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ORIGINAL PAPER

Morphological comparison of the detailed structure of gill rakers from three different feeding habits of marine fish species

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Abstract

The feeding habits and habitat of different fish species influence the morphology and functions of their gill rakers. This study used gross anatomy and scanning electron microscopy to investigate the morphological features of the gill rakers in *Siganus luridus*, *Boops boops*, and *Pagrus pagrus*. The gill rakers appeared as medial and lateral rows in all studied fishes. Except for *Pagrus pagrus*, which had a unique gill rakers arrangement in which the medial row of the 4th gill arch had the most gill rakers, the longest and most gill rakers were on the 1st gill arch in all studied fishes. The gill rakers of *Siganus luridus* were smooth, with various spine-like shapes, such as spine-like gill rakers, which were bifid or trifid spines, or duck toe-shaped gill rakers. According to SEM of the *Siganus luridus'* gill rakers, the trifid end gill rakers resembled caterpillars, and the duck toe-like gill rakers had three or four finger-like spines connected by inter-spine tissue. The *Boops boops* had long conical gill rakers with pointed ends on the lateral sides of the 1st gill arch, and the remaining rows had short gill rakers. According to SEM of the *Boops boops'* gill rakers, the long gill rakers were semi-conical and only had needle-like spines on the medial surface. The short gill rakers were projected as a boat and had three different shapes based on spine distributions. Gill rakers include those with a median crest and long spine laterals, those with only lateral spines, those with usually dorsal spines, and those with long wedge-shaped spines. *Pagrus pagrus'* gill rakers were short, with fine-needle spines covering their tops. By SEM of the *Pagrus pagrus'* gill rakers, they appeared as a cylindrical elevation with spines on top. The spines were conical in shape with pointed curved or straight ends. The maximum value of the gill rakers' lengths was discovered in the lateral row of the 1st gill arch, while the minimum value was in the medial row of the 4th gill arch. As a result, this is the first study of the three fish species' gill rakers. In the studied fishes, the morphological characteristics of gill rakers demonstrated unique structural specifications in feeding behavior.

Keywords Gill rakers · Marine fish · Gross anatomy · Scanning electron microscopy

Introduction

The gill rakers are cartilaginous or bony structures that project to the inside of the pharyngeal cavity, and their structure changes in line with the feeding habits of the fish (Almeida et al. 2013). Gill rakers sit as either single or paired structures on the pharyngeal aspect of the gill arch in Osteichthyes and Chondrichthyes, sometimes also occurring in modified form within epibranchial organs (Howes 1981; Lazzaro 1987; Liston 2013).

Gill rakers' primary function is to guard the fragile respiratory surfaces of the gill filaments from potential damage by particulates within the water taken into the buccal cavity during respiration (Langeland and Nøst 1995). They occur with varying degrees of distribution throughout the

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branchial arches, but the first arch is typically the ultimate site (Drenner et al. 1987; Smith and Sanderson 2007). Gill rakers perform a binary function where they alter the direction of the water as a preliminary step and play as a sieve in a second step in regulating the size of food particles consumed. They direct the water toward the roof of the mouth, where the food particles are trapped by their mucous cover before being ingested (Salman et al. 2005).

Gill rakers are projections on the gill arches that aid food collection and feeding habits. They are typically small and in low numbers among fish that eat large prey. Plankton feeders has elongated, numerous, and variable lamellae or garnish gill rakers that act as a sieve, trapping solid food while passing water (Bond 1996; Kumar and Tembhre 1996). Gill rakers may change as the fish grows (Mummert and Drenner 1986), *Cheilodactylus spectabilis* ontogeny of diet shifts: relationship between feeding mechanics, microhabitat selection, and growth where both juveniles and adults select particular taxa from the available turf micro-fauna, with juveniles consuming smaller sizes of fish feed than adults (McCormick 1998). Number, shape, and gap between gill rakers likely reflect the feeding patterns of the fish species. Fish with a few short rakers are carnivores and omnivores, whereas those with many long rakers are filter feeders (Alsafy et al. 2022; Alsafy 2013; Alsafy and El-Gendy 2022; Moodie 1985; Sanderson et al. 2001; Seghers 1975; Tanaka et al. 2006).

Lateral gill rakers of carnivorous fishes of the 1st gill arch carry minute spines that prevented the escape of the slippery, slimy, and smooth prey, while the rakers on the subsequent rows were shorter (Abuziadah 1995; Alsafy 2013; Salman et al. 2005). The anterior gill rakers on the 1st gill arch appeared as clusters of small tooth patches that adapted to piscivorous feeding. However, they appeared as needle spines in shape, with secondary projections that fit herbivorous feeding. The highest number and length of the anterior gill rakers are found in detritivores and planktivores (Amundsen et al. 2004; Mousa et al. 2016). The diet of the sparsely rakered European whitefish is mollusks, crustaceans, and bug larvae. The densely rakered ones, on the other hand, eat zooplankton, chironomid pupae, and surface insects (Amundsen et al. 2004).

Bony fish uses three filter types to filter its food: sieve filtration, cross-flow filtration, and vortex filtration. In sieve filtration, particle size and the pore size or spaces between rakers determine particle size (LaBarbera 1984). Particles are directed toward the esophagus and do not come into contact with the gills. Instead, they travel parallel to the surface, eventually congregating near the esophageal opening (Callan and Sanderson 2003). Filtration by vortex near the gill openings centrifugal forces cause particles to accumulate in the esophagus as water exits the operculum (Trakumas et al. 2001). Filter-feeding fishes may have an advantage over visual planktivores as they can consult selectively net phytoplankton and thus create situations in which nano-phytoplankton is favored (Lazzaro 1987). Filter feeders' feeding selectivity for motionless particles (phytoplankton and micro-zooplankton, such as protozoans) is governed by their retention capabilities, which are determined by the structure and operation of their branchial filtering apparatus. Filter-feeding in fish has long been thought to be a simple sieving mechanism in which particles too large to pass through the spacing of the filtering mesh are retained. The gill raker structure is the primary representation of the filtering mesh in most fishes. The gill rakers are attached to the anterior part of the gill arches, which are the branchial basket's elements (Gerking 2014; Lazzaro 1987).

Gill rakers were studied in many fishes; between Japanese anchovy, Pacific round herring, and Japanese jack mackerel, the gill raker number was highest in Japanese anchovy, Japanese jack mackerel, and shortest in Pacific round herring (Tanaka et al. 2006), *Epinephelus areolatus*, *Euthynnus affinis*, *Carangoides malabaricus*, *Prestipomides filamentous*, and *Lethrinus mahsena* explained the typical aspects of carnivorous fish that had cylindrical gill rakers with hook-like ends and firm structures, blade-like structures, and triangular gill rakers at mixed feeding types as *Pomadasys maculatus* and *Aprion virescens* (Salman et al. 2005). The importance of gill rakers in tropical (Panama) and Canadian freshwater fish species is that the number and length of gill rakers in tropical species is greater than the number of gill rakers in Canadian species (Moodie 1985). Long filiform and adhered gill rakers were found in *Parapimelodus*, *Hypostomus commersonii*, and *Parapimelodus nigribarbis*, while *Serrasalmus maculatus* and *Hoplias malabaricus* had piscivorous gill characters (Almeida et al. 2013). *Sparus aurata*, *Diplodus noct*, *Rhapdosargus haffara*, *Mugil cephalus*, *Mugil capito*, and *Liza aurata* belonged to the *Sparidae* family and had gill rackers of the 1st gill arch with a short and conical shape. The frontal gill rakers of the first-gill arch are long with a height number of *Siganus rivulatus* and have a needle-like spine modified for herbivorous behavior. *Saurida undosquamis*, *Synodus saurus*, on the 1st gill arch, the front of gill rakers resemble clusters of small tooth spots adapted to piscivore behavior. *Herklotsichthys quadrimaculatus* and *Caranx sexfasciatus* had numerous and elongated gill rakers organized into one row adapted for plankton feeding (Mousa et al. 2016). *European whitefish* had a high density of sparsely gill rakers that were shorter, thicker, and less dense than densely gill rakers adapted to plankton feeding (Amundsen et al. 2004; Kahilainen et al. 2011).

The herbivorous *Siganus luridus* (Rüppell, 1828) inhabits the Mediterranean and Pacific oceans (Bariche et al. 2004; Golani et al. 2006). The carnivorous red porgy (*Pagrus pagrus*) (Linnaeus, 1758) is a Mediterranean sparid highly

valued for aquaculture and fishing (Kentouri et al. 1994; Manooch 1978). It is usually related to reefs and sand habitats (Labropoulou et al. 1999). The omnivorous bogue, *Boops boops* (Linnaeus, 1758) is a marine species in the *Sparidae* family. It is common in the Mediterranean and the East Atlantic (FAO 2019).

The shape of gill rakers, their relative sizes, and their distribution patterns vary across many groups of fish. Data on commercially important *Siganus luridus*, *Pagrus pagrus*, and *Boops boops* gross anatomy and scanning electron microscopy are lacking. The current study aims to distinguish differences in the morphological characteristics of *Siganus luridus*, *Pagrus pagrus*, and *Boops boops* gill rakers.

Materials and methods

Samples and morphometric analysis

The study was carried out on 15 fish belonging to three families: Siganidae (5 of dusky spinefoot (*Siganus luridus* Rüppell, 1828); Sparidae (5 of red porgy; *Pagrus pagrus* Linnaeus, 1758); and 5 of bogue (*Boops boops* Linnaeus, 1758). The fish were collected in an icebox tank by fishermen from the Mediterranean Sea coasts of Matrouh and Damietta Governorates and the Red Sea coast of Suez Governorate, Egypt. The gills and oropharyngeal cavities were first washed with normal saline and examined to be free from injuries or abnormalities. Then we dissected the gill operculum, and the gills were extracted and photographed (Dimech et al. 2012), then preserved in 10% formalin solution and directly transported to the dissecting laboratory. The fish samples' number, source, length, weight, and feeding behavior were recorded in Table 1.

The number of gills rakers in each row from the first to the fourth gill arch was counted using the gross specimens and SEM images (Table 2). The obtained SEM and photographic images were processed using ImageJ software to measure the five long gill rakers in the middle of the gill arch, the width of the spaces between them at the base of the gill rakers, and the spines on their surfaces on the four-gill arches (Tables 3 and 4) (Alsafy and El-Gendy 2022; Tanaka et al. 2006).

Table 2 Number of gill rakers on the medial and lateral sides of the four-gill arches for the three studied species

	Siganus luridus	*Boops boops*	*Pagrus pagrus*
1st gill arch			
Lateral	19 ± 0.3162	21 ± 0.894	13 ± 0.4472
Medial	19 ± 0.3162	21 ± 0.894	13 ± 0.4472
2nd gill arch			
Lateral	17 ± 0.4472	16 ± 0.3162	9 ± 0.3162
Medial	17 ± 0.4472	16 ± 0.3162	9 ± 0.3162
3rd gill arch			
Lateral	13 ± 0.4472	14 ± 0.3162	9 ± 0.3162
Medial	13 ± 0.4472	14 ± 0.3162	9 ± 0.3162
4th gill arch			
Lateral	10 ± 0.894	13 ± 0.894	6 ± 0.894
Medial	10 ± 0.894	13 ± 0.4472	18 ± 0.4472

Gross morphology and scanning electron microscopy examination

Five fish were used to demonstrate the morphological features of the gills. The opercula were dissected, and the gills were photographed in situ. Then, the gills were removed from the fish, the gill rakers on each gill arch were counted, and the shapes of all rakers were recorded grossly and photographed by a digital camera (Cannon style IXY 32S, Japan).

The gills of the examined fish were carefully isolated. Small samples of the gill arches of each fish were taken and fixed in a mixture of 2.5% paraformaldehyde and 2.5% glutaraldehyde in 0.1 M phosphate buffer for 4 h at 4 °C. After washing in the same buffer solution, the samples were post-fixed in 1% osmium tetroxide in a phosphate buffer for 2 h. The samples were dehydrated in increasing concentrations of ethanol before critical point dried in carbon dioxide. Then they were sputter-coated with gold and investigated by

Table 1 Examined fish sample numbers, feeding behavior, and sampling source

Fish name	Dusky spinefoot (*Siganus uridus* Rüppell, 1828)	Bogue (*Boops boops* Linnaeus, 1758)	Red porgy (*Pagrus* pagrus, Linnaeus, 1758)
Family	Siganidae	Sparidae	Sparidae
Feeding behavior	Herbivorous	Omnivorous	Carnivorous
Fish source	Mediterranean Sea (Damietta Governorate)	Mediterranean Sea (Martouh Governorate)	Red Sea (Suez Governorate)
Fish number	5	5	5
Mean length(cm)	15.2 ± 0.863	17.1 ± 0.158	19.7 ± 0.663
Mean weight (gm)	98 ± 4.0914	50 ± 0.3162	101.8 ± 4.188

Table 3 Length of gill rakers (µm) at the middle of each gill arch for each of the three studied species

	Rakers row	*Siganus luridus*	*Boops boops*	*Pagrus pagrus*
Gill rakers of the 1st gill arch	Lateral	787 ± 21.07	3043.4 ± 163.2	1397 ± 110.2
	Medial	780 ± 19.1	759.2 ± 21.4	980 ± 8.9
Gill rakers of the 2nd gill arch	Lateral	437 ± 28.18	628 ± 11.8	854.8 ± 54.8
	Medial	430 ± 34.3	620 ± 13.7	790.8 ± 88.9
Gill rakers of the 3rd gill arch	Lateral	433.2 ± 23.9	618 ± 19.45	706.4 ± 39.72
	Medial	427.2 ± 40.8	546.8 ± 36.02	685 ± 65.7
Gill rakers of the 4th gill arch	Lateral	320 ± 19.2	543 ± 14.9	539.4 ± 68.543
	Medial	300 ± 7.914	542.4 ± 19.9	295.2 ± 26.77

Table 4 Space between the bases of gill rakers at the middle of each gill arch for each of the three studied species

	Siganus luridus	*Boops boops*	*Pagrus pagrus*
1st gill arch			
Lateral	437 ± 60.8	563.2 ± 20.6	1233.2 ± 107.50
Medial	426 ± 77.6	561.6 ± 11.73	1030 ± 44.8
2nd gill arch			
Lateral	395.6 ± 32.41	540 ± 13.6	985.4 ± 75.19
Medial	374.6 ± 14.78	540 ± 13.6	850 ± 90.5
3rd gill arch			
Lateral	363.6 ± 25.10	388 ± 9.7	801 ± 40.71
Medial	360.6 ± 75.3	379 ± 3.66	749 ± 59.7
4th gill arch			
Lateral	354 ± 30.10	336.4 ± 20.6	730 ± 77.8
Medial	344 ± 70.3	270.2 ± 18.04	396.6 ± 42.27

a JEOL JSM-IT200 scanning electron microscope operating at the Faculty of Science, Alexandria University (Goldstein et al. 2017).

Results

Gross morphology

In *Siganus luridus*, the gill arches are L-shaped. Each gill arch has two different forms of rakers with asymmetrical arrangements on most parts of the gill arches: spine-like rakers on the rostral side, which are bifid or trifid spines, and duck toe-shape rakers on the caudal side (Fig. 1). The mean number of the rakers on the 4th gill arches is 19, 17, 13, and 10 (Table 2).

In *Boops boops*, the gill arches are semilunar in shape. The long rakers appears conical with pointed ends on the lateral side of the first arch, while the rakers on the medial side of the 1st arch and the medial and lateral sides of the 2nd, 3rd, and 4th gill arches are short and has spines (Fig. 3 A, B, C). The rakers' mean number of each gill arch is 21, 16, 14, and 13 on the 1st to the 4th gill arches (Table 2).

In *Pagrus pagrus*, the gill arches look like a hook. The gill rakers are short, had fine-needle spinules covering the rakers' top and arrange into medial and lateral rows (Fig. 4 A, B). The rakers of the first three gill arches are parallel to each other, while on the 4th gill arch, the rakers of the lateral row correspond to only three small rakers on the medial row (Fig. 4C, D). The mean raker numbers are 13, 9, and 9 on the lateral and medial sides of the 1st, 2nd, and 3rd gill arches, respectively, while at the 4th gill arch, the lateral rakers are 6, and the medial row had 18 rakers (Table 2).

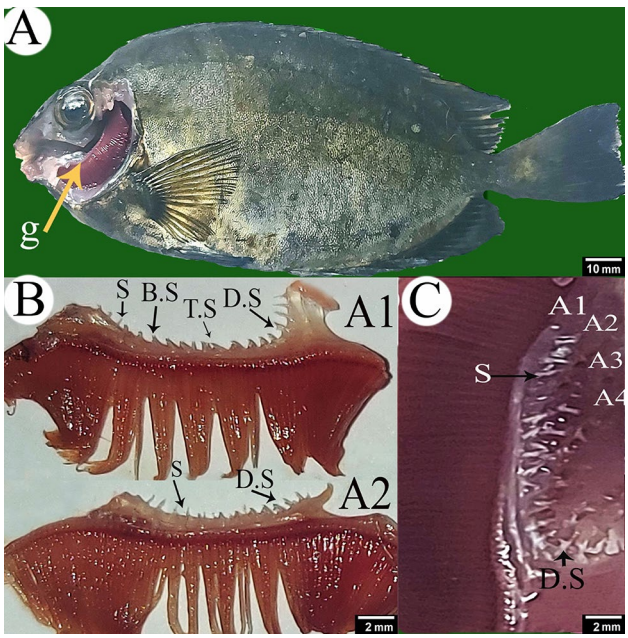

Fig. 1 Overview images of the gills of *Siganus luridus*. **A** Lateral view of the gills after removing the operculum. **B** Lateral view of the 1st and 2nd gill arch. **C** Dorsal view of the gill arches. g The gills, (A1, A2, A3, and A4) the 1st, 2nd, 3rd, and 4th gill arches, S spine gill rakers, (B.S) bifid spine gill rakers, (T.S) trifid spine gill rakers, (D.S) duck toe-like gill rakers

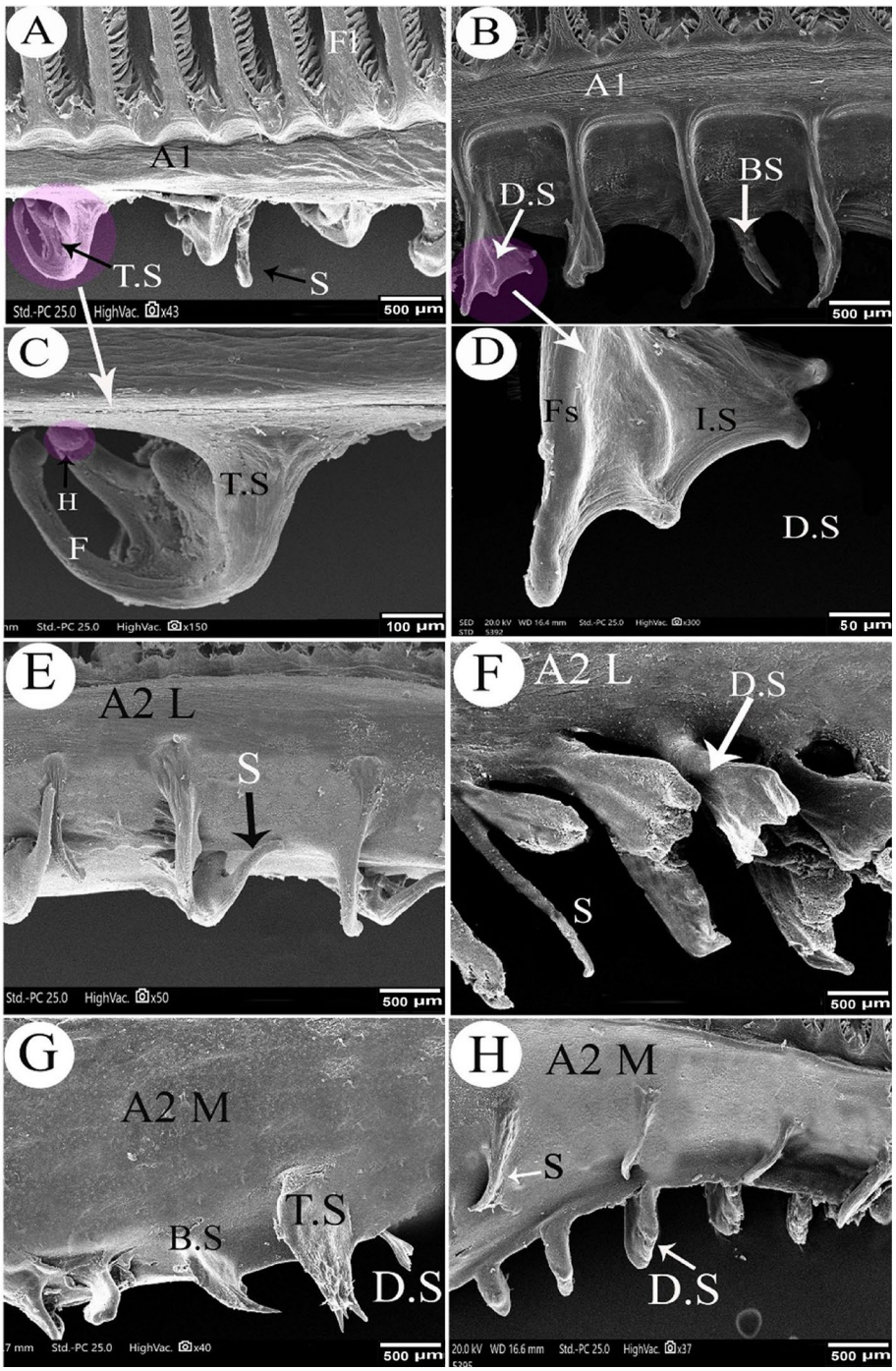

Fig. 2 Scanning electron microscopic images of the gill rakers of *Siganus luridus* (**A**-**D**) of the 1st gill arch (**E**–**H**) of the 2nd gill arch. **A** Medial view of the 1st gill arch, **B** Lateral view of the 1st gill arch, **C** Magnification of the trifid curved spines gill rakers (T.S). **D** Magnification of the duck toe-like gill rakers (D.S). (**E** and **F**) Lateral aspect of the rostral and caudal part of the 2nd gill arch (A2L). (**G** and **H**) Medial aspect of the rostral and caudal part of the 2nd gill arch (A2M). (A1) the 1st gill arch, (S) spine gill rakers, (B.S) bifid spines gill rakers, (F) finger-like spines of the trifid spines, (H) spherical head, (Fs) finger spines of the duck toe spine, (I.S) inter-spine connection, (FI) gill filament

Scanning electron microscopy

In *Siganus luridus*, the first-gill arch carried different shapes of rakers (Fig. 2). The gill rakers were relatively smooth and their ends looked like a curved spine (Fig. 2A/S), or a bifid with two pointed ends (Fig. 2B/BS), or curved trifid end gill rakers looked like the caterpillar head that had two long finger-like processes with a spherical and one finger-like with a short blunt end (Fig. 2A, C/TS). Another shape of gill raker that looked like the duck toe consisted of three or four finger-like spines with the blunt end connected by inter-spine tissue (Fig. 2B, D/DS). On the 2nd, 3rd, and 4th gill arches, there were many types of gill rakers which appeared to be curved or straight spine-like gill rakers, bifid spine rakers with a pointed end and small spines on their base, and trifid pointed straight spine gill rakers and duck toe-like gill rakers (Fig. 3).

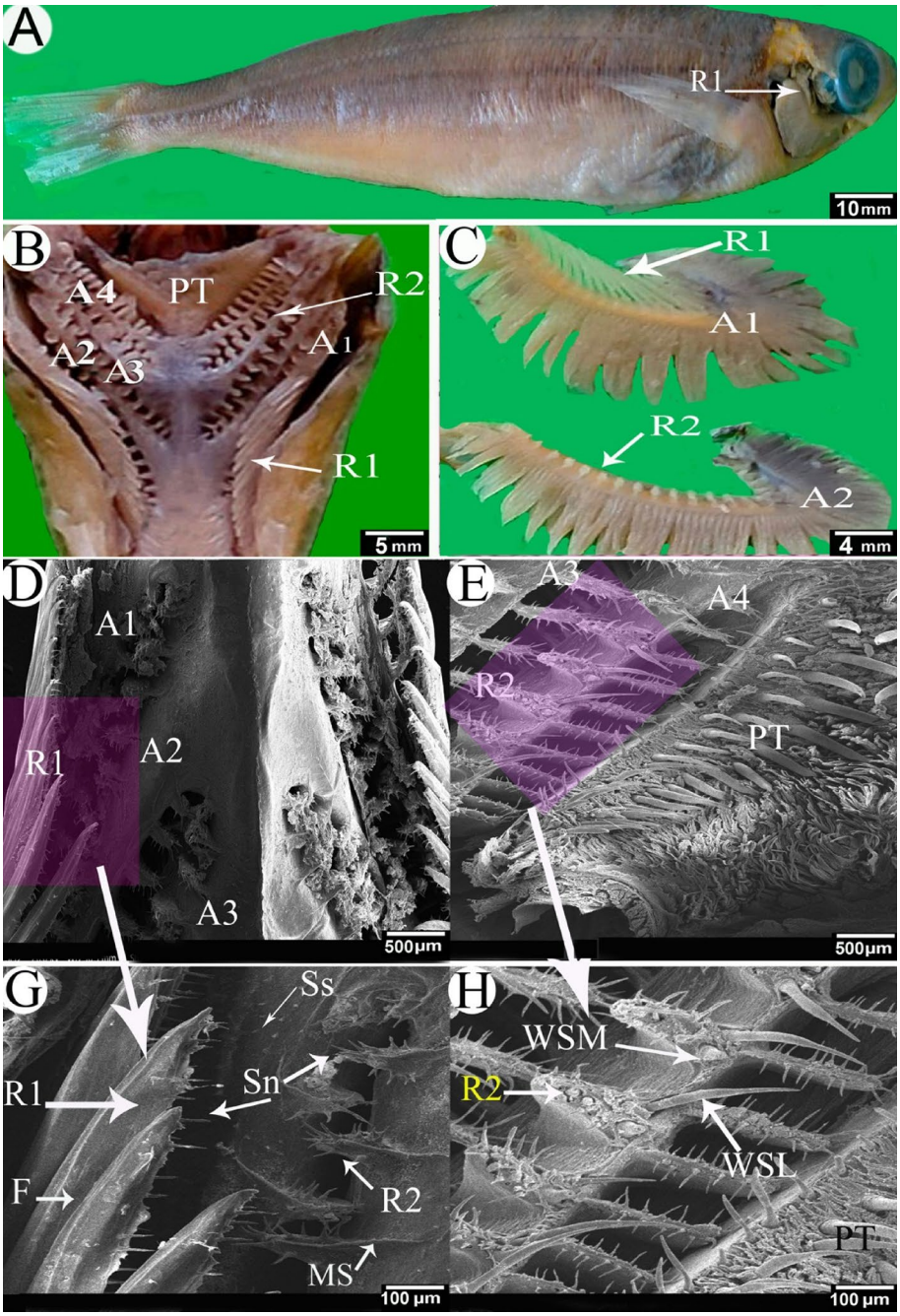

Fig. 3 Overview images (**A**, **B**, and **C**) and scanning electron microscopic images (**D**, **E**, **F**, and **G**) of the gills of *Boops boops*. **A** Lateral view of the gills after removing the operculum. **B** Rostral view to the gills chamber. **C** Lateral view of the 1st and 2nd-gill arch. (D&E) SEM images of the dorsal aspect of the gill arches. (**F** and **G**) SEM images showing the magnification of the colored areas on G&E. (A1, A2, A3, and A4) 1st-4th gill arches. **R**1 long gill rakers. **R**2 short gill rakers. (PT) pharyngeal teeth. (Ss) Small spines. (Sn) needle-like spines. (F) Wavy folds. (WSL) wedge-shaped long spines. (WSM) wedge-shaped medium-length spines. (MS) median crest on the short gill rakers of the 1st gill arch and the gill rakers of the 2nd gill arch

In *Boops boops*, the long gill rakers were semi-conical in shape with tapered ends, and their medial surfaces had needle-like spines (sewing needles), while their lateral surfaces were curved and had wavy folds (Fig. 3D, E, F, G). The short gill rakers projected like a boat shape on the lateral side (Fig. 3/F, G). The short gill rakers had three shapes according to the arrangement of spines. The 1st and 2nd gill arch's short gill rakers were expanded to the lateral side and had a dorsal median crest and needle spines on their margins (Fig. 3/F, G). The medial gill rakers on the 3rd and 4th gill arches had many spines on their margin (Fig. 3E, G). Lateral rows of short gill rakers at the 3rd and 4th gill arches had needle-like spines on the dorsal parts of the gill rakers, and wedge-shaped spines appeared from the arch at the base of the gill rakers.

In *Pagrus pagrus*, the gill rakers appeared at a cylindrical elevation with spines on their top. The gradual decrease in the gill rakers' height was from the 1st to 4th gill arch. The spines were conical in shape with pointed curved or straight ends. There were wavy folds on the gill arches and

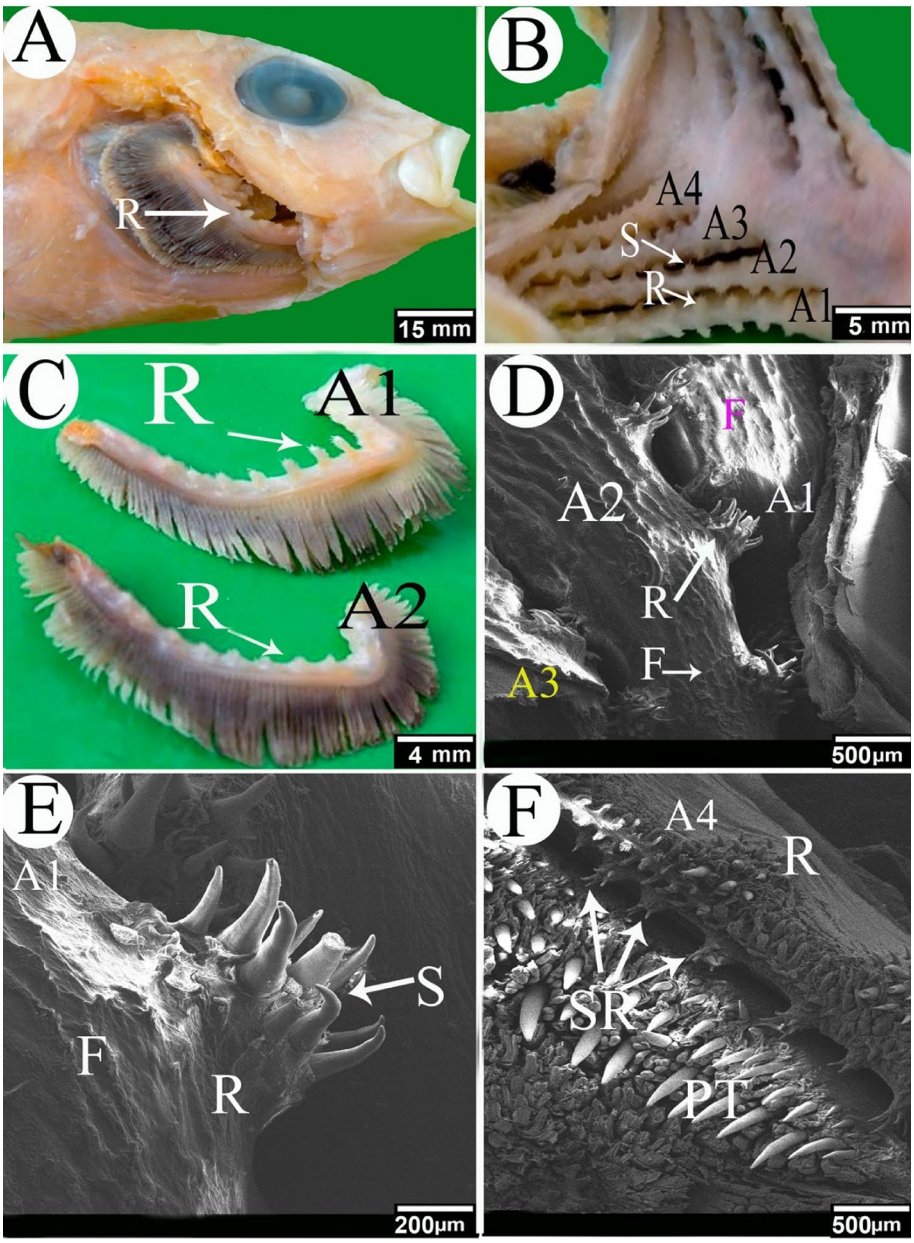

Fig. 4 Overview images (**A**, **B**, and **C**) and scanning electron microscopic images (**D**, **E**, and **F**) of the gills of *Pagrus pagrus*. **A** Lateral view of the gills after removing the operculum. **B** Rostral view to the gills chamber. **C** Lateral view of the 1st and 2nd gill arch. (**D**, **E**, and **F**) SEM images of the dorsal aspect of the gill arches. (A1, A2, A3, and A4) 1st–4th gill arches. **R** Short gill rakers. **S** Spines on the top of the gill rakers. F Folded dorsal surface of the gill rakers. (SR) three small gill rakers on the medial side of the 4th gill arch to one gill raker on the lateral side. (PT) pharyngeal teeth

gill rakers. In addition, epithelium protrusions were demonstrated between the two rows of gill rakers on the 1st gill arch (Fig. 4D, E, and F).

Morphometric analysis

In *Siganus luridus*, the length of the gill rakers of the lateral and medial rows of the 1st gill arch was 787 ± 21.07 µm and 780 ± 19.1 µm, and they decreased gradually on the 2nd and 3rd-gill arch until they reached 320 ± 19.2 µm and 300 ± 7.914 µm on the lateral and medial rows of the 4th-gill arch (Table 3). The space between the bases of gill rakers at the middle of each gill arch was 437 ± 60.8 µm and 426 ± 77.6 µm of the lateral and medial rows of the 1st gill arch, and they decreased gradually on the 2nd and 3rd-gill arch until they reached 354 ± 30.10 µm and 344 ± 70.3 µm on the lateral and medial rows of the 4th-gill arch (Table 4). The length of the spine gill rakers measured 280–780 µm, the bifid spine-like gill rakers measured 357.2–605.12 µm, the trifid curved spine gill rakers measured 630 µm, and the duck toe spine gill rakers measured 300.45–742.176 µm (Table 3).

In *Boops boops*, the length of the gill rakers of the lateral and medial rows of the 1st gill arch was 3043.4 ± 163.2 µm and 759.2 ± 21.4 µm, and they decreased gradually on the 2nd and 3rd-gill arch until they reached 543 ± 14.9 µm and 542.4 ± 19.9 µm on the lateral and medial rows of the 4th-gill arch (Table 3). The space between the bases of gill

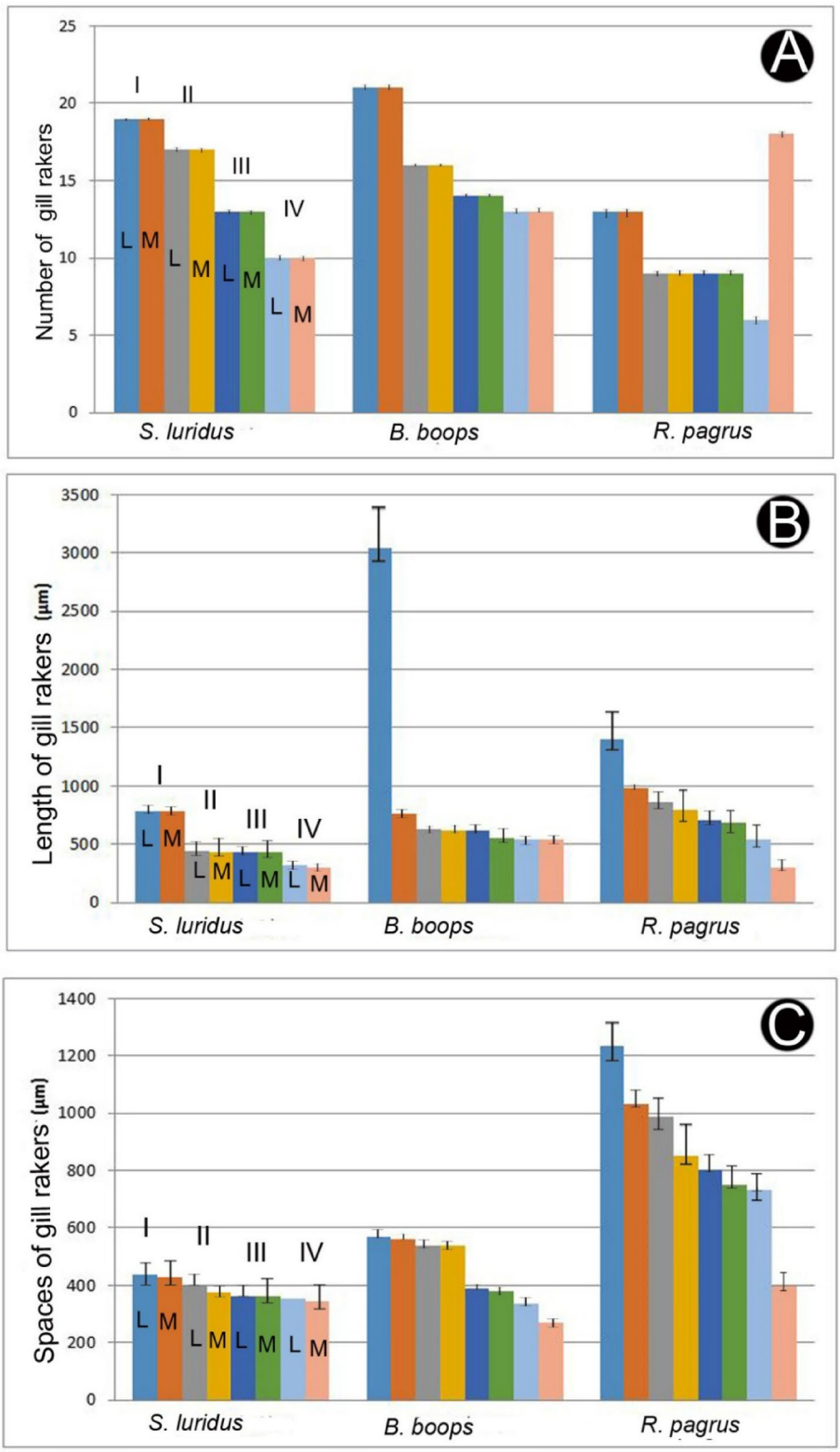

Fig. 5 **A**) the number of the gill rakers (mean ± SD), **B**) the average length of the gill rakers (mean ± SD) by µm at the middle of each gill arch., and **C**) the spaces between the bases of the gill rakers (mean ± SD) by µm at the middle of each gill arch. I–IV: 1st to 4th-gill arch. L. lateral row, M. Medial row

rakers at the middle of each gill arch was 563.2 ± 20.6 µm and 561.6 ± 11.73 µm of the lateral and medial rows of the 1st gill arch, and they decreased gradually on the 2nd and 3rd-gill arch until they reached 336.4 ± 20.6 µm and 270.2 ± 18.04 µm on the lateral and medial rows of the 4th-gill arch (Table 4). The needle-like spine length was about 109–158 µm. The long wedge spines were about

430–590 µm, while the moderate wedge spines were about 280–460 µm.

In *Pagrus pagrus*, the length of the gill rakers of the lateral and medial rows of the 1st gill arch was 1397 ± 110.2 µm and 980 ± 8.9 µm, and they decreased gradually on the 2nd- and 3rd-gill arch until they reached 539.4 ± 68.543 µm and 295.2 ± 26.77 µm on the lateral and medial rows of the 4th-gill arch (Table 3). The space between the bases of gill rakers at the middle of each gill arch was 1233.2 ± 107.50 µm and 1030 ± 44.8 µm of the lateral and medial rows of the 1st gill arch, and they decreased gradually on the 2nd and 3rd-gill arch until they reached 730 ± 77.8 µm and 396.6 ± 42.27 µm on the lateral and medial rows of the 4th-gill arch (Table 4).

From the analysis of the measurements shown in Tables 2, 3, 4 and Fig. 5, we discovered that the highest number of gills rakers were in *Boops boops*, and, *Pagrus pagrus* had a low number of gill rakers but a large number in the last row. The longest gill rakers were in *Pagrus pagrus* except for the lateral row of boops 1st-gill arch rakers, while the interval or the spaces between gill rakers were in *Pagrus pagrus*.

Discussion

The morphological characteristics of gill rakers have demonstrated unique structural specifications that are visible in feeding behavior in the studied fish. The current study examined the gill rakers of *Siganus luridus*, *Boops boops*, and *Pagrus pagrus*.

The gill rakers of *Siganus luridus* were relatively smooth. Their ends appeared spine-like with different shapes; single spine, bifid, trifid, and quadrate, like duck toe, that act as filters and catch the algae particles. In addition to trifid and quadrate-like duck toes adapted to vegetarian feeders, the *siganid* fish are herbivorous; they progress from feeding on zoo- and phytoplankton as larvae to finer algae (De Bruin et al. 1995; Mousa et al. 2016). *Siganus luridus* is primarily herbivorous and live on a variety of plant foods. Its preferred food is algae (99.73%), seagrass, and rubble (El-Sadek et al. 2022). For herbivorous fish, the gill rakers were mainly short. The gill rakers act as branchial sieves as an adaptation for efficient filtering of small food particles in the water gulped by the fish (Kumari et al. 2009). The herbivorous black fish's gill rakers direct water toward the oral cavity roof, where food particles are trapped by the mucous covering before being ingested (Sanderson et al. 1991). It was suggested that the gill rakers perform a dual function; they change the direction of the water as a first step and filter food particles as a second (Sanderson et al. 1996).

Boops boops had long rakers that appeared conical with pointed ends on the medial and lateral sides of the first-gill arch. The following gill arches had long gill rakers on their medial sides and short gill rakers on their lateral sides. All gill rakers carried different shapes of spines. These long and short spinated gill rakers and the narrow spaces between the gill rakers in *Boops boops* are specialized for different types of food particles, and the *Boops boops* are omnivorous (Bond 1996; Gibson 1988; Mousa et al. 2016; Salman et al. 2005). The long gill rakers were semi-conical in shape with tapered ends, and their medial surfaces had needle-like spines (sewing needles) adapted for the sorting of plankton, similar to observations stated by Mousa et al. (2016). In addition, the presence of wedge-shaped spines that appear from the arch at the base of gill rakers acts and increases the seizing of prey that are slippery and smooth prey (De Bruin et al. 1995).

The rakers of *Pagrus pagrus* were short and had fine-needle spines covering their tops. The gradual decrease in the gill rakers' height has appeared from the 1st to the 4th gill arch. The spines were conical in shape with pointed curved or straight ends. These findings confirm the carnivorous *Sparidae* fish described (Khalaf Allah 2013; Mousa et al. 2016; Salman et al. 2005). *Pagrus pagrus* has a low number of gill rakers but a large number in the last row, which may increase the seizing of slippery, smooth, and slimy prey and act as a save (Abuziadah 1995).

The gill rakers were arranged into medial and lateral rows in *Pagrus pagrus*, *Boops boops*, and *Siganus luridus*. The number of the gill rakers on the medial and lateral rows was equal in all gill arches of the studied fishes except in the last gill raker row of *Pagrus pagrus*. The highest number of the gill rakers was always on the 1st gill arch and was in *Boops boops*, *Siganus luridus*, and *Pagrus pagrus*. An increasing number of gills rakers enhances cross-flow filtering, and the closely spaced gill rakers limit the escape possibilities of small prey (Kahilainen et al. 2011; Mousa et al. 2016; Robinson and Parsons 2002; Smith and Sanderson 2007). The prey size relationship is a consequence of the strong correlation between gill raker gap and standard length (McCormick 1998). The herbivorous *Siganus luridus* had a high number of gills rakers and narrow spaces between them, while the carnivorous *Pagrus pagrus* had a low number of gills rakers and wide spaces between them, and the omnivorous *Boops boops* had an intermediate range between the previous two fishes. This indicates that herbivorous species prefer small food particles over carnivorous and omnivorous species, which prefer large food particles.

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Declarations

Conflict of interest None of the authors has any financial or personal relationships that could inappropriately influence or bias the content of the paper.

Ethics approval All methods and ethics were approved by the ethical committee, Faculty of Veterinary Medicine, Alexandria University, Egypt.

Consent to participate Not applicable.

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