourlani* Petit, 1934 and absence of taste buds on the tongue of *Diretmus sp.* Johnson, 1864. These two mesopelagic species possess poorly developed taste receptors, for they inhabit areas of low prey abundance and diversity (MEYER- ROCHOW, 1981).

In fish, food items seized, grasped, snapped, or nibbled with jaws, in general, are retained in the mouth cavity. During the retention period these are subjected to final sensory judgement. As a result, a food item can then be either rejected or swallowed (For review of the literature see KASUMYAN & DOVING, 2003). In *R. rita,* prominent taste buds may be useful in assessing the palatability of the food and decide whether to swallow or spit it out (e.g., KASUMYAN & DOVING, 2003). The decision is made when contact of food with taste buds results into a mechanical impulse perceived and transmitted from the sensory cells to the brain centres (ATEMA, 1971; REUTTER et al., 1974; REUTTER & BREIPOHL, 1975). Furthermore, the location of the taste buds (type I and type II) at the summit of the conspicuous epithelial protrusions may increase the probability of contact between the receptors and the food items when retained in the mouth cavity. The latter may result in enhanced efficiency in perception and sorting of food types as well as in assessing the quality and palatability of food items. MEYER-ROCHOW (1981), who observed taste buds on distinct dome-like elevations on the surface of tongue of several fish species, suggested that elevated taste buds could have a superior perception of taste, in contrast with non-elevated ones or with receptors sunken below the level of the tongue. The same was also suggested for *Salmo gairdneri* (EZEASOR, 1982).

Structures similar to the type III taste buds in the mouth cavity of *R. rita* were also observed on the snout, lips and barbel epithelium of *Gadus morhua* Linnaeus, 1758 (HARVEY & BATTY, 1998), on the head, lips and gill rakers of *Danio rerio* Hamilton, 1822 (HANSEN et al., 2002), on the lips and mouth of some blenniid and gobiid fishes (FISHELSON & DELAREA, 2004), and in the oro-pharyngeal cavity in a number of cardinal fishes (FISHELSON et al., 2004). Further, FISHELSON et al. (2004) in addition to the taste buds belonging to the type III category reported yet another category the type IV.

The presence of ridge-like structures on the tongue and in between the dentaries of *R. rita* is important, for it results in the projection of taste buds above the level of the surface of the epithelium. In addition, the occurrence of taste buds on these structures may be associated with the high degree of competence of the fish in taste preference and selection of food. Furthermore, these ridges may be considered to guide the food particles in the mouth cavity towards the pharynx. ISLAM (1951) while describing the mouth cavity of *R. rita* made no reference of such structures. KHANNA (1962) also did not report such a ridge in between the dentaries in *R. rita*. However, he reported the presence of a prominent longitudinal ridge on the tongue but made no reference of epithelial protrusions and taste buds on it. No additional information on similar structures was found in the literature for other fishes.

Presence of taste buds on the velum in *R. Rita* may serve to screen the quality of food before it is passed onto the mouth cavity. FISHELSON et al. (2004) also reported a large number of taste buds in the oral valves in cardinal fishes. The same, however, was not true for *Salmo gairdneri* (EZEASOR, 1982).

The free surface of the epithelial cells at different locations (e.g., skin, lips, mouth cavity, pharynx, gills) of different fishes, is characteristically differentiated into series of microridges, and referred to as cytoplasmic folds, microvilli, microfolds, microvillar ridges, ridges or microridges (For review of literature see GARG et al., 1995). The microridges are organized in different ways to form intricate patterns and are thought to be involved in various functions; e.g., absorptive or secretory activities, to aid in laminar flow, holding mucous secretions to the cell surface, to provide reserve surface area for stretching or distortion, to facilitate the spread of mucus away from the goblet cells, to provide mechanical protection, to enhance mechanical flexibility (For review of literature see WHITEAR, 1990; OLSON, 1995).

The form of microridges corresponds to type and rate of secretion at the cell apex. Some variations in surface pattern may reflect the stage of maturation of a particular cell, or groups of cells that have recently reached the surface. Furthermore, the development of microridges are then a consequence of the arrival of new membranes, as vesicles carrying the secretion fuse with the apical plasmalemma and high ridges would indicate a rapid sequence of arrival of secretory vesicles at the surface (WHITEAR, 1990). In the mouth cavity of *R. rita*, presence of prominent microridges could thus be considered to reflect high secretory activity of epithelial cells.

Compactly arranged microridges, often interconnected with microbridges, may also be considered to provide rigidity to the free surfaces of the epithelium, in order to protect against physical abrasions, when manoeuvring of ingested prey (e.g., MITTAL et al., 2004).

Invaginations and shallow depressions of the epithelium at the lateral sides of molariform teeth and the tongue of *R. rita* may also enhance plasticity and allow the stretching of the epithelial cells during the manipulation of food consumed by the fish. Mucus is elaborated by mucous cells distributed in the mouth cavity of *R. rita*. Secreted mucus is used to lubricate both the epithelium and ingested food items, in order to assist the smooth passage of food and thus protect the epithelium from possible mechanical injury (EZEASOR & STOKOE, 1980; MARTIN & BLABER, 1984; SINHA & CHAKRABARTI, 1985, 1986; ANDERSON, 1986; CHAKRABARTI & SINHA, 1987; PARK & KIM, 2001; PODKOWA & GONIAKOWSKA-WITALINSKA, 2003). Mucus has also been associated with various food-processing activities : e.g., particle entrapment (FRIEDLAND, 1985; TIBBETTS, 1997; EIRAS-STOFELLA & CHARVET-ALMEIDA, 1998); pregastric digestion (MURRAY et al., 1994); absorption process (GRAU et al., 1992; EZEASOR & STOKOE, 1980); and extraction of nutrients from plant material digested by fish (TIBBETTS, 1997).

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