Received: 29 March 2023 | Accepted: 19 June 2023

DOI: 10.1111/ahe.12943

ORIGINAL ARTICLE

Anatomia Histologia Embryologia WILEY

Anatomical oropharyngeal cavity specialisations in the cutlassfish (*Trichiurus lepturus*, Linnaeus, 1758)

Neveen E. R. El-Bakary[1] | Mohamed A. M. Alsafy[2] | Catrin S. Rutland[3] | Samir A. A. El-Gendy[2] | Basma M. Kamal[4]

[1]Faculty of Science, Department of Zoology, Damietta University, Damietta, Egypt

[2]Faculty of Veterinary Medicine, Department of Anatomy and Embryology, Alexandria University, Alexandria, Egypt

[3]Faculty of Medicine and Health Sciences, School of Veterinary Medicine and Science, University of Nottingham, Nottingham, UK

[4]Faculty of Veterinary Medicine, Department of Anatomy and Embryology, University of Sadat City, Sadat City, Egypt

Correspondence

Mohamed A. M. Alsafy, Faculty of Veterinary Medicine, Department of Anatomy and Embryology, Alexandria University, Alexandria, Egypt.
Email: safy73@yahoo.com, mohamed.alsafy@alexu.edu.eg

Catrin S. Rutland, Faculty of Medicine and Health Sciences, School of Veterinary Medicine and Science, University of Nottingham, Nottingham, UK.
Email: catrin.rutland@nottingham.ac.uk

Funding information

Alexandria University; Damietta University; University of Nottingham; University of Sadat City

Abstract

Trichiurus lepturus is a carnivorous fish, and most of the previous anatomical research has focused on computed tomography imaging and histology of their teeth and fangs, while the remaining structures of pharyngeal cavity remain unexplored. The present research is the first to use anatomical examinations alongside scanning electron microscopy to investigate the *T. lepturus* oral cavity. The oropharyngeal roof included teeth, upper lip, rostral and caudal velum and the palate. The middle of the palate showed a median groove flanked by two folds, followed by a median band flanked by micro-folds, thereafter the palate became crescent shaped. The lateral regions of the palate exhibited longitudinal folds that extended rostrally towards the fangs. The oropharyngeal floor had two cavities which acted as a scabbard for the premaxillary fangs and upper velum, while the caudal sublingual cavity contained two oyster-shaped structures on the outer surface plus sublingual ridges and sublingual clefts. The tongue apex exhibited a spoon-like shape, its body demonstrated a median elevation and the root with two lateral branches contained only dome-shaped papillae. Taste buds were located on the upper velum, lower lip and the caudal part of the interbranchial septum. Images and descriptions of *T. lepturus* tooth structure are also provided. The present research, using anatomical dissection and morphological observation using scanning electron microscopy, has identified the structures of the dentition system, a variety in shapes of the folds and microridges, and identified the taste buds and mucous pores in the *T. lepturus* oropharyngeal cavity.

KEYWORDS

oropharyngeal cavity, scanning electron microscopy, teeth, tongue, *Trichiurus lepturus*

1 | INTRODUCTION

The largehead hairtail (*Trichiurus lepturus*) or beltfish is a member of the cutlessfish family, *Trichiuridae* is found in tropical and temperate oceans throughout the world (Muhammad et al., 2017; Nakamura & Parin, 1993). The Food and Agriculture Organization of the United Nations included this fish on its list of highest commercially harvested aquatic animals. In 2020, 1,143,578 tonnes of these fish were harvested worldwide, nearly double that fished in 1980, with a value of $1,143,578.373 (FAO, 2022a, 2022b).

The carnivorous *T. lepturus* feeds on cephalopods, bony fishes and euphausiids as sub-adults and adults (Martial et al., 2020; Martins et al., 2005). Bakhoum (2007) revealed that *Trichiurus* from the Egyptian coast, especially at AbuQir, fed on crustaceans when they were smaller than 30 cm in size, while fish larger than 59 cm tended to eat fish. The oropharyngeal cavity in predatory fish plays several roles including seizing and maintaining grip on prey (including other fish), food selection and the rejection of unwanted excretory particles swallowed by the fish. In fish, the lips and accompanying structures can be classified based on how their food is selected, captured, pre-digested and the deglutition process (Elgendy et al., 2016; Nandi & Saikia, 2021; Sayed et al., 2019). Several studies have also been conducted on differing fish species on the role of food uptake and intra-oral mechanics with a focus on the close relationships between fish adaptation to their environments and changes in the oral cavity anatomy (Alsafy et al., 2021, 2022; El Bakary, 2012; Elgendy et al., 2016; Fishelson et al., 2014; Rønnestad et al., 2013).

The oropharyngeal cavity roof and floor, and especially the teeth and sublingual floor, velum, tongue, palate, micro ridge and the pore system play significant roles in carnivorous fish feeding and their ability to adapt to their environment (Alsafy et al., 2022; Elgendy et al., 2016; Madkour et al., 2022). Most fish have a premaxilla and a maxilla (caudal to the premaxilla) in their upper jaw. In comparison to other vertebrates, the caudal region of the maxilla often has a greater range of movement in fish. A more complicated series of muscular and skeletal movements are therefore required to produce an effective gape (open mouth) for food prehension. The premaxilla protrudes rostrally during feeding to give the gape's dorsolateral appearance. This action increases the suction required in order to eat most prey fish. The presence of a ligament linking the caudal side of the premaxilla to the caudal end of the mandible's dentary bone allows for passive premaxillary protrusion by enabling ventral and posterior movement of the jaw (Gibb et al., 2015; Roberts-Sweeney, 2016).

Dentition in differing fish species also varies enormously. Several combinations observed include no teeth, few teeth, numerous columns of teeth, pharyngeal teeth (upper alone or both upper and lower plate-like teeth) and teeth on gill rakers (Alibardi, 2013). Dentition morphotypes include, front-fanged macrodont, back-fanged macrodont, villiform and edentulate, all of which differ in terms of individual tooth morphology, biomechanical properties, description and inferred function based on tooth size, position along the jaw, number of teeth, number of teeth rows and distance between teeth (Mihalitsis & Bellwood, 2019).

Morphological studies of the fish tongue both with or without taste buds, the distribution of taste buds, the teeth in general and the surface organisation of the mucosa of the oropharyngeal cavity have also received much attention from researchers (Abbate et al., 2006, 2012, 2020; Alsafy et al., 2018, 2021; Elgendy et al., 2016). For example in the carnivorous fish *Rita rita* and *Sparus aurata* (commonly called the gilthead seabream), papilliform teeth were associated with holding the prey, whereas molariform teeth were used for crushing and grinding the food (Elgendy et al., 2016; Yashpal et al., 2006). In addition, three types of taste buds were present to enable gustation. The rigid-free surface observed in the epithelial cells may contribute towards the compactly arranged microridges which help protect against physical abrasions during swallowing.

Despite knowledge about the anatomy and histology of some species, little is known about the *T. lepturus* oropharyngeal cavity. Understanding more about the anatomy may aid future cross-species comparisons and functional studies, especially in relation to eating, predation and respiration. The present work provides a comprehensive understanding of the anatomy, morphology and architecture of the oropharyngeal cavity in *T. lepturus*.

2 | MATERIALS AND METHODS

Seven sub-adult *T. lepturus* fish measuring 30–55 cm were collected from the Mediterranean Sea near Damietta-Egypt by professional fishermen following the guidance set out in ‘Sampling protocol for the pilot collection of catch, effort and biological data in Egypt’ (Dimech et al., 2012). The specimens were euthanized operating under standard commercial fishing conditions (cervical dislocation) and was conducted by a trained veterinary surgeon, in accordance with local, national and international ethics guidelines and checked for abnormalities. Specimens were placed on ice and then transported to the laboratory facilities. The specimens were considered subadults (at 30–55 cm long), with juveniles classified as 5–30 cm long, and full adults measuring more than 70 cm. The roof and the floor of the oropharyngeal region were then separated in each fish.

Two specimens were used to undertake the morphology study (observations and photographs) and the remaining five specimens were prepared for scanning electron microscopy (SEM). SEM specimens were fixed in 2% formaldehyde, 1.25% glutaraldehyde and 0.1 M sodium cacodylate buffer at pH 7.2 for 1 h at 4°C, thereafter the specimens were washed in 0.1M sodium cacodylate containing 5% sucrose, processed through tannic acid, and dehydrated through a graded series of ethanol and critical point dried. The samples were attached to aluminium stubs facing upwards and covered with carbon tabs and gold, prior to SEM examination (using a JEOL JSM-IT200 at Alexandria University, Faculty of Science). The term ‘fang’ was used to refer to large teeth, as used previously for the trichiurids by Tucker (1956), similarly ‘dagger-shaped teeth’ was used as described by Bemis and coauthors (2019).

3 | RESULTS

3.1 | Morphology

The oropharyngeal cavity appeared relatively wide with the mouth open, with an elongated jaw relative to the head size and opened rostrally through a pointed opening (Figure 1). The maxilla was shorter than the mandible. The oropharyngeal cavity was divided into two distinct parts. The characteristic features of the teeth within the *T. Lepturus* oral cavity, especially the fangs, were observed. The mouth was bordered by the upper and the lower jaws (Figure 1). The roof teeth contained three premaxillary fangs in five out of seven specimens, and four in the two remaining cases. The floor contained two

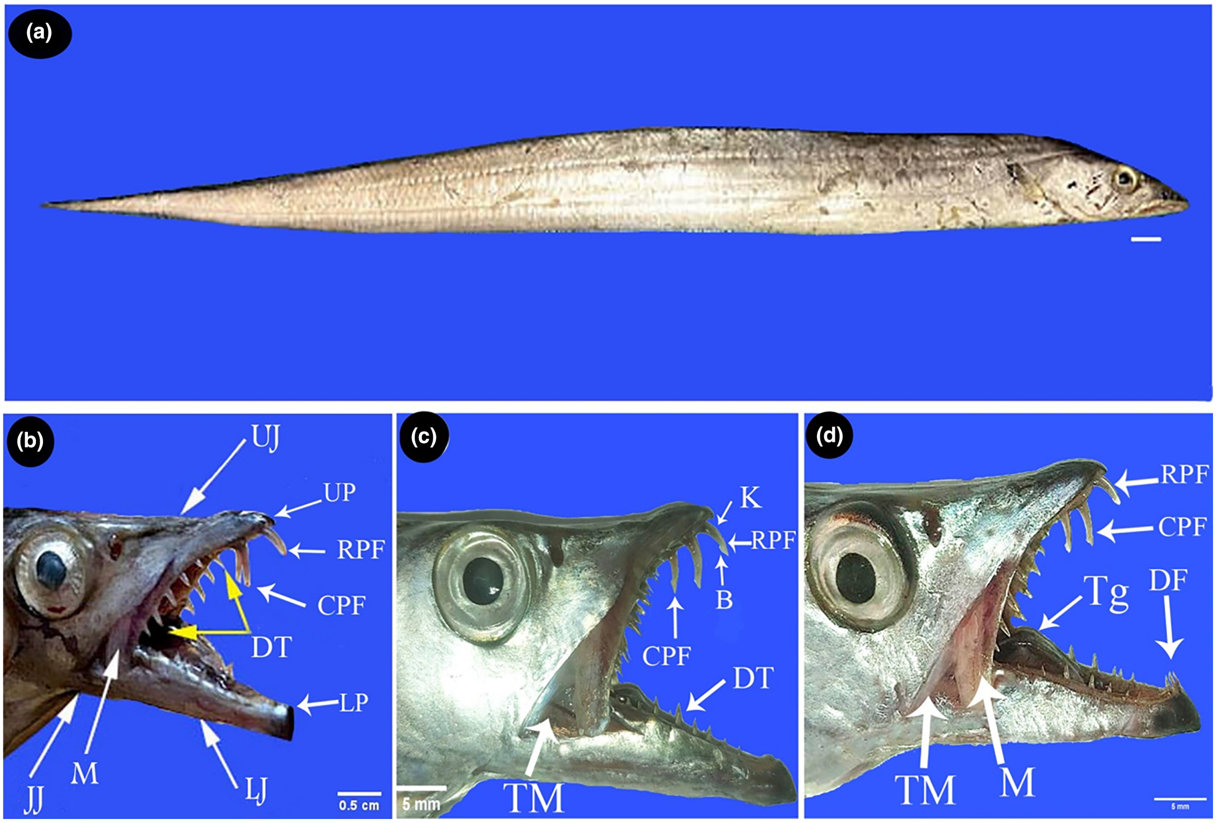

FIGURE 1 Morphology of the oropharyngeal cavity in *Trichiurus lepturus*. (a) Lateral aspect of *T. lepturus*. (b–d) Lateral aspect of the opened buccal cavity showing the different teeth and anatomical structures. (b) Three premaxillary fangs: one positionally rostrally and two caudally. (c) Three premaxillary fangs, two positioned rostrally and one caudally. (d) Three premaxillary fangs, one positioned rostrally and two caudally, with three dentary fangs. B, barb; CPF, caudal premaxillary fangs; DF, dentary fangs; DT, dagger teeth; JJ, jaw joint; K, keel; LJ, lower jaw; LP, lower lip; M, maxilla; RPF, rostral premaxillary fangs; Tg, teeth groove; TM, translucent membrane; UJ, upper jaw; UP, upper lip.

dentary fangs in the majority of the samples, these were often broken, one specimen had three fangs. On the roof, the dagger-shaped teeth increased in length gradually just rostral to the maxilla in a caudal direction, whereas on the floor of the mouth these teeth started to decrease in length in the middle of the mandible. The roof of the oropharyngeal cavity was marked by an elevation between the fangs and the palate (Figure 2a). The floor was further characterized by two depressions or cavities, a pigmented apical pouch and the spoon-shaped tip of the tongue along with two lateral branches of the tongue root which were attached to the medial side of the upper jaw (Figure 2b).

3.2 | The roof of the oropharyngeal cavity

The roof of the oropharyngeal cavity had a truncated triangular shape, its apex was located rostrally and its base was positioned caudally (Figure 3a). The roof consisted of the upper jaw, upper lip, velum, palate and teeth. The roof was divided into three parts: rostral, middle and caudal. The teeth consisted of rostral and caudal premaxillary fangs, two premaxillary teeth and dagger-shaped teeth.

The rostral part of the roof had a round margin upper lip and two premaxillary teeth that appeared in front of either one or two rostral premaxillary fangs (Figures 3a and 4a). Caudal to the rostral premaxillary fangs, there were either one or two caudal premaxillary fangs (growing fangs) their apex was wide and directed caudally (Figures 4a and 5a). The lateral dagger-shaped teeth of the upper jaw consisted of 3–4 teeth on each side (Figure 2a). There were two premaxillary ankylosed fangs directed rostroventrally, they appeared as long-pointed conical-shaped curved teeth and had barbs on their apices (hook-shaped enamelled cap), the lateral surface of the fang had regular longitudinal folds and the epithelium on their bases formed a socket, resembling a tie around a neck (Figure 4a). The two premaxillary teeth were folded on their outside surface and their apices appeared long and cylindrical, reminiscent of implements used to core fruit and vegetables such as a squash corer.

The epithelial surface of the upper lip had several microridges and epithelium protrusions, on the rostral margin, the epithelium protrusions took on a shape similar to mountain ridges, and caudally they appeared more leaf-like in shape (Figure 4b). In the mid and lateral regions of the lip, several microridges ran in the middle and lateral areas, these were transverse and oblique microridges, respectively (Figure 4c,d).

The velum differentiated into two portions: the rostral and caudal parts. The surface of the velum had irregular epithelium protrusions that contained taste buds, microfolds and pores (Figure 2). The caudal

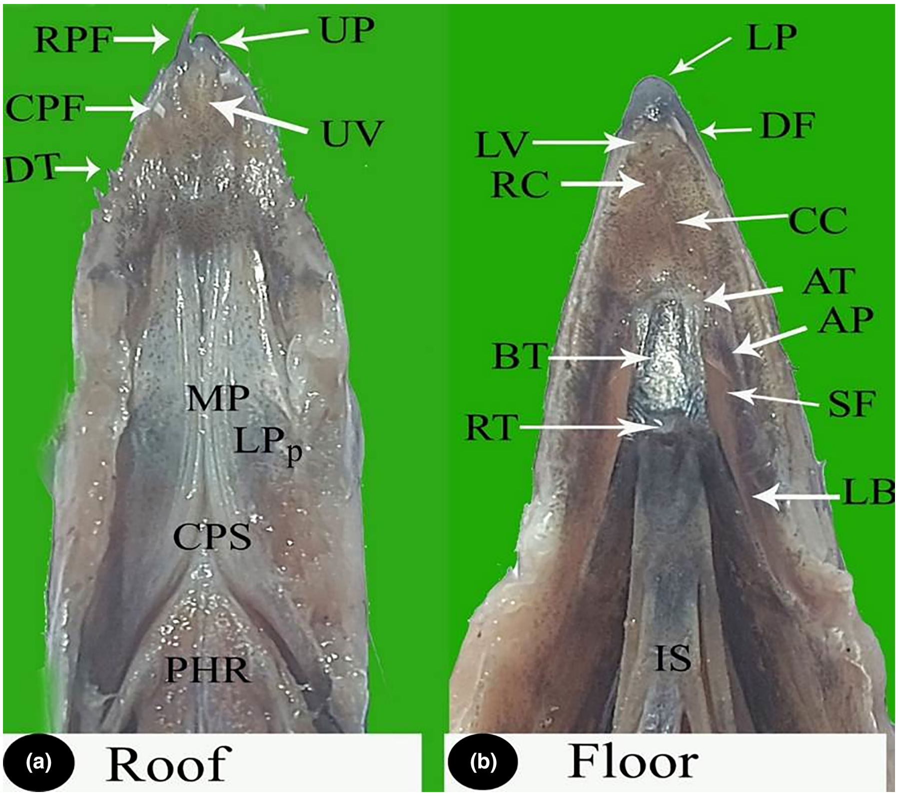

FIGURE 2 Morphology of the *Trichiurus lepturus* oropharyngeal cavity floor and roof. (a) Roof and (b) floor. AP, apical pouch; AT, apex of the tongue; BT, body of the tongue; CC, caudal sublingual cavity; CPF, caudal premaxillary fangs; CPS, crescent shaped part of the palatine; DF, dentary fang; DT, dagger-shaped teeth; IS, interbranchial septum; LB, lateral branch of the root of the tongue; LP, lower lip; LPp, lateral part of the palate; LV, lower velum; MP, median part of the palate; PHR, pharyngeal roof; RC, rostral sublingual cavity; RPF, rostral premaxillary ankylosed fangs; RT, root of the tongue; SF, sublingual floor; UP, upper lip; UV, upper velum.

portion had an elongated elevation and appeared tongue-like, the lateral part and central elevation had more protrusions and taste buds than that observed in the anterior region (Figure 4a).

The middle region of the oropharyngeal roof was represented mainly by the palate (Figure 5), the middle palatine part exhibited a median groove flanked by two folds, followed by a median band (with an appearance resembling a bamboo stem) flanked by epithelium with microfolds (Figure 5b,c). Thereafter, the middle palatine part became wider, forming a more crescentic shape. The lateral palatine part was characterized by longitudinal folds and extended rostrally towards the fangs (Figure 5b).

The upper jaw formed a central groove or a canal where five dagger-shaped teeth were arranged in this area on each side, the length of these teeth gradually increased caudally. Erupted and growing teeth were also present (Figures 4a and 5a).

The caudal region of the roof appeared rectangular in shape and had several regular and parallel longitudinal folds with longitudinal clefts. On the edges of this region, some upper pharyngeal teeth bands contained spiny curved teeth which were directed caudally and laterally (inwards) to direct food towards the oesophagus (Figure 6a). The end of this region was covered by several longitudinal folds that contained irregular microfolds and micro-clefts (Figure 6d).

3.3 | The floor of the oropharyngeal cavity

The floor of the oropharyngeal cavity comprised of the lower lip, lower jaw, lower velum, sublingual floor, apical pouch, tongue, lateral side of the floor, pharynx floor and the teeth. The two dentary fangs were present and did not have barbs and the dagger-shaped teeth lingual teeth band and interbranchial teeth band were both present.

The lower lip appeared thicker in the central rostral part and thinner in the periphery areas. Epithelium covered the internal surface of the rostral part of lips. The epithelium was characterized by several epithelial protrusions that carried taste buds, whereas the middle and the hind parts exhibited no taste buds (Figure 7a,b).

The lower velum had one pair of longitudinal velum ridges, plus a transverse velum ridge and a velum notch (Figure 7a). Caudal to the lower velum, there was a sublingual cavity that was divided into a rostral cavity just behind the upper velum cavity that acted as a scabbard (sheath) for the rostral premaxillary fangs and rostral velum, and a caudal cavity for the caudal premaxillary fangs and the caudal velum (Figures 3b and 7a,c). The caudal sublingual cavity contained three types of structures, (1) two structures resembling the shape of a closed oyster shell, (2) sublingual ridges and (3) sublingual clefts (Figures 3b and 7c,d).

The lateral part of the apical pouch was characterized by parallel paralingual longitudinal folds, and its caudal margin was shaped like a crescent (Figures 3b and 7c,d). Meanwhile, the tongue was located at the mid-region of the oropharyngeal floor and appeared as an elongated thickening of the underlying hyoid skeleton. The tongue was immobile and was divided into three parts: an apex, a body and a root. The apex of the tongue was pointed, thin and extended caudally to form a thin lingual border, the epithelium of the apex surface had irregular transverse folds and microfolds, in addition, no taste buds were present in this region (Figure 7d,e). The body of the tongue was characterized by a central elevation with a small depression at its beginning from the root (Figure 8a).

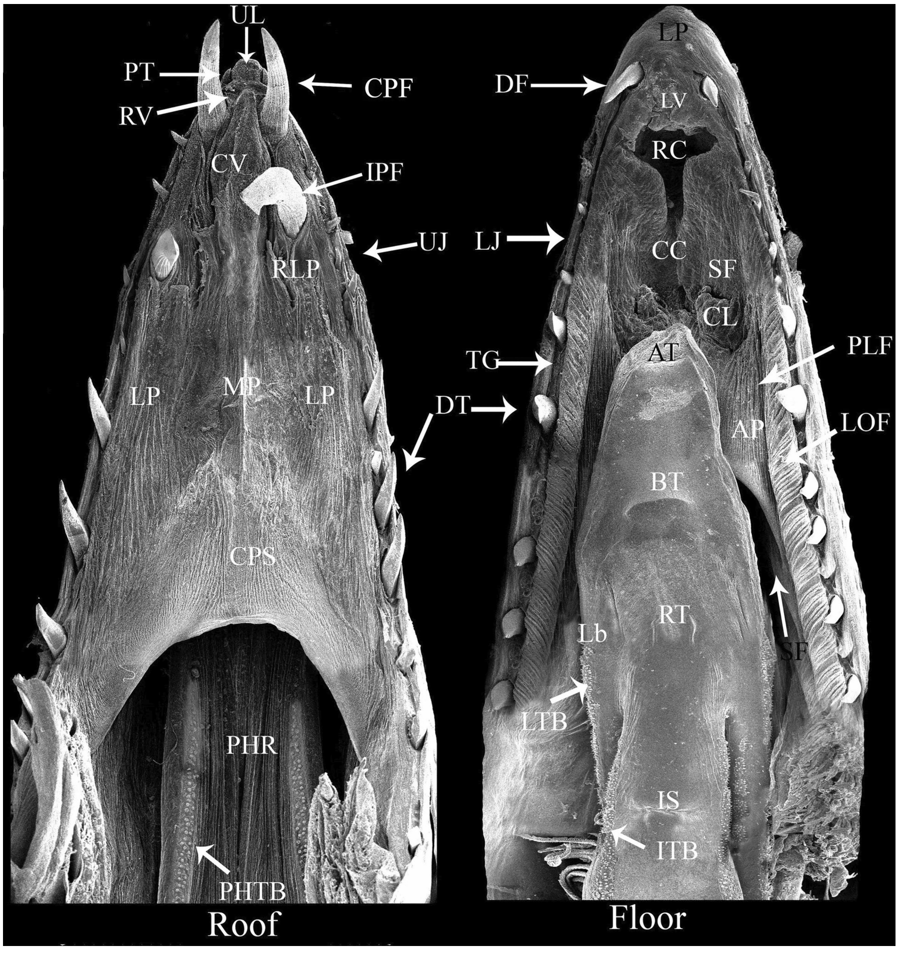

FIGURE 3 Scanning electron micrographs showing morphology of the *Trichiurus lepturus* oropharyngeal cavity floor and roof. (a) The roof and (b) floor of the oropharyngeal cavity. AP, apical pouch; AT, apex of the tongue; B, barbs on the fang apex; BT, body of the tongue; CC, caudal sublingual cavity; CD, caudal part of the velum; CL, closed oyster shell-shaped structure; CPF, caudal premaxillary fangs; CPS, crescentic palatine shape; DF, dentary fang; DT, dagger-shaped lateral teeth; Lb, lateral branch of the tongue root; LJ, lower jaw; LOF, lateral oblique's fold band; LP, lower lip; LPL, lateral part of the lower lip; LPp, lateral part of the palate; LV, lower velum; MP, middle part of the palate; PHTB, pharyngeal teeth band; PLF, paralingual longitudinal folds on the apical pouch; PT, two premaxillary teeth; RC, rostral sublingual cavity; RLP, rostral part of the lateral palatine part; RPF, rostral premaxillary ankylosed fangs; RT, root of the tongue; RV, rostral part of the velum; SF, sublingual floor; TG, teeth groove; UJ, upper jaw; UL, upper lip.

The tongue root was characterized by two lateral branches that attached to the inner side of the lower jaw. The epithelium of the body and root were characterized by dome shape papillae in addition to a lingual teeth band that had spiny teeth rows with a circular groove around their bases (Figure 8c–e).

The caudal part of the oropharyngeal floor had a long interbranchial septum which contained an interbranchial teeth band on the two lateral margins; the interbranchial teeth were rows of spiny teeth and had oblique folds (Figures 8e and 9a,b). The caudal part of the interbranchial septum was characterized by oblique folds, oblique clefts, oblique and transverse ridges and several taste buds (Figure 9c,d).

The lower jaw had a teeth groove that began from the dentary fang and contained the dagger shaped teeth, the groove had two sides the medial and lateral sides of the lower lip, the medial side had a lateral oblique fold band, its shape resembled a steel wire rope with the oblique folds and oblique grooves (Figures 2b and 8a,b).

4 | DISCUSSION

There are 45 species of cutlassfish the family *Trichiuridae* within the order *Scombriformes*. It is a valued food source around the world, for example in Egypt, 1812 tons were caught in 2010 (General Authority for Fishery Resources Development, 2010) and in China it was identified as the most important commercial marine fish species in terms of weight accounting for 10%–20% of their total marine (Luo, 1991). Previous research had concentrated on teeth, looking at histological and computed tomography results. The present study was the first to research the oropharyngeal cavity of this species using SEM.

The importance of breathing valves has been shown in several studies (Alsafy et al., 2022; El Bakary, 2012; Elgendy et al., 2016; Kaushik & Bordoloi, 2017; Nandi & Saikia, 2021). The breathing valve (velum) is crucial in preventing water reflux and food escape (Dahlgren, 1898; Hughes & Hughes, 1963). The automated operation of the maxillary (also known as upper) and mandibular (also known as lower) breathing valves, prevent water from entering the cavity while also preventing water from exiting through the mouth. Some *Actinopterygii* species such as *Catostomidea* have no lower valve, *Siluridea* have equally sized valves whereas some teleosts have a larger upper velum compared to the lower (Mitchell, 1904). The present work shows that the cutlassfish, *T. lepturus* also has a larger upper velum compared to the lower velum. The functional significance of this has been attributed to the upper velum catching the returning water stream needing and therefore needing to be heavy enough to resist the outward pressure from water (Mitchell, 1904).

It has previously been noted that the oropharyngeal cavity morphology of the cutlassfish, *T. lepturus* is potentially related to

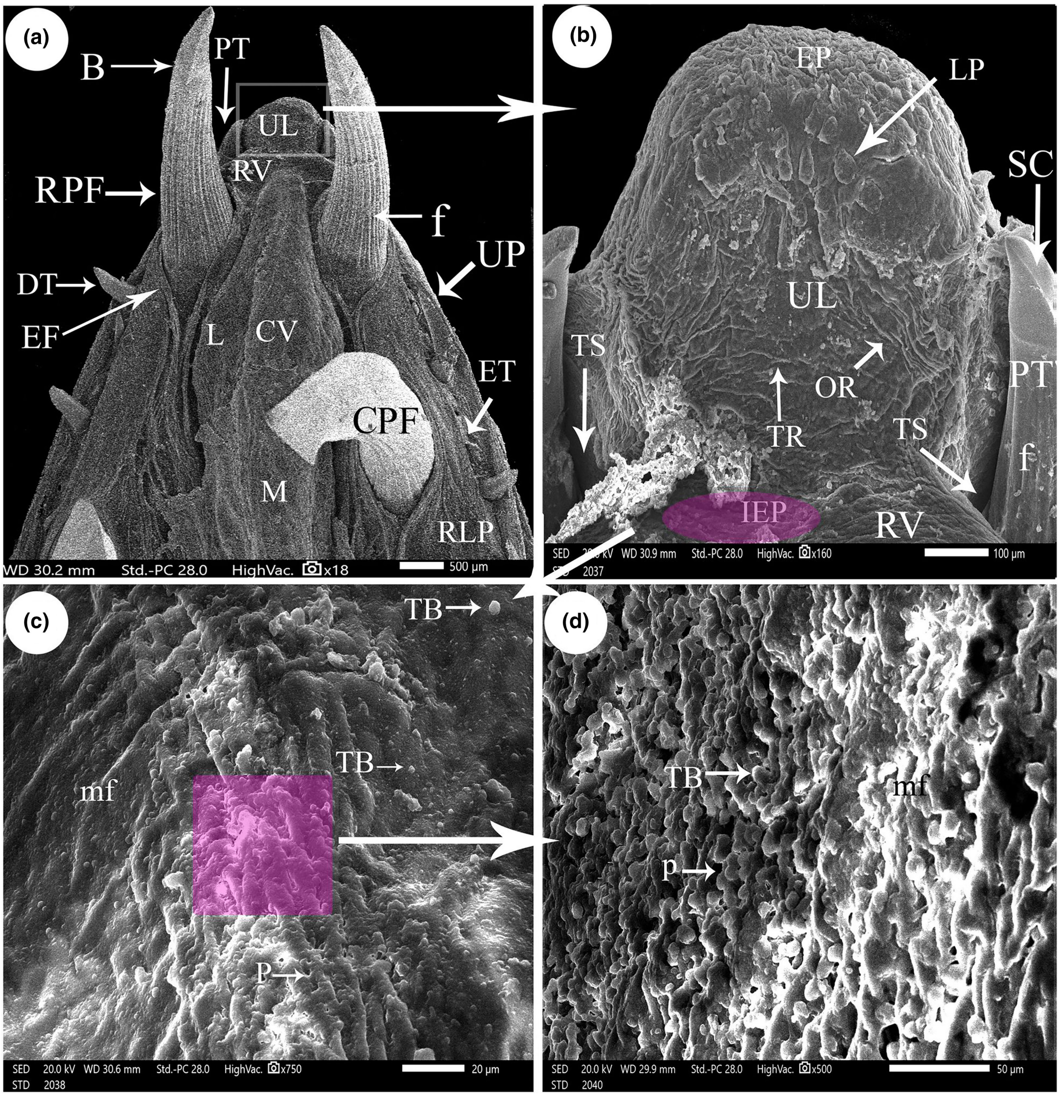

FIGURE 4 Scanning electron micrographs showing the surface morphology of the rostral part of the oropharyngeal cavity roof. (a–d) Increasing magnifications, the boxed (a) and pale red shaded areas (b and c) indicate the areas depicted in (b)–(d), respectively. B, barbs on the fangs apex; CPF, caudal premaxillary fangs; CV, caudal part of the velum; DT, dagger-shaped lateral teeth; EF, epithelium surrounding the base of the fangs (socket of the fangs); EP, epithelium lining; ET, erupted lateral teeth; f, longitudinal folds on the outer surface of the fangs; IEP, irregular epithelium protrusion; L, lateral part of the caudal velum; LP, leaf-like epithelium projection; M, median elevation of the caudal velum; mf, microfolds in the epithelial protrusions;OR, oblique microridges; P, epithelium protrusion shaped like mountain ridges; PT, two premaxillary tooth; RLP, rostral lateral region of the palatine part; RPF, rostral premaxillary ankylosed fangs; RV, rostral part of the velum; SC, cylindrical teeth apex, similar in shape to a squash corer; TB, taste buds; TR, transverse microridges; TS, tooth socket; UJ, upper jaw; UL, upper lip.

the type of food and feeding habits of this fish. For example, *T. lepturus* is characterized by a large mouth and jaw, and increased gape that enables it to engulf its prey (de Schepper et al., 2008). Previous research has shown these features are effective for capturing the movable and evasive prey, as this predators depends on high-velocity mouth closure when catching prey (Ferry-Graham et al., 2001; Kammerer et al., 2005; Norton & Brainerd, 1993; Porter & Motta, 2004).

The teeth consisted of different types of teeth, which varied in shape. These included premaxillary and dentary fangs, and sharp dagger-shaped teeth (sharp papillary form shape). In addition, the two small premaxillary teeth, the pharyngeal teeth band in the roof and the lingual and interbranchial teeth bands were present, given the shape and location we hypothesis these may help with the fine grinding actions exerted on the prey, but further functional studies are required to ascertain their functions. The current study agrees with a previous study in Atlantic cutlassfish (Bemis et al., 2019) as *T. lepturus* also have large, barbed, premaxillary and dentary fangs and sharp dagger-shaped teeth (sharp papillary form shape) in one row their oral jaws. In addition, the functional teeth firmly ankylose to the dentigerous bones. While Bemis et al. (2019) concentrated on tooth development and replacement, the present research elucidated anatomical and morphological aspects of the entire oropharyngeal cavity. The morphology and arrangement of these fangs may play essential roles in capturing, retaining and eating food these types of teeth are generally found in carnivorous (predatory)

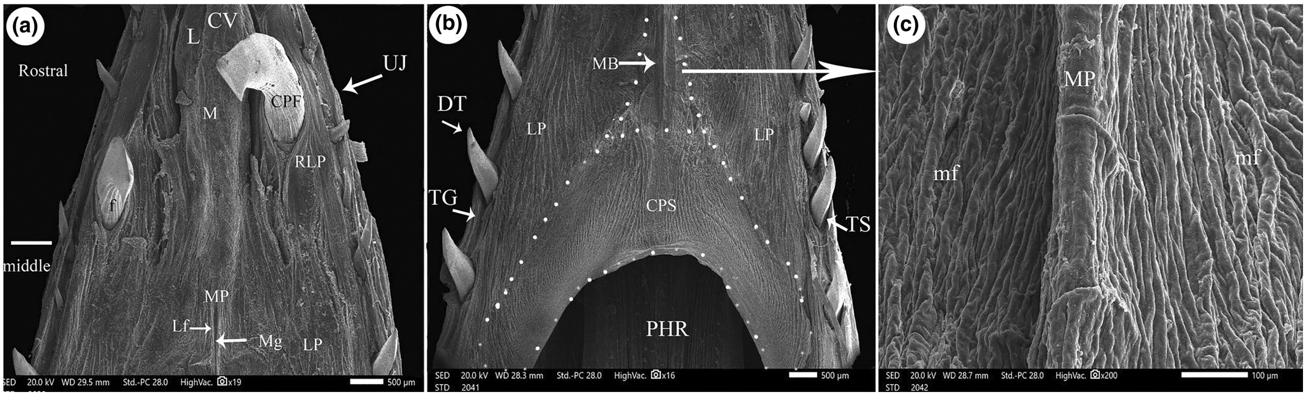

FIGURE 5 Scanning electron micrographs showing the surface morphology of the mid-region of the oropharyngeal roof (a–c). CD, the caudal part of the velum; CPF, caudal premaxillary fangs; CPS, crescentic shaped part of the palate; DT, dagger-shaped teeth; L, the lateral part of the caudal velum; Lf, lateral fold; LP, the lateral part of the palate; M, median elevation of the caudal velum; MB, median band with a bamboo stem like appearance; mf, microfold; Mg, median groove; MP, the middle part of the palate; PHR, pharyngeal roof; RLP, the rostral of the lateral palatine part; TG, teeth groove; TS, teeth socket; UJ, the upper jaw, the dotted area represents the median part of the palate. Rostral = the rostral part of the roof. Middle = the middle part of the roof.

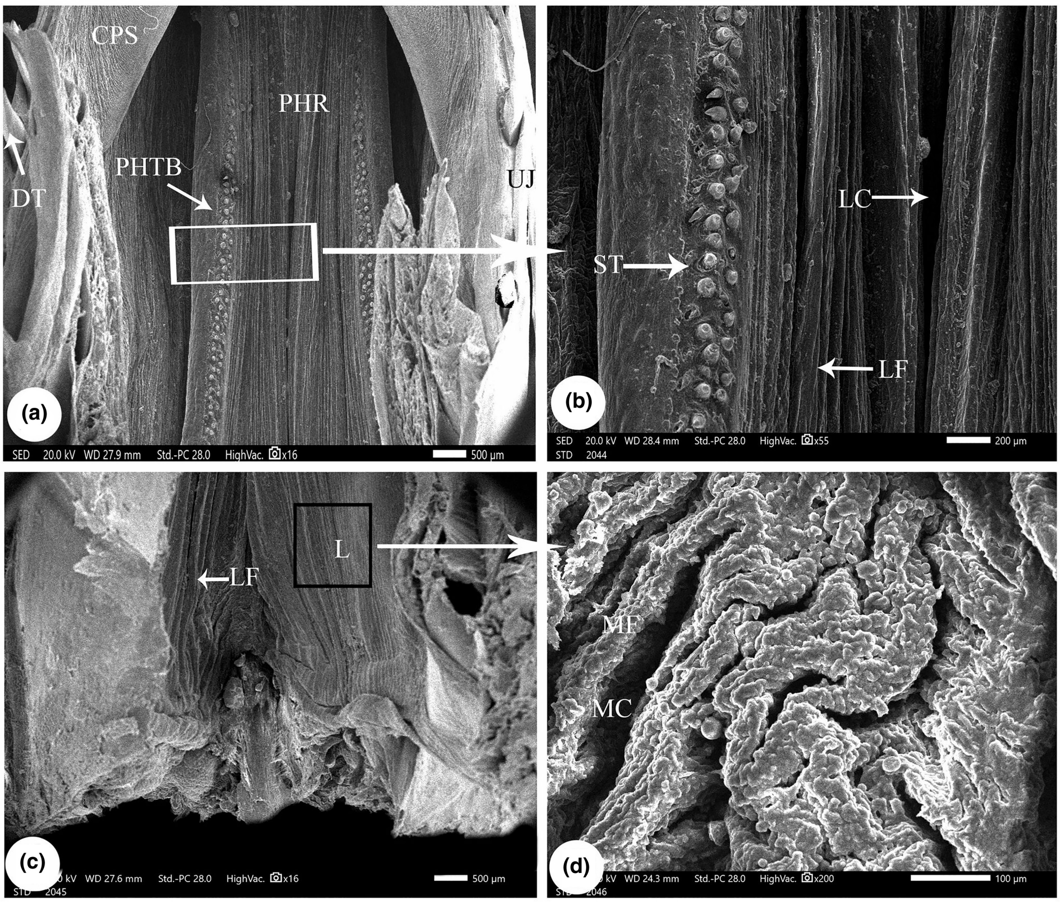

FIGURE 6 Scanning electron micrographs showing oropharyngeal cavity roof surface morphology. (a and b) caudal region of the oropharyngeal cavity roof, (c and d) end of the caudal region containing microfolds and micro-clefts. CPS, crescentic palatine shape; DT, dagger-shaped teeth; LC, longitudinal clefts; LF, regular parallel longitudinal folds; MC, micro-cleft; MF, microfolds; PHR, pharyngeal roof; PHTB, pharyngeal teeth band; ST, spiny curved teeth; UJ, upper jaw.

fish (Kaushik & Bordoloi, 2017). It was indicated that in *Oxycheilinus digramma* the fangs were primarily to capture prey ensuring puncturing of prey skin, whereas the short conical teeth for gripping and cutting prey after capture, whereas others mentioned that the jaws and pharyngeal teeth in some fish species assisted with mastication and crushing of the food prior to swallowing (Mihalitsis &

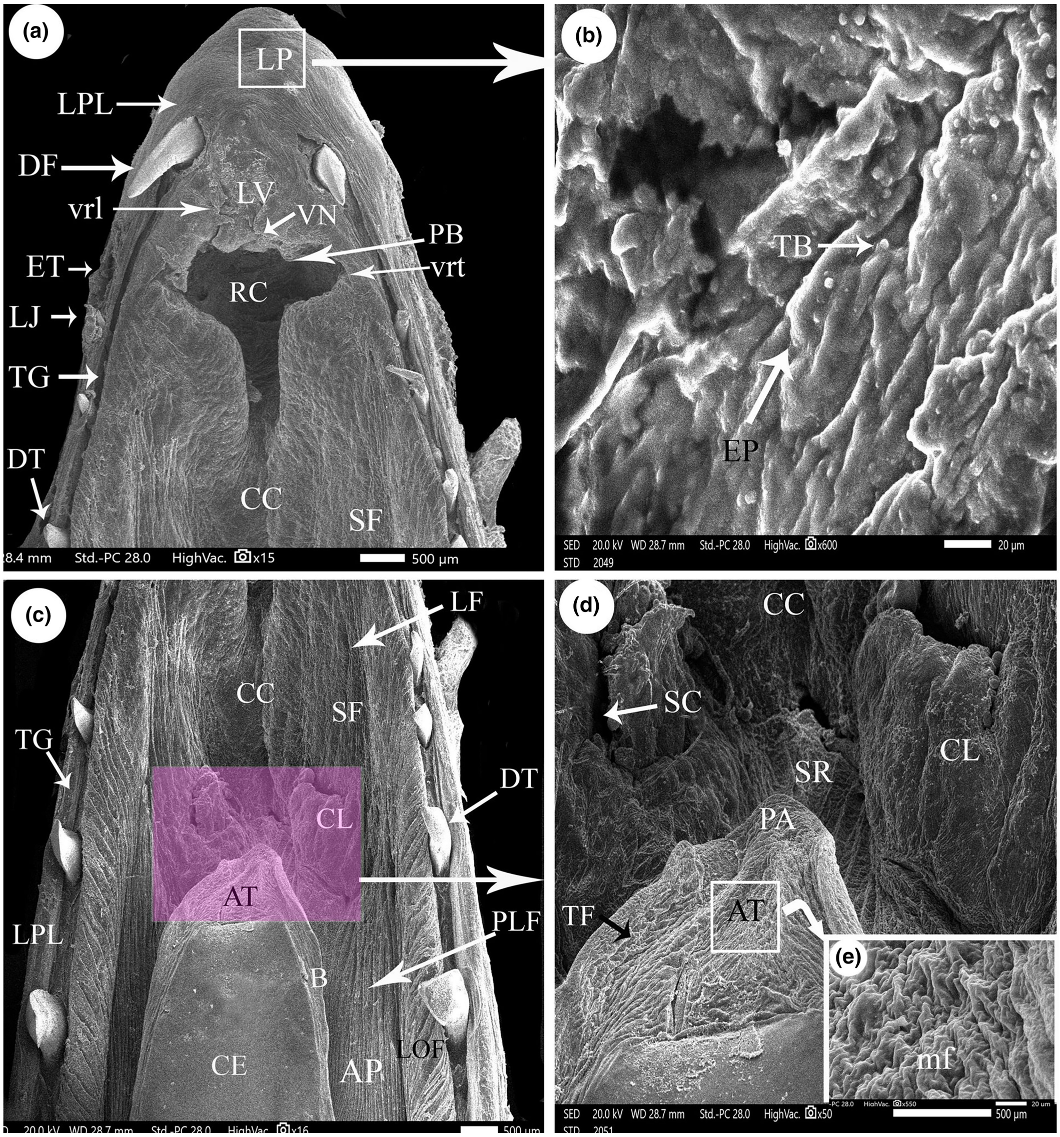

FIGURE 7 Scanning electron micrographs showing the surface morphology of the rostral part of the oropharyngeal floor (a–e). (a + c) The lower lip through to the tongue apex. Higher magnifications of (b) rostral part of the lower lip surface, (d) sublingual floor and the tongue apex, and (e) dorsal surface of the tongue apex. AP, apical pouch; AT, apex of the tongue; B, thin tongue borders; CC, caudal cavity for the caudal premaxillary fangs and caudal upper velum; CE, transvers folds; CL, closed oyster-shaped structure; CP, thick epithelium projections; DF, dentary fang; LF, longitudinal folds at the sublingual floor; LJ, lower jaw; LOF, lateral oblique fold band; LP, lower lip; LPL, lateral part of the lower lip; LV, lower velum; mf, microfolds; PA, pointed apex of tongue; PB, posterior border of the velum; PLF, paralingual parallel longitudinal folds at the apical pouch; RC, rostral cavity for the rostral premaxillary fangs and rostral upper velum; SC, sublingual clefts; SF, sublingual floor; SR, sublingual ridges; TB, taste buds; TF, central elevation of the tongue body; TG, teeth groove; VN, velum notch; vrl, longitudinal valum ridge; vrt, transverse valum ridge.

Bellwood, 2019; Sibbing, 1982; Vandewalle et al., 1994). Martins and coauthors also reported field observations of large *T. lepturus* inhaling and cutting their prey (Martins et al., 2005). Given the carnivorous diet of *T. lepturus* these fangs and teeth may increase the chances of capturing prey, create deep punctures into evasive prey and/or prey with hard structures, and the dagger-shaped teeth also function to help catch, retain and cut the seized prey following capture.

The current research investigating *T. lepturus* noted that the tongue was immobile and did not protrude out of the buccal cavity, and that an apical pouch was present. This type of immobile tongue is similar to that of the European sea bass *Dicentrarchus labrax* (Abbate et al., 2012), the common sole flatfish *Solea solea* (El Bakary, 2014), gilthead seabream *S. aurata* (El Bakary, 2012; Elgendy et al., 2016), white grouper *Epinephelus aeneus* (Alsafy et al., 2021) and the grey gurnard *Eutrigla gurnards* (Abumandour et al., 2021). The apical pouch discovered in *T. lepturus* may provide a protective feature to the apex of the tongue, similar findings were also observed in the white sea bream *Diplodus sargus sargus* and the gilthead seabream *S. aurata* (Elgendy et al., 2016; Guerrera et al., 2015).

The current work observed that the *T. lepturus* tongue was differentiated into three regions, apex, body, and root. It contained several

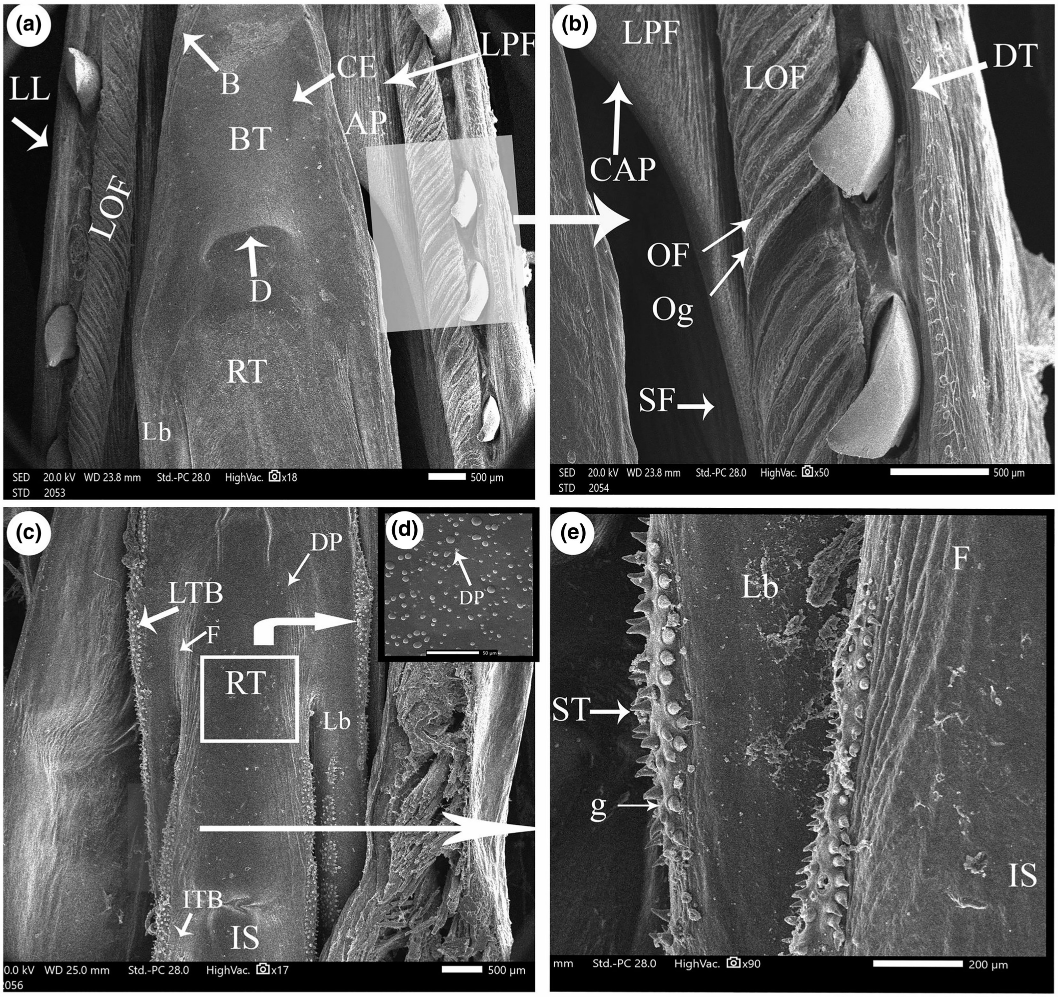

FIGURE 8 Scanning electron micrographs showing the surface morphology of the mid-region of the oropharyngeal floor. (a + c) Mid-region of the buccal cavity floor. Higher magnifications of (b) boundaries of the teeth groove, (d) surface epithelium to the root of the tongue, (e) teeth bands. AP, the apical pouch; B, thin tongue borders; BT, the body of the tongue; CAP, the caudal margin of the apical pouch; D, the depression on the caudal part of the tongue body; DP, dome shape papillae; DT, dagger-shaped teeth; F, oblique folds on the interbranchial septum; g, circular groove around the base of the teeth; IS, interbranchial septum; ITB, interbranchial teeth band; LL, the lateral part of the lower lip; LOF, lateral oblique's fold band; Lp, the lateral branch of the tongue root; LTB, lingual teeth band; PLF, paralingual parallel longitudinal folds; OF, oblique folds; Og, oblique grooves; RT, the root of the tongue; SF, sublingual floor; ST, spiny teeth rows; TF, the central elevation of the tongue body; TG, teeth groove.

rows of teeth in its lateral regions, and interbranchial teeth and pharyngeal teeth, in addition to taste buds located on the upper velum, lower lip and on the caudal part of the interbranchial septum. We hypothesize that these anatomical features could assist with food ingestion, food processing and taste. The presence of small teeth and dome shape papillae on the tongue, the pharynx, and the presence of taste buds, indicate potential interplay between the mechanics of food processing, taste and swallowing. The presence of teeth on the tongues dorsal surface in fish differs among predatory teleostean species. In the European sea bass *D. labrax* (Levanti et al., 2017) and Short mackerel *Rastrelliger brachysoma* (Kettratad et al., 2017) there were canine-like teeth with a different distribution arrangement to those seen in the present study. In addition, the median part of the European sea bass tongue body is covered with teeth while the tongue root dorsal surface is characterized by the absence of teeth (Levanti et al., 2017). It has also been suggested the pattern and the distribution of the teeth and taste bud on the tongue of the *Micropterus salmoide*s were related to food processing and taste (Linser et al., 1998).

The oral cavities of most fish lack salivary glands and are instead lined by a stratified epithelium containing various mucous cells (Abbate et al., 2020; Roberts-Sweeney, 2016; Yashpal et al., 2014). The cutlassfish in the present study exhibited invaginations and shallow depressions within the epithelium on the lateral sides of the dagger-shaped teeth (sharp papilliform teeth) and in the tongue, in addition to mucous pores. These may have many functions including filtration of food, increasing plasticity, flexibility, absorption and mucus secretion which could aid the smooth passage of food, while also protecting the epithelium from potential dangers such as abrasions (Gibb et al., 2015;

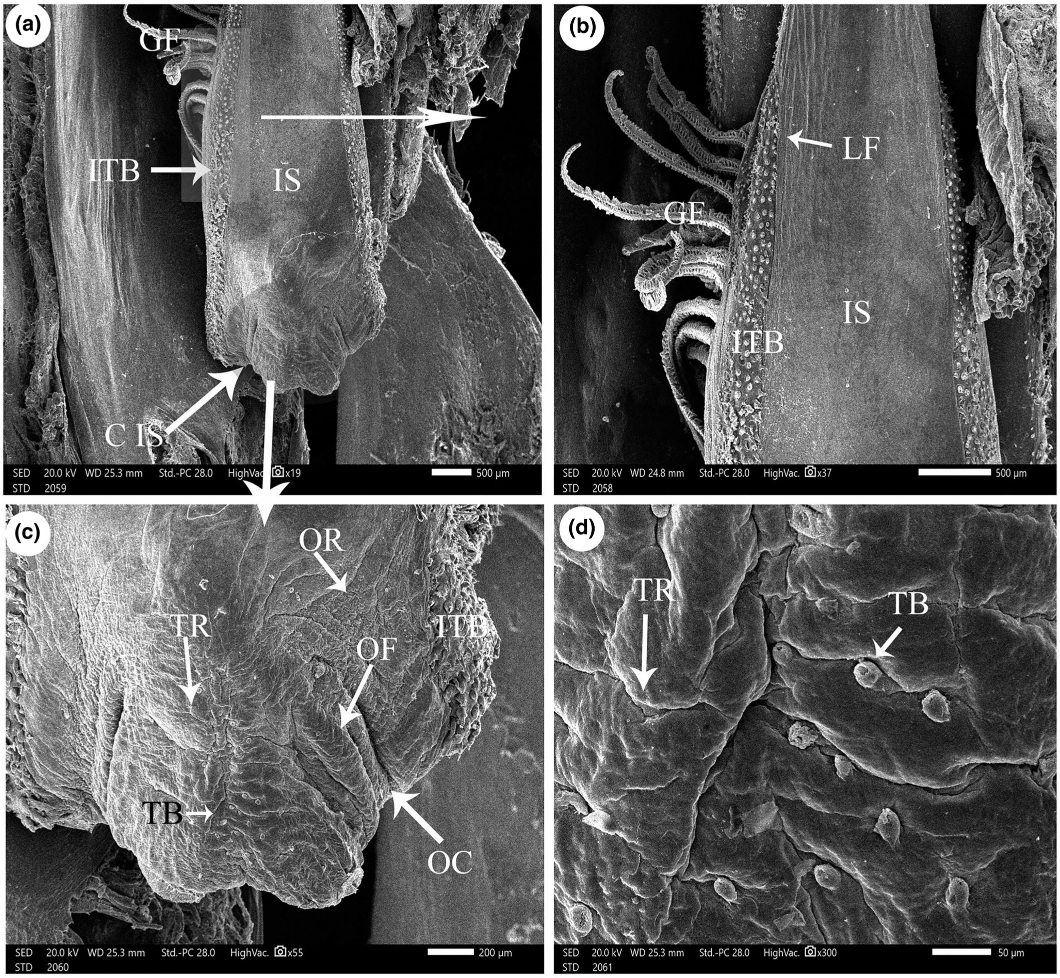

FIGURE 9 Scanning electron micrographs showing the surface morphology of the hind region of the oropharyngeal floor. (a) Interbranchial septum appeared as a caudal extension of the root of the tongue. Higher magnifications of (b) dorsal surface to inter branchial septum, and (c + d) the caudal part of the interbranchial septum. GF, gill filaments; IS, interbranchial septum; ITB, interbranchial teeth band; LF, longitudinal folds; OC, oblique clefts; OF, oblique folds; OR, oblique ridges; TB, several taste buds; Tr, transverse ridges.

Harabawy et al., 2008; Whitear, 1990; Yashpal et al., 2006, 2009), but further studies are required to elucidate the functions.

The presence of taste buds was observed on the lip velum and pharynx in *T. lepturus*. In addition, the dome-shaped papillae were only located on the tongue and on the folds at the apex, in this species. The dorsal lingual surface of different carnivorous fish have been shown to contain several taste buds similar to those observed in the present study, including species such as the carnivorous Chub mackerel *Scomber japonicus* (Baaoom et al., 2018), the ray-finned fish *Cirrhinus mrigala* (Yashpal et al., 2014), and in gilthead seabream *S. aurata* (El Bakary, 2012), and the sea bass *D. labrax* (Abbate et al., 2012). In contrast, no taste buds were observed on the dorsal surface of swordfish *Xiphias gladius* (Levanti et al., 2017) or the white grouper *E. aeneus* tongue (Alsafy et al., 2022). It has previously been suggested that the presence of taste buds might indicate a high taste capacity, which could assist with discriminate between different types of nourishment (Baaoom et al., 2018), but this functional link needs further investigation. It is also of note that the eventual rejection of food has been demonstrated in other species including the gilthead seabream *S. aurata* and the carnivorous freshwater catfish *R. rita* (Abbate et al., 2012; Yashpal et al., 2006), therefore this could also be the case for *T. lepturus*.

The present research has also shown the presence of a lateral oblique folded band on the medial side of teeth groove, shaped like a steel wire rope. In the middle of the palate there was a median band, with a bamboo stem-like structure and shape. It is possible that these structures may harden or strengthen the cavity to accommodate and tolerate the hard structures within the prey. In addition, the presence of cavities on the floor may act as sockets for fangs to prevent any destruction at the floor during feeding activities, but further studies are required to confirm their function.

T. lepturus is in the top 10 species of fish caught by fisheries worldwide, with 1,144,000 tonnes caught in 2020 alone (FAO, 2022a). Despite the importance of *T. lepturus* as a food source for people, and their importance to fisheries, little is known about its oropharyngeal cavity anatomy. The present research provides greater insights into the anatomy, morphology and structure of the *T. lepturus* oropharyngeal cavity, an important food resource worldwide.

AUTHOR CONTRIBUTIONS

Basma M. Kamal and Samir A.A. El-Gendy designed and organized the research. Neveen E.R. El-Bakary undertook the anatomical dissections and electron microscopy. All authors (Neveen E.R. El-Bakary, Mohamed A.M. Alsafy, Catrin S. Rutland, Samir A.A. El-Gendy, Basma M. Kamal) analysed the results, undertook literature searches, wrote the manuscript and then read and approved the final manuscript.

ACKNOWLEDGEMENTS

The authors would like to thank Damietta University, Alexandria University, University of Nottingham and University of Sadat City for funding this research.

FUNDING INFORMATION

The current study was funded by Damietta University, Alexandria University, University of Nottingham and University of Sadat City.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

ORCID

Neveen E. R. El-Bakary https://orcid.org/0000-0001-8774-0121
Mohamed A. M. Alsafy https://orcid.org/0000-0001-6236-4801
Catrin S. Rutland https://orcid.org/0000-0002-2009-4898
Samir A. A. El-Gendy https://orcid.org/0000-0002-6180-389X
Basma M. Kamal https://orcid.org/0000-0002-9541-0621

REFERENCES

Abbate, F., Germana, G., De Carlos, F., Montalbano, G., Laura, R., Levanti, M., & Germana, A. (2006). The oral cavity of the adult zebrafish (*Danio rerio*). *Anatomia, Histologia, Embryologia*, *35*(5), 299–304. https://doi.org/10.1111/j.1439-0264.2006.00682.x

Abbate, F., Guerrera, M., Montalbano, G., Ciriaco, E., & Germanà, A. (2012). Morphology of the tongue dorsal surface of gilthead seabream (*Sparus aurata*). *Microscopy Research and Technique*, *75*(12), 1666–1671.

Abbate, F., Guerrera, M. C., Levanti, M., Laurà, R., Aragona, M., Mhalhel, K., Montalbano, G., & Germanà, A. (2020). Anatomical, histological and immunohistochemical study of the tongue in the rainbow trout (*Oncorhynchus mykiss*). *Anatomia, Histologia, Embryologia*, *49*(6), 848–858.

Abumandour, M. M., Massoud, E., El-Kott, A., Morsy, K., El-Bakary, N. E., & Kandyle, R. (2021). An ultrastructural focus on the buccal cavity of the grey gurnard *Eutrigla gurnardus* (Linnaeus, 1758): Adaptative dietary implications. *Microscopy Research and Technique*, *84*(9), 2130–2139.

Alibardi, L. (2013). Observations on the ultrastructure and distribution of chromatophores in the skin of chelonians. *Acta Zoologica*, *94*(2), 222–232.

Alsafy, M., Madkour, N. F., El-Bakary, R., Karkoura, A., El-Gendy, S., & Abumandour, M. M. (2022). Ultrastructural comparison between the oral cavity floor of the juvenile and adult *Epinephelus aeneus*: New vision of aging development and its carnivorous adaptation. *Microscopy Research and Technique*, *85*(2), 767–780.

Alsafy, M., Madkour, N. F., el-Bakary, R., Karkoura, A., el-Gendy, S., Zaki, M. A., Tanekhy, M., & Abumandour, M. M. A. (2021). Age-related ultrastructural characterizations of the teeth of the white grouper (*Epinephelus aeneus*) in the different three age-stages. *Microscopy Research and Technique*, *84*(6), 1115–1134.

Alsafy, M. A., Bassuoni, N. F., & Hanafy, B. G. (2018). Gross morphology and scanning electron microscopy of the Bagrus Bayad (Forskal, 1775) oropharyngeal cavity with emphasis to teeth-food adaptation. *Microscopy Research and Technique*, *81*(8), 878–886.

Baaoom, K. A., Basmidi, A. A., & Obbed, M. H. (2018). Surface architecture of the mouth cavity in a carnivorous fish *Scomber japonicus* (Houttuyn, 1782) (Scombridae). *University of Aden Journal of Natural and Applied Sciences*, *22*(2), 427–435.

Bakhoum, S. A. (2007). Diet overlap of immigrant narrow–barred Spanish mackerel *Scomberomorus commerson* (Lac., 1802) and the largehead hairtail ribbonfish *Trichiurus lepturus* (L., 1758) in the Egyptian Mediterranean coast. *Animal Biodiversity and Conservation*, *30*(2), 147–160.

Bemis, K. E., Burke, S. M., St. John, C. A., Hilton, E. J., & Bemis, W. E. (2019). Tooth development and replacement in the Atlantic Cutlassfish, *Trichiurus lepturus*, with comparisons to other Scombroidei. *Journal of Morphology*, *280*(1), 78–94.

Dahlgren, U. (1898). The maxillary and mandibular breathing valves of teleost fishes. *Zoological Bulletin*, *2*(3), 117–124.

de Schepper, N., Van Wassenbergh, S., & Adriaens, D. (2008). Morphology of the jaw system in trichiurids: Trade-offs between mouth closing and biting performance. *Zoological Journal of the Linnean Society*, *152*(4), 717–736. https://doi.org/10.1111/j.1096-3642.2008.00348.x

Dimech, M., Stamatopoulos, C., El-Haweet, A., Lefkaditou, E., Mahmoud, H., Kallianiotis, A., & Karlou-Riga, C. (2012). *Sampling protocol for the pilot collection of catch, effort and biological data in Egypt*. Food and Agriculture Organization of the United Nations. https://www.fao.org/publications/card/en/c/2f11ce49-f36a-5f43-8f66-d77b2388d893/

El Bakary, N. (2012). Morphology of the buccal cavity of sea bream (*Sparus aurata*) and its relation to the type of feeding using scanning electron-microscopy. *Global Veterinaria*, *9*(6), 779–784.

El Bakary, N. E. S. R. (2014). Morphological study of the asymmetrical buccal cavity of the flatfish common solea (*Solea solea*) and its relation to the type of feeding. *Asian Pacific Journal of Tropical Biomedicine*, *4*(1), 13–17.

Elgendy, S. A., Alsafy, M. A., & Tanekhy, M. (2016). Morphological characterization of the oral cavity of the gilthead seabream (*Sparus aurata*) with emphasis on the teeth-age adaptation. *Microscopy Research and Technique*, *79*(3), 227–236. https://doi.org/10.1002/jemt.24245

FAO. (2022a). *The state of world fisheries and aquaculture 2022*. Towards Blue Transformation.

FAO. (2022b). *Trichiurus lepturus* Linnaeus, 1758. https://www.fao.org/fishery/en/aqspecies/2468/en

Ferry-Graham, L. A., Wainwright, P. C., Hulsey, C. D., & Bellwood, D. R. (2001). Evolution of mechanics of long jaws in Butterflyfishes (family Chaetodontidae). *Journal of Morphology*, *248*, 120–143.

Fishelson, L., Golani, D., & Diamant, A. (2014). SEM study of the oral cavity of members of the Kyphosidae and Girellidae (Pisces, Teleostei), with remarks on Crenidens (Sparidae), focusing on teeth and taste bud numbers and distribution. *Zoology*, *117*(2), 122–130.

General Authority for Fishery Resources Development. (2010). *Fish statistics book*. The Ministry of Agriculture and Land Reclamation.

Gibb, A. C., Staab, K., Moran, C., & Ferry, L. A. (2015). The teleost intramandibular joint: A mechanism that allows fish to obtain prey unavailable to suction feeders. *Integrative and Comparative Biology*, *55*(1), 85–96.

Guerrera, M. C., Montalbano, G., Germana, A., Maricchiolo, G., Ciriaco, E., & Abbate, F. (2015). Morphology of the tongue dorsal surface in white sea bream (*Diplodus sargus sargus*). *Acta Zoologica*, *96*(2), 236–241. https://doi.org/10.1111/azo.12071

Harabawy, A. S. A., Mekkawy, I. A. A., Mahmoud, U. M., Abdel- Rahman, G. H., & Khidr, B. M. (2008). Surface architecture of the oropharyngeal cavity and the digestive tract of Bagrus docmak (Forsskal 1775) and *Clarias gariepinus* (Burchell, 1822) (Teleostei) from the Nile River: A scanning electron microscope study. *Journal of the Egyptian–German Society of Zoology*, *56*, 171–198.

Hughes, G. M., & Hughes, G. M. (1963). *Comparative physiology of vertebrate respiration*. Harvard University Press.

Kammerer, C. F., Grande, L., & Westneat, M. W. (2005). Comparative and developmental functional morphology of the jaws of living and fossil gars (Actinopterygii: Lepisosteidae). *Journal of Morphology*, *267*, 1017–1031.

Kaushik, G., & Bordoloi, S. (2017). Ultrasurface structure of oromandibular area in a hill stream teleost *Glyptothorax trilineatus* Blyth, 1860. *Acta Zoologica*, *98*(4), 362–369.

Kettratad, J., Senarat, S., Boonyoung, P., & Jiraungkoorskul, W. (2017). Tongue anato-histology of the oceanodromous adult *Rastrelliger brachysoma* (Bleeker, 1851) with a note on the comparison with the tongue structure of adult *R. kanagurta* (Cuvier, 1816). *Songklanakarin Journal of Science & Technology*, *39*(1), 117. https://doi.org/10.14456/sjst-psu.2017.13

Levanti, M., Germanà, A., Montalbano, G., Guerrera, M., Cavallaro, M., & Abbate, F. (2017). The tongue dorsal surface in fish: A comparison among three farmed species. *Anatomia, Histologia, Embryologia*, *46*(2), 103–109.

Linser, P. J., Carr, W. E., Cate, H. S., Derby, C. D., & Netherton, J. C. (1998). Functional significance of the co-localization of taste buds and teeth in the pharyngeal jaws of the largemouth bass, *Micropterus salmoides*. *The Biological Bulletin*, *195*, 273–281.

Luo, B. (1991). Cutlessfish. In C. Q. Fan (Ed.), *Marine fishery biology* (pp. 111–160). Agriculture Press.

Madkour, N. F., Abumandour, M. M. A., El-Bakary, R., Karkoura, A., El-Gendy, S., & Alsafy, M. (2022). Ultrastructural focus on the oral cavity roof of the juvenile and adult white grouper (*Epinephelus aeneus*): Novel view of its development with carnivorous adaptation. *Microscopy Research and Technique*, *85*(12), 3804–3816. https://doi.org/10.1002/jemt.24227

Martial, K. K., Issa, O. N., Marcelle, B. I., Tapé, J., & Toussaint, G. (2020). Paramètres de croissance et d'exploitation des stocks de *Trichiurus lepturus* Linnaeus, 1758 (Perciformes, Trichiuridae) vivant au large des côtes ivoiriennes. *Journal of Applied Biosciences*, *150*, 15434–15447.

Martins, A., Haimovici, M., & Palacios, R. (2005). Diet and feeding of the cutlassfish *Trichiurus lepturus* in the subtropical convergence ecosystem of southern Brazil. *Journal of the Marine Biological Association of the United Kingdom*, *85*(5), 1223–1229.

Mihalitsis, M., & Bellwood, D. (2019). Functional implications of dentition-based morphotypes in piscivorous fishes. *Royal Society Open Science*, *6*(9), 190040.

Mitchell, E. G. (1904). Oral breathing valves of teleosts, their modifications and relation to the shape of the mouth. *American Naturalist*, *38*, 153–164. https://doi.org/10.1086/278386

Muhammad, A., Farooq, S., Rabbaniha, M., Jahangir, S., Malik, A., Hameed, A., & Baloch, A. (2017). Current fishery status of ribbonfish (*Trichiurus lepturus* Linnaeus, 1758) (Trichiuridae) from Makran coast (northeast Arabian Sea).

Nakamura, I., & Parin, N. (1993). Snake mackerels and cutlassfishes of the world. *FAO Fisheries Synopsis*, *15*(125), I.

Nandi, S., & Saikia, S. K. (2021). Scanning electron microscopic and histological studies of the buccal cavity of a phytoplanktivorous small freshwater fish, *Amblypharyngodon mola*. *Microscopy Research and Technique*, *84*(1), 119–124.

Norton, S. F., & Brainerd, E. L. (1993). Convergence in the feeding mechanics of ecomorphologically similar species in the Centrarchidae and Cichlidae. *Journal of Experimental Biology*, *176*, 11–29.

Porter, H. T., & Motta, P. J. (2004). A comparison of strike and prey capture kinematics of three species of piscivorous fishes: Florida gar (*Lepisosteus platyrhincus*), redfin needlefish (*Strongylura notata*), and great barracuda (*Sphyraena barracuda*). *Marine Biology*, *145*, 989–1000.

Roberts-Sweeney, H. E. (2016). Anatomy and disorders of the oral cavity of ornamental fish. *Veterinary Clinics: Exotic Animal Practice*, *19*(3), 669–687.

Rønnestad, I., Yúfera, M., Ueberschär, B., Ribeiro, L., Sæle, Ø., & Boglione, C. (2013). Feeding behaviour and digestive physiology in larval fish: Current knowledge, and gaps and bottlenecks in research. *Reviews in Aquaculture*, *5*, S59–S98.

Sayed, A. E. D. H., Mahmoud, U. M., & Essa, F. (2019). The microstructure of buccal cavity and alimentary canal of *Siganus rivulatus*: Scanning electron microscope study. *Microscopy Research and Technique*, *82*(4), 443–451.

Sibbing, F. A. (1982). Pharyngeal mastication and food transport in the carp (*Cyprinus carpio*): A cineradiographic and electromyographic study. *Journal of Morphology*, *172*(2), 223–258.

Tucker, D. W. (1956). Studies on the trichiuroid fishes – 3: A preliminary revision of the family Trichiuridae. *Bulletin of the British Museum of Natural History and Zoology*, *4*, 73–130. https://www.biodiversitylibrary.org/page/26203328#page/107/mode/1up

Vandewalle, P., Huysseune, A., Aerts, P., & Verraes, W. (1994). The pharyngeal apparatus in teleost feeding. In V. L. Bels, M. Chardon, & P. Vandewalle (Eds.), *Biomechanics of feeding in vertebrates. Advances in comparative and environmental physiology* (Vol. *18*, pp. 59–92). Springer. https://doi.org/10.1007/978-3-642-57906-6_4

Whitear, M. (1990). Causative aspects of microridges on the surface of fish epithelia. *Journal of Submicroscopic Cytology and Pathology*, *22*(2), 211–220.

Yashpal, M., Kumari, U., Mittal, S., & Kumar Mittal, A. (2006). Surface architecture of the mouth cavity of a carnivorous fish *Rita rita* (Hamilton, 1822) (Siluriformes, Bagridae). *Belgian Journal of Zoology*, *136*(2), 155.

Yashpal, M., Kumari, U., Mittal, S., & Mittal, A. (2014). Glycoproteins in the buccal epithelium of a carp, *Cirrhinus mrigala* (Pisces, Cyprinidae): A histochemical profile. *Anatomia*, *Histologia*, *Embryologia*, *43*(2), 116–132.

Yashpal, M., Kumari, U., Mittal, S., & Mittal, A. K. (2009). Morphological specializations of the buccal cavity in relation to the food and feeding habit of a carp *Cirrhinus mrigala*: A scanning electron microscopic investigation. *Journal of Morphology*, *270*(6), 714–728.

How to cite this article: El-Bakary, N. E. R., Alsafy, M. A. M., Rutland, C. S., El-Gendy, S. A. A., & Kamal, B. M. (2023). Anatomical oropharyngeal cavity specialisations in the cutlassfish (*Trichiurus lepturus*, Linnaeus, 1758). *Anatomia, Histologia, Embryologia*, *00*, 1–12. https://doi.org/10.1111/ahe.12943