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Comparative morphology of the urohyal bone of fishes collected from the Persian Gulf and Oman Sea

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The urohyal is incorporated within the hyoid and branchial arches and performs a significant role in the mouth opening-closing mechanism of fishes, and is considered a synapomorphy of teleostean fishes. Morphological variation of the urohyal, in terms of size and shape parameters, can allow species identification. Morphology of the urohyal in 49 species belonging to 43 genera and 29 families from the Persian Gulf and from the Oman Sea were compared using size and shape measurements. The results examine the suitability of using the urohyal morphology in differentiating fish species from this region; highlighting the taxonomic value of the urohyal, which until now, had been studied little in terms of use as a diagnostic feature in the classification of teleosts.

Keywords: fish skeleton, taxonomy, teleost, osteology, identification

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INTRODUCTION

The urohyal is an unpaired median bone located ventral to the basibranchial region within the hyoid and branchial arches, and is important in the mechanism of mouth opening and closing in fishes (Arratia & Schultze, 1990; Chollet-Villalpando *et al*., 2014). The description of this structure in different fish groups dates back to Cuvier (1835). The morphology of the urohyal is used for taxonomic and phylogenetic purposes for several fish species (Bianchi, 1984; Murray & Attia, 2004; Otero, 2004; Mabee *et al*., 2011; De La Cruz-Agüero & Chollet-Villalpando, 2012; Marceniuk *et al*., 2012; Chollet-Villalpando *et al*., 2014). It is also used in feeding studies to quantify the food ingested by piscivorous fish and other aquatic animals (Hansel *et al*., 1988; Scharf *et al*., 1997, 1998; Johal *et al*., 2001; Gosztonyi *et al*., 2007; Gonzalez-Zevallos *et al*., 2010; Tombari *et al*., 2010; Perez-Comesaña *et al*., 2013). This can often be species-specific and used in various studies of diet in fishes (Kusaka, 1974; Esmaeili & Teimori, 2006; De La Cruz-Agüero & Chollet-Villalpando, 2012).

There are several qualitative descriptive studies of the urohyal in fishes, for example Aprieto (1974) on some species of Carangidae, Sato *et al*. (1988) on Clupeidae, and De La Cruz-Agüero & Chollet-Villalpando (2012) on different species of Gerreidae. However, the quantitative information for the urohyal in most past studies is very limited, despite it often being diagnostic (Chollet-Villalpando *et al*., 2014) and variable (Kusaka, 1974; Esmaeili & Teimori, 2006).

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The morphology of the urohyal of Iranian fishes is not well studied. Esmaeili & Teimori (2006) have described the urohyal of some freshwater fishes and they included in their study the urohyal of *Tenualosa ilisha*. Jahromi *et al*. (2010) studied the morphology of two scarid species, *Scarus ghobban* and *S. persicus*.

Accordingly, this study was initiated to provide an additional osteological description of the fish species inhabiting the Persian Gulf and Oman Sea. The data and observations from this study will facilitate future taxonomic analyses regarding the fish groups studied.

MATERIALS AND METHODS

Urohyals were obtained from fishes collected from landing sites at Bandar Abbas and Bushehr cities, Iran. The fish specimens were kept on ice during the trip back to the laboratory where their total and standard lengths in mm were recorded. The flesh was removed by placing the fish specimen in boiling water for a few minutes and the urohyal extracted from the ventral side of the head, washed and stored dry in small envelopes. Families of species studied were arranged according to Eschmeyer (2014) and are presented in Table 1 together with the number of specimens for each species and size range. In total, 148 fish specimens of 49 species belonging to 43 genera and 28 families were studied. Eschmeyer (2014) and Fricke (2014) were used for the updated taxonomic status of the species, spelling of species names, and taxonomic references. Digital images for the dorsal, ventral and left sides of the urohyals extracted from specimens were taken (as described by Kusaka, 1974), using a Canon 7D camera. The graphical software Corel Draw X7 was used in the production

Table 1. Number of samples (N), standard length range (SL, mm) and mean (m SL) of fishes collected from the Iranian marine waters and used in the urohyal morphology analysis.

Species	Figures	Catalogue number	Family	N	Standard length (mm) Range
Anodontostoma chacunda	4, 9, 14	ZM-CBSU10712	Clupeidae	1	142.10
Ilisha megaloptera	4, 9, 14	ZM-CBSU7674	=	2	215–252
Ilisha melanostoma	4, 9, 14	ZM-CBSU7675	=	1	235.00
Nematalosa nasus	4, 9, 14	ZM-CBSU10715	=	1	170.00
Chirocentrus nudus	4, 9, 14	ZM-CBSU7700	Chirocentridae	3	145–490
Saurida tumbil	4, 9, 14	ZM-CBSU7590	Synodontidae	3	215–311
Tylosurus crocodilus	4, 9, 14	ZM-CBSU4322	Belonidae	3	960–1120
Platycephalus indicus	4, 9 , 14	ZM-CBSU7586	Platycephalidae	3	320–340
Cephalopholis hemistiktos	4, 9, 14	ZM-CBSU7526	Serranidae	2	150–228
Epinephelus stoliczkae	4, 9, 14	ZM-CBSU7577	=	3	250–275
Sillago sihama	4, 9, 14	ZM-CBSU 7524	Sillaginidae	3	144–197
Alepes djedaba	4, 9, 14	ZM-CBSU7566	Carangidae	3	238–254
Atropus atropus	5, 10, 15	ZM-CBSU7688	=	2	112–195
Carangoides armatus	5, 10, 15	ZM-CBSU7598	=	2	304–162
Carangoides malabaricus	5, 10, 15	ZM-CBSU7612	=	3	152–166
Parastromatus niger	5, 10, 15	ZM-CBSU7601	=	3	132–143
Scomberoides commersonianus	5, 10, 15	ZM-CBSU7603	=	3	267–272
Secutor insidiator	5, 10, 15	ZM-CBSU10724	Leiognathidae	2	62–64
Lutjanus fulviflamma	5, 10, 15	ZM-CBSU7573	Lutjanidae	6	164–221
Lutjanus lutjanus	5, 10, 15	ZM-CBSU7563	=	6	164–207
Gerres filamentosus	5, 10, 15	ZM-CBSU7570	Gerreidae	2	152–173
Plectorhinchus schotaf	5, 10, 15	ZM-CBSU7661	Haemulidae	3	190–198
Pomadasys furcatus	5, 10, 15	ZM-CBSU7664	=	1	155.30
Pomadasys maculatus	5, 10, 15	ZM-CBSU7521	=	3	214–273
Pomadasys stridens	6, 11, 16	ZM-CBSU10706	=	2	188–190
Acanthopagrus arabicus	6, 11, 16	ZM-CBSU7679	Sparidae	5	176–201
Argyrops spinifer	6, 11, 16	ZM-CBSU7618	=	3	167–198
Cheimerius nufar	6, 11, 16	ZM-CBSU10503	=	3	180–201
Diplodus sargus kotschyi	6, 11, 16	ZM-CBSU7692	=	3	170–231
Nemipterus japonicus	6, 11, 16	ZM-CBSU7616	Nemipteridae	3	130–175
Nibea maculata	6, 11, 16	ZM-CBSU7670	Sciaenidae	3	243–265
Otolithes ruber	6, 11, 16	ZM-CBSU7671	=	3	180–230
Eleutheronema tetradactylum	6, 11, 16	ZM-CBSU7504	Polynemidae	3	184–233
Polydactylus sextarius	6, 11, 16	ZM-CBSU10709	=	2	198–210
Upeneus sulphureus	6, 11, 16	ZM-CBSU7685	Mullidae	1	124–167
Drepane punctata	7, 12, 17	ZM-CBSU7669	Drepanidae	3	119–223
Planiliza subviridis	7, 12, 17	ZM-CBSU7528	Mugilidae	3	117–129
Scarus ghobban	7, 12, 17	ZM-CBSU7592	Scaridae	3	186–303
Ephippus orbis	7, 12, 17	ZM-CBSU7682	Ephippidae	3	107–130
Siganus sutor	7, 12, 17	ZM-CBSU7694	Siganidae	3	224–252
Sphyraena putnamae	7, 12, 17	ZM-CBSU7610	Sphyraenidae	3	353–377
Rastrelliger kanagurta	7, 12, 17	ZM-CBSU7518	Scombridae	3	175–186
Scomberomorus guttatus	7, 12, 17	ZM-CBSU4327	=	3	440
Pampus argenteus	7, 12, 17	ZM-CBSU4399	Stromateidae	3	285
Psettodes erumei	7, 12, 17	ZM-CBSU7606	Psettodidae	2	239–243
Pseudorhombus elevatus	7, 12, 17	ZM-CBSU7677	Paralichthyidae	2	230–233
Brachirus orientalis	8, 13, 18	ZM-CBSU7699	Soleidae	3	173–180
Cynoglossus arel	8, 13, 18	ZM-CBSU7594	Cynoglossidae	3	144–195
Cynoglossus bilineatus	8, 13, 18	ZM-CBSU7596	=	6	180–240

of all figures. The description of the features of the urohyal was studied using the terminology of Chollet-Villalpando *et al.* (2014) modified from Kusaka (1974). In this description the following abbreviations are used: Ba, basibranchial attachment; Co, condyle; De, dorsal extension; Dp, dorsal plate; Ha, hypohyal attachment; Lp, lateral plate; Pde, postero-dorsal edge; Pe, posterior edge; Rb, radial band; Ve, ventral extension; Vp, ventral plate (Figure 1). These features are defined as short (length $<$ height), or broad if height $>$ 1/2 length; long (length $>$ height) or narrow if height $<$ 1/2 length).

All proportions of the urohyal were measured following Kusaka (1974), these are: DL, urohyal dorsal length; FL, urohyal frontal length; MH, urohyal maximum height; UH, urohyal height; UL, urohyal length; UW, urohyal width; VL, ventral length (Figure 2). Linear measurements were standardized as a function of the length of the urohyal and the angle values to eliminate the effect of fish size. Accordingly, the following features of the urohyal were calculated:

$$\text{Size of urohyal} = \frac{\text{Length of the urohyal}}{\text{Head length}} \times 100$$

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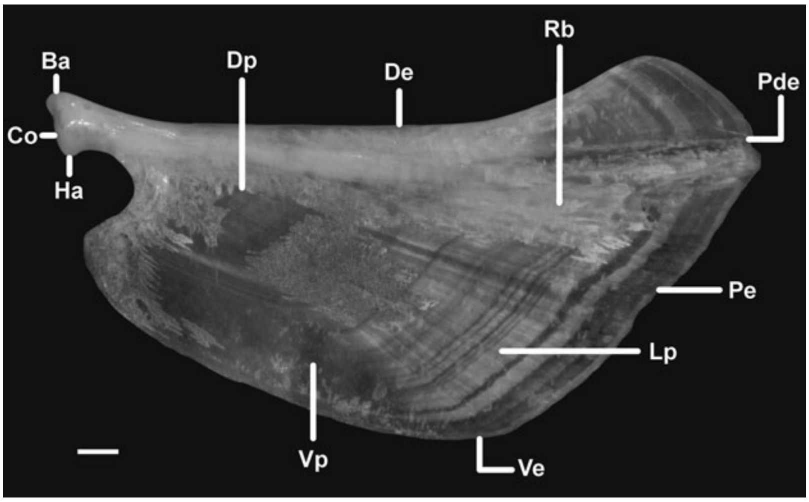

Fig. 1. Left side view of a urohyal of *Gerres filamentosus*. Terminology of urohyal as follows: Ha, hypohyal attachment; Ba, basibranchial attachment; Ve, ventral extension; De, dorsal extension; De, dorsal plate; Pde, postero-dorsal edge; Rb, radial band; Lp, lateral plate; Pe, posterior edge; Ve, ventral edge; Vp, ventral plate; Co, condyle (modified from Kusaka, 1974).

$$\text{Height of the lengthwise extension} = \frac{\text{Urohyal height}}{\text{Urohyal length}} \times 100$$

$$\text{Lateral development or spread} = \frac{\text{Urohyal width}}{\text{Urohyal length}} \times 100$$

$$\text{Aspect ratio} = \frac{\text{Urohyal length}}{\text{Urohyal width}}$$

The values of the angles, ventral angle (VA, angle 3; ACB), condylar angle (CA, angle 1; BAC) and postero-dorsal angle (PDA, angle 2; ABC) were measured using an online digital screen protractor (ICONICO) (Figure 3). The urohyals are deposited in the collection of the Zoological Museum of Shiraz University (ZMCBSU), Biology Department, Shiraz, Iran (Table 1).

RESULTS

The urohyals are illustrated in Figures 4–18.

The dorsal, ventral and lateral sides of the urohyal are variable in shape in the examined species of fishes. The dorsal side shows 18 main shapes (Table 2, Figures 4–8). Out of this number there are seven shapes subdivided into several sub-shapes with the number of species represented by the shapes ranging from two to 10. The remaining 11 shapes are represented by one or two species. The shaft shape with its sub-shapes (10 species) is the most common among the fish species studied. The next most common shapes are wedge and penholder with their sub-shapes (six and seven, respectively). The slender shape category with its two sub-shapes holds two species. The flask shape and irregular shapes with their sub-shapes contain four species each.

The dorsal side of the urohyal of the studied species showed 18 main shapes. Such a high number of shapes originated from well diversified families involved in this morphological comparison. Some of the shapes succeeded in encompassing the species belonging to the same genera or families. For example, the four species of the family Haemulidae all have a flask shape. The four sparid species belong to four genera. *Acanthopagrus arabicus* and *Diplodus sargus kotschyi* have a

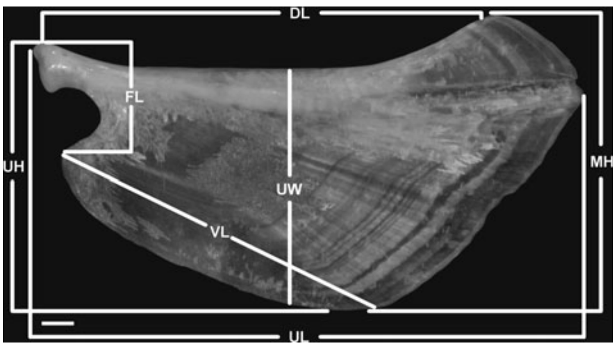

Fig. 2. Dimension measurements of the left side view of a urohyal of *Gerres filamentosus*. DL, dorsal length; FL, frontal length; MH, maximum height; UH, urohyal height; UL, urohyal length; VL, ventral length (Kusaka, 1974).

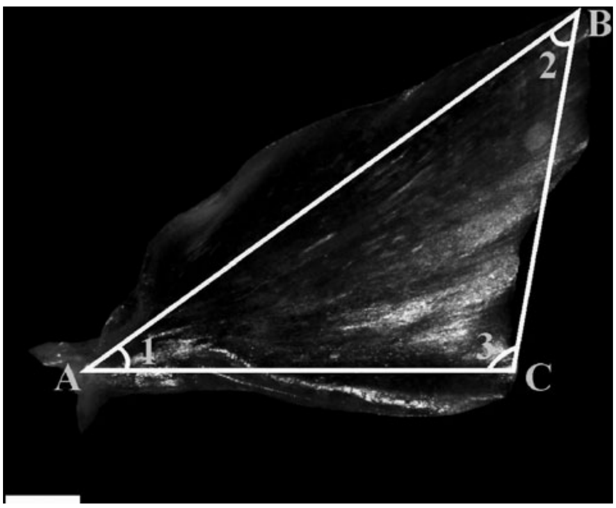

Fig. 3. Angles of the left side view of a urohyal of *Gerres filamentosus*. Ventral angle (VA, angle 3; ACB); condylar angle (CA, angle 1; BAC); postero-dorsal angle (PDA, angle 2; ABC).

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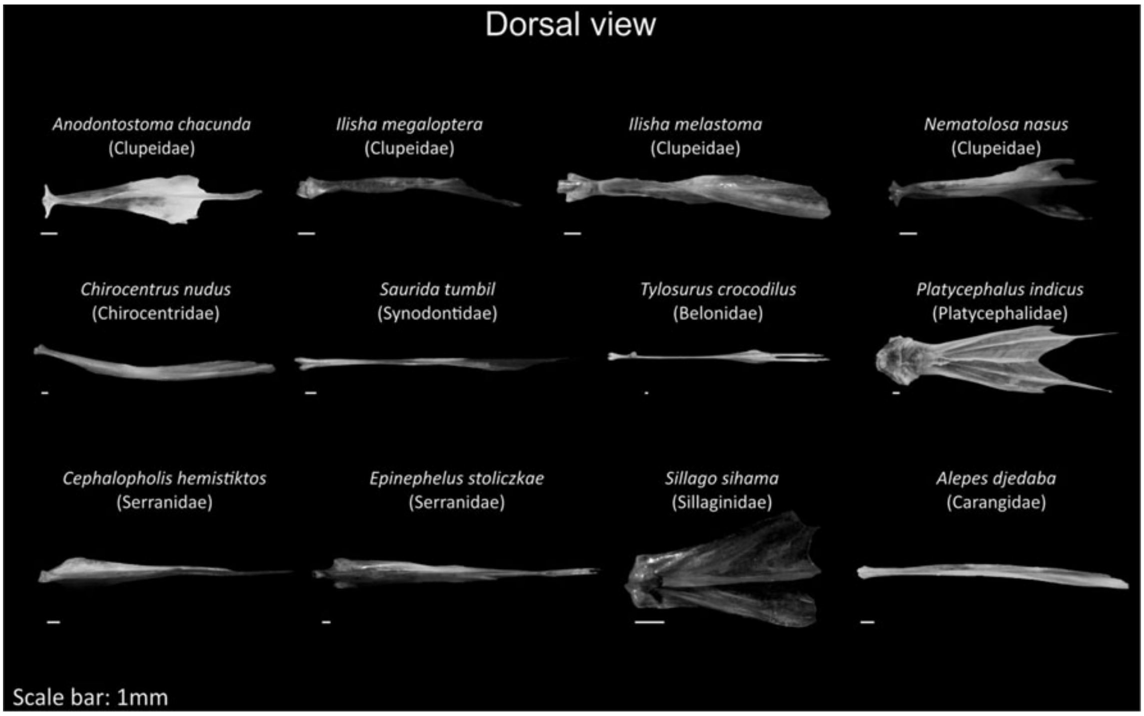

Fig. 4. Dorsal view of the urohyal of *Anodontostoma chaucunda* (Clupeidae) to *Alepes djedaba* (Carangidae). Scale bar = 1 mm.

wedge-tailed shape, while *Argyrops spinifer* and *Cheimerius nufar* have an irregular shaft shape. The two polynemid species *Eleutheronema tetradactylum* and *Polydactylus sextarius* have a two-headed ovate shape. The five clupeid species belong to four genera, two species of the genus *Ilisha* have a penholder shape, *Anodontostoma chacunda* and *Nematalosa nasus* have an irregular triangular shape, and *Chirocentrus nudus* Swainson, 1839 has a curved sword shape. On the other hand, several species belonging to different families have a similar shape of urohyal in dorsal view (Table 2).

There are 16 shapes of the urohyal in ventral view (Table 3, Figures 9–13). In the lateral view, the urohyal showed 22 shapes (Table 4, Figures 14–18). Viewing the urohyal of the species examined in the present study, it was possible to

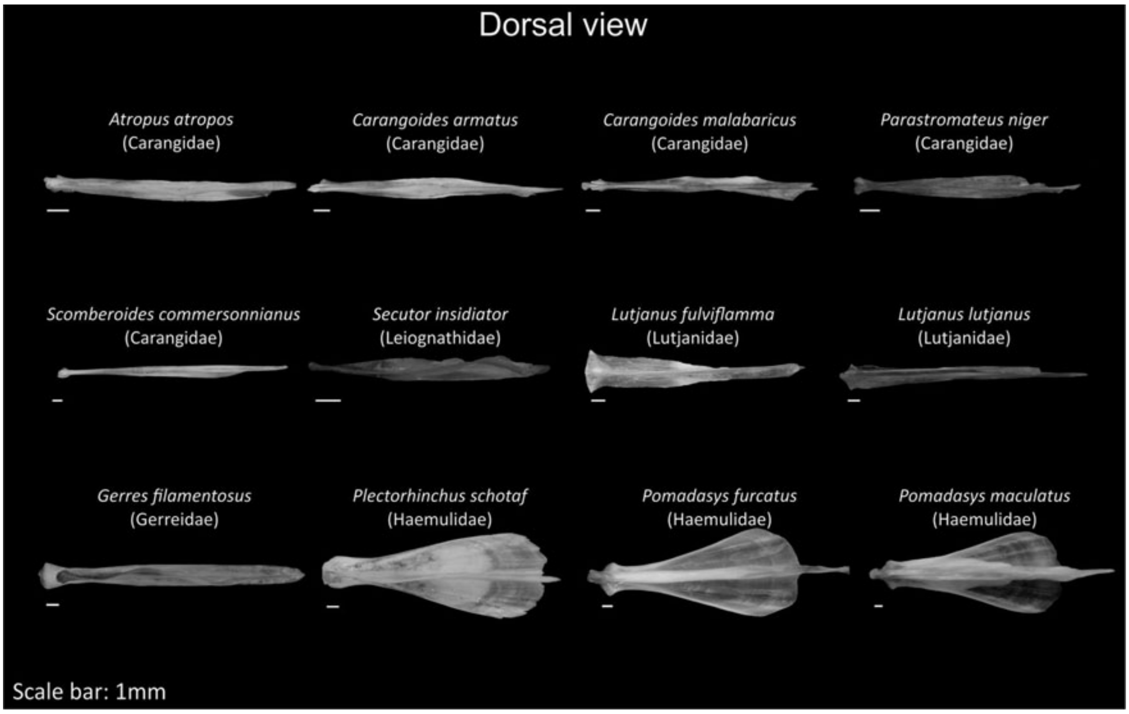

Fig. 5. Dorsal view of the urohyal of *Atropus atropus* (Carangidae) to *Pomadasys maculatus* (Haemulidae). Scale bar = 1 mm.

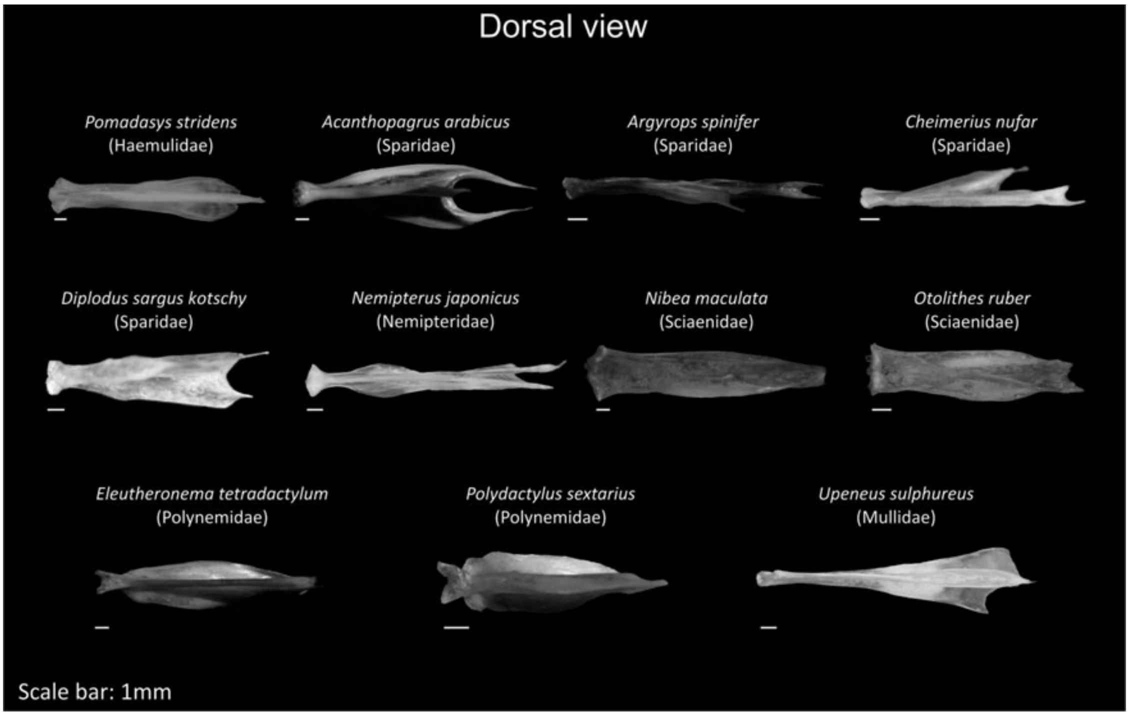

Fig. 6. Dorsal view of the urohyal of *Pomadasys stridens* (Haemulidae) to *Upeneus sulphureus* (Mullidae). Scale bar = 1 mm.

recognize the following 11 features (Figure 1). These features showed considerable variations in shape between the studied species (Table 5, Figures 4–8).

Proportions

The majority of the species has a large urohyal (48 species), a medium to large size is found in *Ilisha megaloptera, Ilisha melanostoma*, and medium is seen in *Tylosurus crocodilus*.

The lengthwise extension has three criteria, these being slender, medium and high. The majority of the studied species falls in the medium criterion (30 species) followed by slender (13 species) and the high criterion (eight species).

For the lateral development spread of the studied species there are only two criteria, laterally unexpanded (23 species) and ordinary spread (12 species). The following species are shown to have criteria falling between the laterally unexpanded and ordinary spread criteria: *Scomberoides*

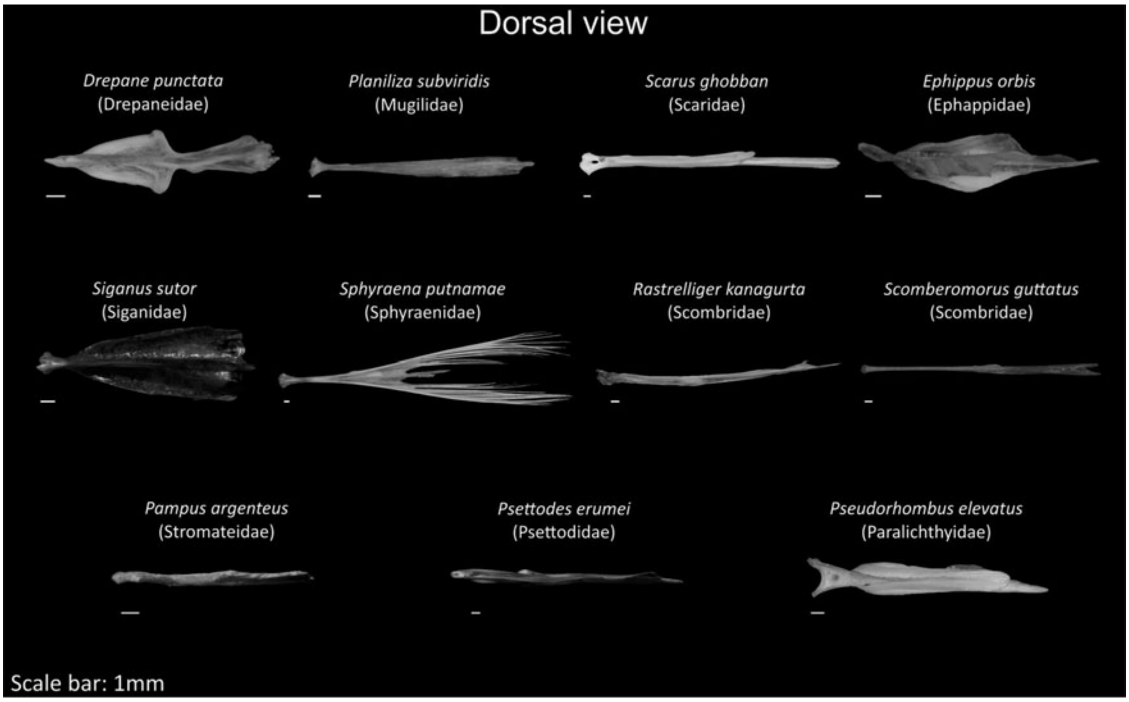

Fig. 7. Dorsal view of the urohyal of *Drepane punctata* (Drepaneidae) to *Pseudorhombus elevatus* (Paralichthyidae). Scale bar = 1 mm.

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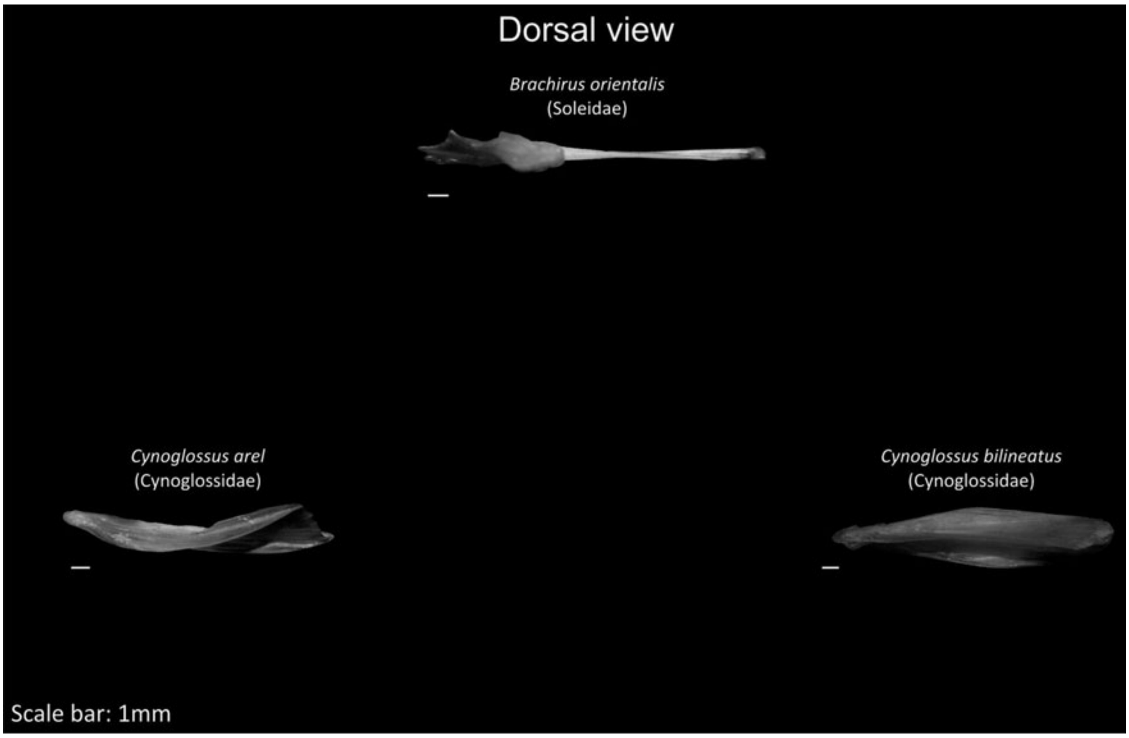

Fig. 8. Dorsal view of the urohyal of *Brachirus orientalis* (Soleidae) to *Cynoglossus bilineatus* (Cynoglossidae). Scale bar = 1 mm.

commersonianus, Alepes djedaba, Lutjanus lutjanus, Acanthopagrus arabicus, Argyrops spinifer and *Cheimerius nufar*. For the species such as *Anodontostoma chacunda, Plectorhinchus schotaf, Lutjanus fulviflamma, Polydactylus sextarius, Otolithes ruber, Nibea maculata, Sillago sihama, Diplodus sargus kotschyi* and *Brachirus orientalis*, the urohyal showed a lateral spread intermediate between ordinary and wide.

The minimum and maximum values of the urohyal dorsal height are 0.18 and 0.34% in SL as shown in *Drepane punctata* and *Scomberoides commersonianus* respectively. The minimum value of the frontal length is 0.02% of SL and revealed by *Nibea maculata*, while the maximum value is 0.16% SL and shown by *Upeneus sulphureus*. The urohyal maximum height ranges from 0.02 and 0.19% SL for *Platycephalus indicus* and *Siganus sutor* respectively. The

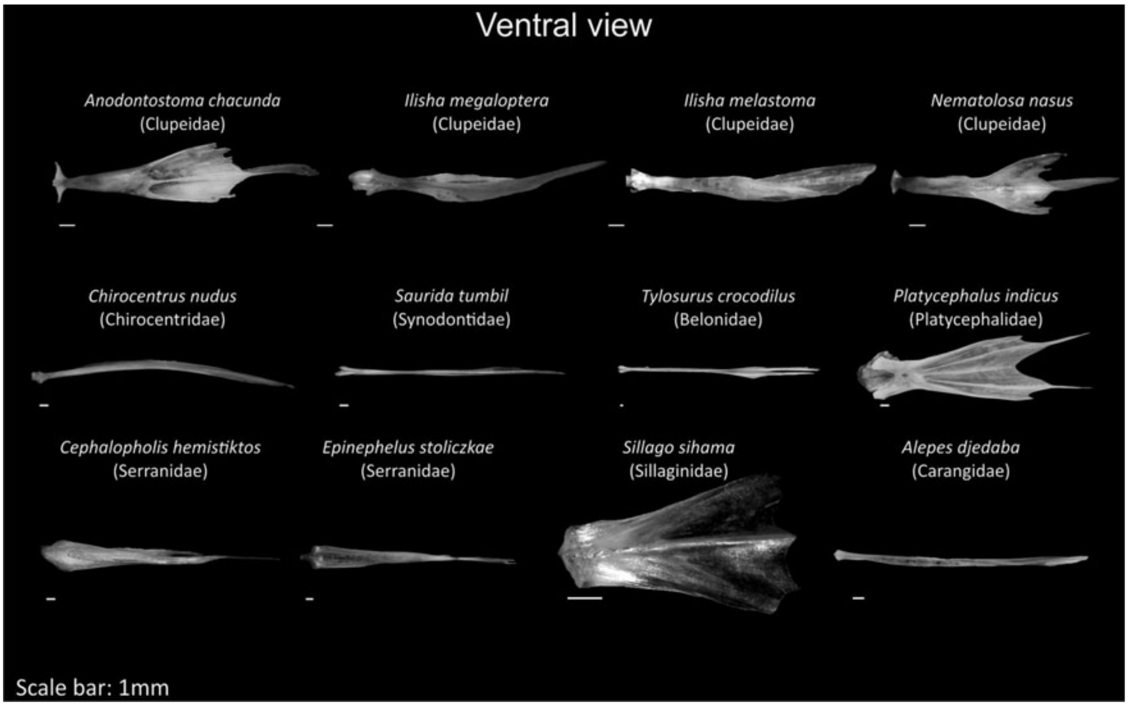

Fig. 9. Ventral view of the urohyal of *Anodontostoma chaucunda* (Clupeidae) to *Alepes djedaba* (Carangidae). Scale bar = 1 mm.

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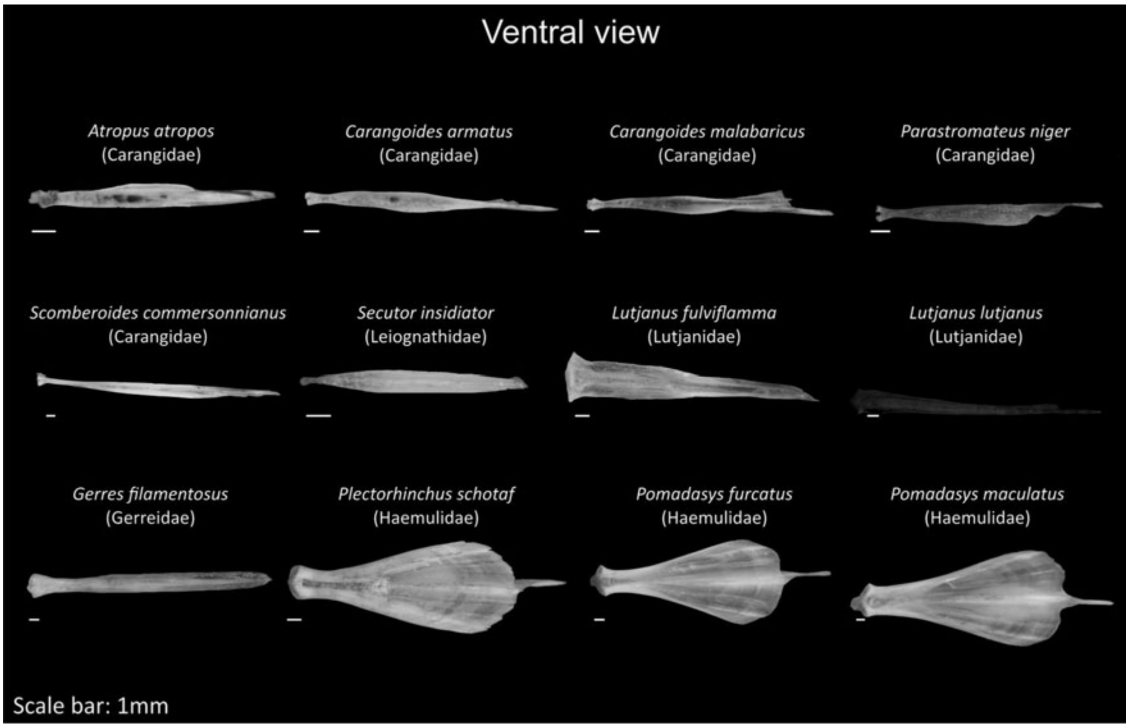

Fig. 10. Ventral view of the urohyal of *Atropus atropus* (Carangidae) to *Pomadasys maculatus* (Haemulidae). Scale bar = 1 mm.

lower value obtained for the urohyal height is 0.01% SL shown by *Sphyraena putnamae* and the higher value was 0.34% SL revealed by *Eleutheronema tetradactylum*. The urohyal length showed lower value of 0.29% SL as in *Ephippus orbis* and higher value of 0.35% SL as in *Scomberoides commersonianus*. The minimum and maximum values shown by the ventral length of the urohyal are 0.02 and 0.28% SL as in *Tylosurus crocodilus* and *Scarus ghobban* respectively.

Angles

The three angles of the urohyal, condylar, ventral and postero-dorsal showed ranges of 4–79°, 18–179° and 3–155° respectively. The lowest value of the condylar angle (BAC) 4° is observed in *Tylosurus crocodilus* and the highest, 79° in *Ephippus orbis*. For the ventral angle (ACB), the lowest value 18° is found in *Cynoglossus arel* and the highest value in *Tylosurus crocodilus*. The postero-dorsal angle has values

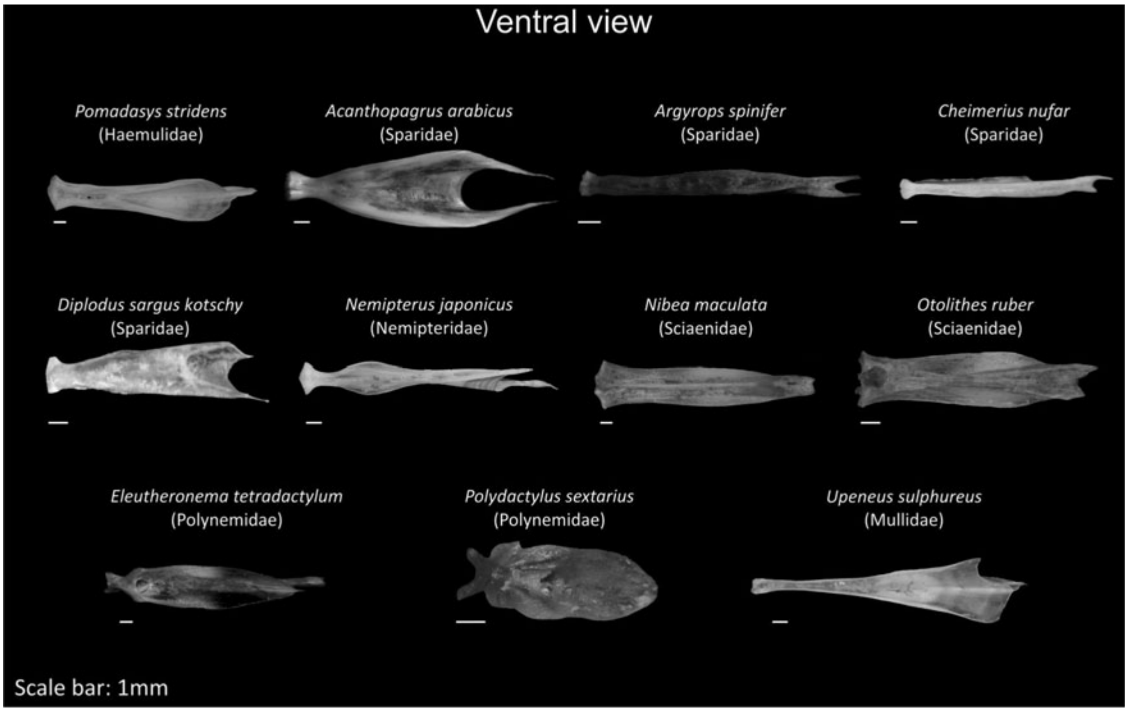

Fig. 11. Ventral view of the urohyal of *Pomadasys stridens* (Haemulidae) to *Upeneus sulphureus* (Mullidae). Scale bar = 1 mm.

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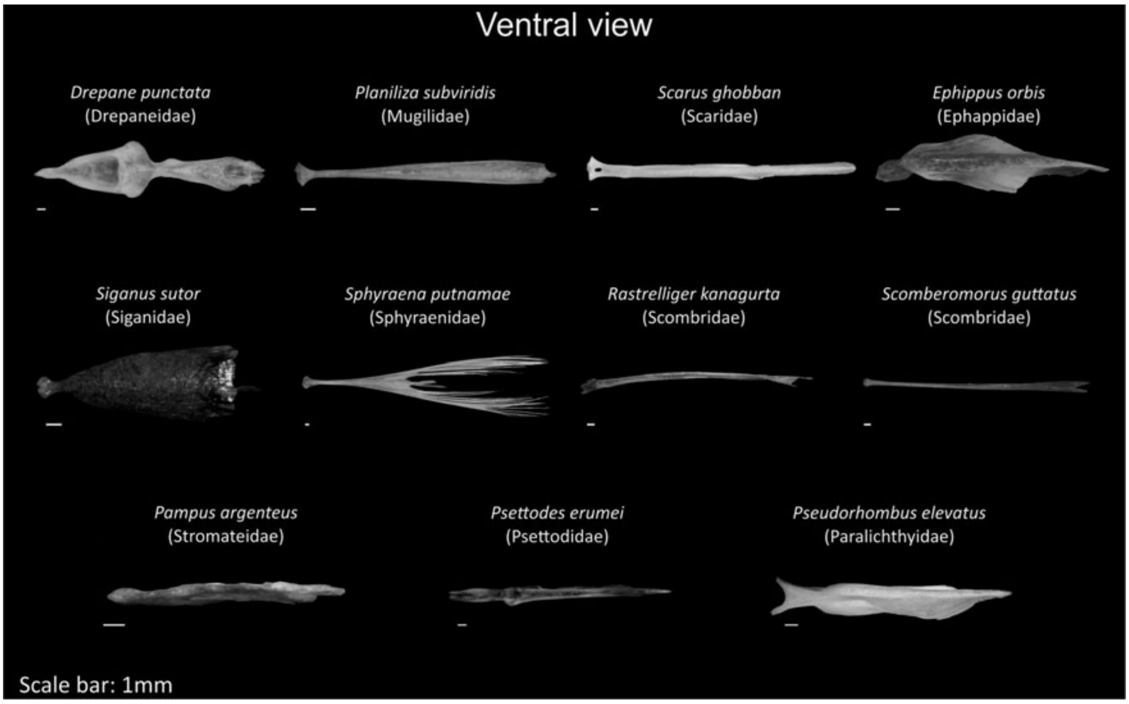

Fig. 12. Ventral view of the urohyal of *Drepane punctata* (Drepaneidae) to *Pseudorhombus elevatus* (Paralichthyidae). Scale bar = 1 mm.

ranging from 3° as in *Tylosurus crocodilus* and 155° as shown in the urohyal of *Cynoglossus arel*.

DISCUSSION

This osteological study of the urohyal illustrates the wide range of characters present in the members of the studied families. This study must be considered preliminary because, out of 36 orders of Actinopterygii described (Eschmeyer, 2014), only 22.2% of the known orders have been examined and out of a total of 144 families present in the order Perciformes (Eschmeyer, 2014), only 14.6% of the known families have been examined. Nevertheless, 49 species belonging to 43 genera have been studied, so a reasonable survey was possible. It is possible to

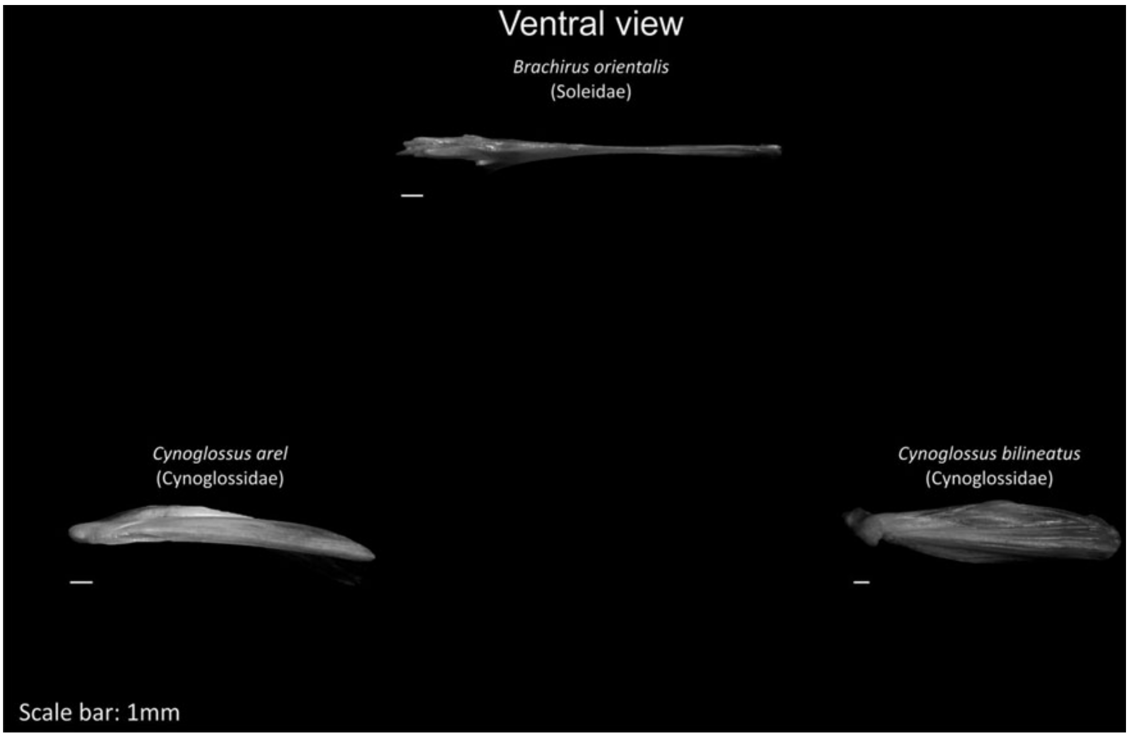

Fig. 13. Ventral view of the urohyal of *Brachirus orientalis* (Soleidae) to *Cynoglossus bilineatus* (Cynoglossidae). Scale bar = 1 mm.

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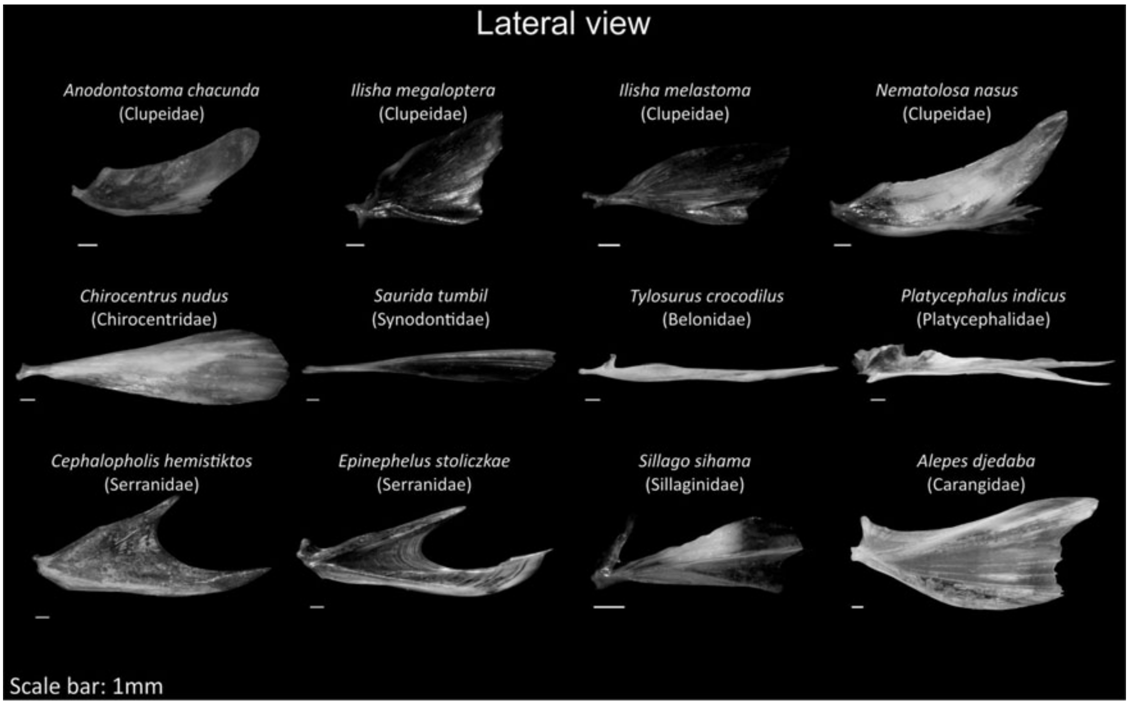

Fig. 14. Lateral view of the urohyal of *Anodontostoma chaucunda* (Clupeidae) to *Alepes djedaba* (Carangidae). Scale bar = 1 mm.

distinguish exclusive characters that are confined to particular taxa.

The present study enriches knowledge about the urohyal morphology, underlining its diagnostic value for teleostean taxonomy. The present research is the first comprehensive, comparative and quantitative assessment of the urohyal for some fish species from the marine waters of Iran, following the setting of its diagnostic characteristics by Arratia & Schultze (1990).

As the fish size effect has been eliminated, the variations in the morphology of urohyal between the studied species in the present work could reflect their natural variation. In several instances, fish species can be identified using the morphological differences in the shape of the urohyal (e.g. Kusaka, 1974; Esmaeili & Teimori, 2006). Accordingly, Aprieto (1974) has shown that the family Carangidae has revealed differences in the morphology of the skull and urohyal between individuals from wild and cultivated populations.

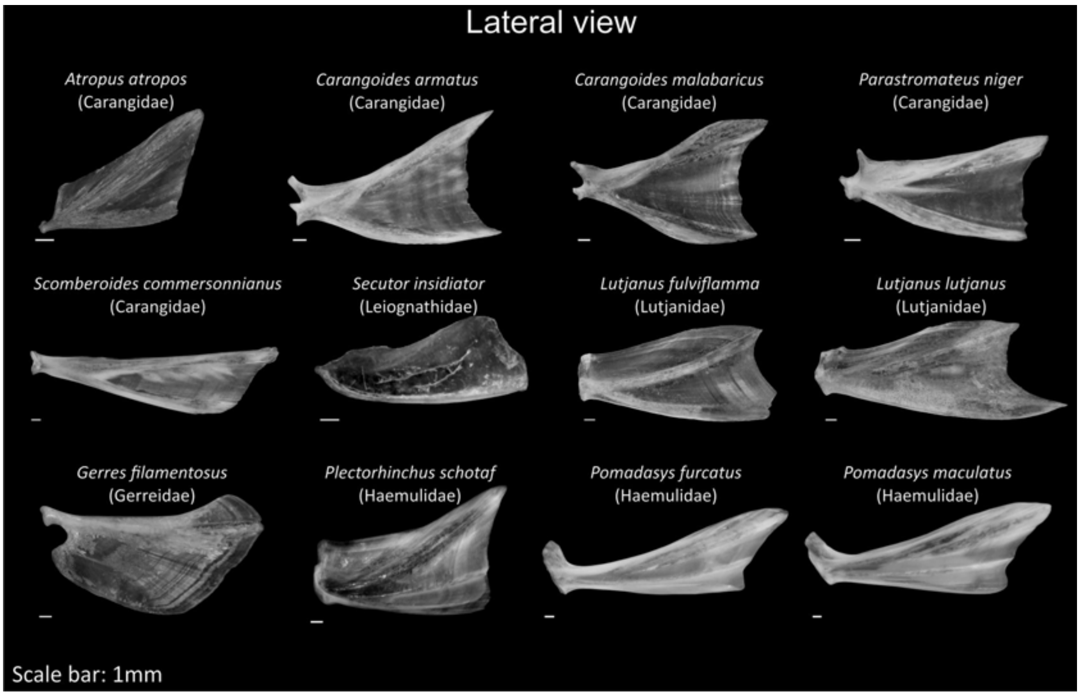

Fig. 15. Lateral view of the urohyal of *Atropus atropus* (Carangidae) to *Pomadasys maculatus* (Haemulidae). Scale bar = 1 mm.

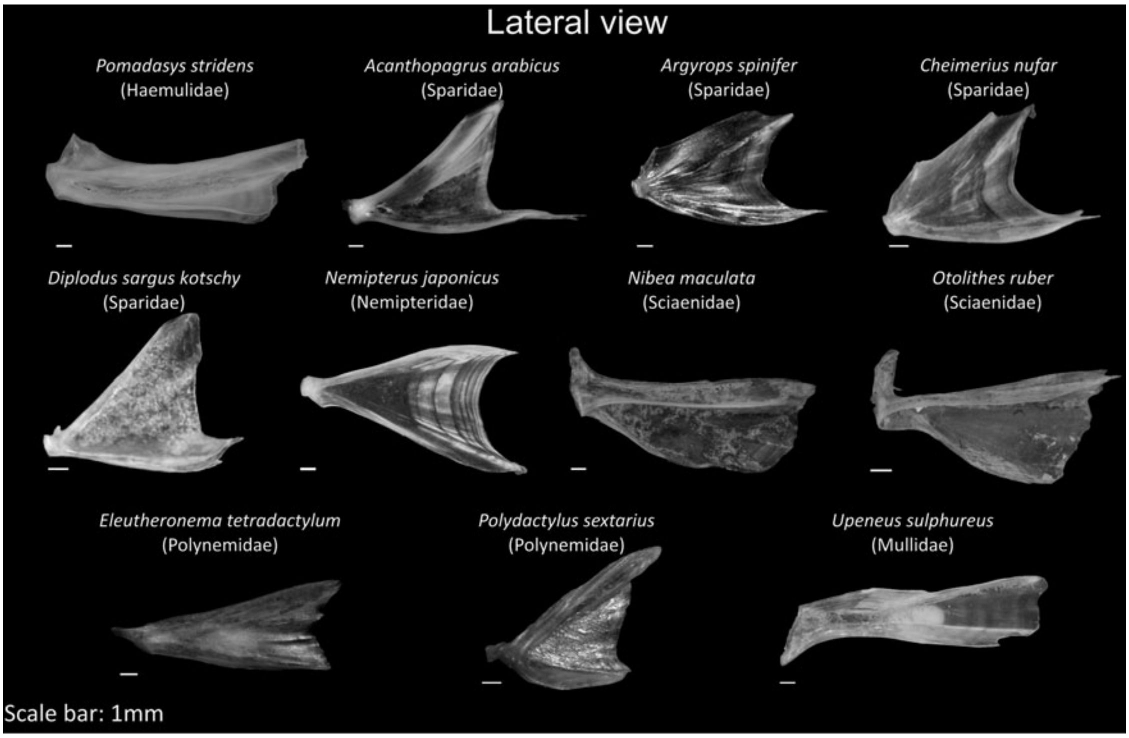

Fig. 16. Lateral view of the urohyal of *Pomadasys stridens* (Haemulidae) to *Upeneus sulphureus* (Mullidae). Scale bar = 1 mm.

Furthermore, the morphology of the urohyal was used in the description of a subspecies of the genus *Merluccius* (Lloris *et al.*, 2003), and recently Chollet-Villalpando *et al.* (2014) have separated species of the family Gerreidae using the morphological characteristics of the urohyal.

In most previous studies on the urohyal, the description was considered from the qualitative point of view and no quantitative or comparative attempts were made (Andreata & Barbieri, 1981; Andreata, 1989; Gonzalez-Acosta *et al.*, 2005, 2007; De La Cruz-Agüero & Chollet-Villalpando, 2012), but recently Chollet-Villalpando *et al.* (2014) have shown the useful quantitative characters in separating some species of the family Gerreidae. In the present study both the quantitative and qualitative characteristics of the urohyal

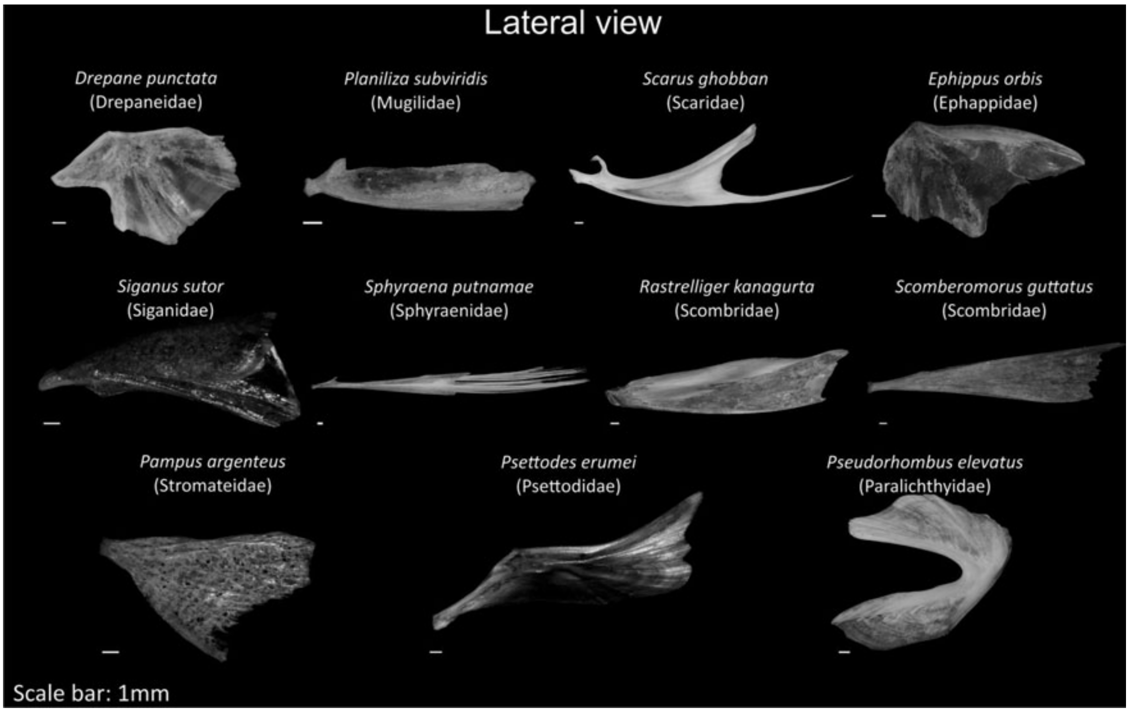

Fig. 17. Lateral view of the urohyal of *Drepane punctata* (Drepaneidae) to *Pseudorhombus elevatus* (Paralichthyidae). Scale bar = 1 mm.

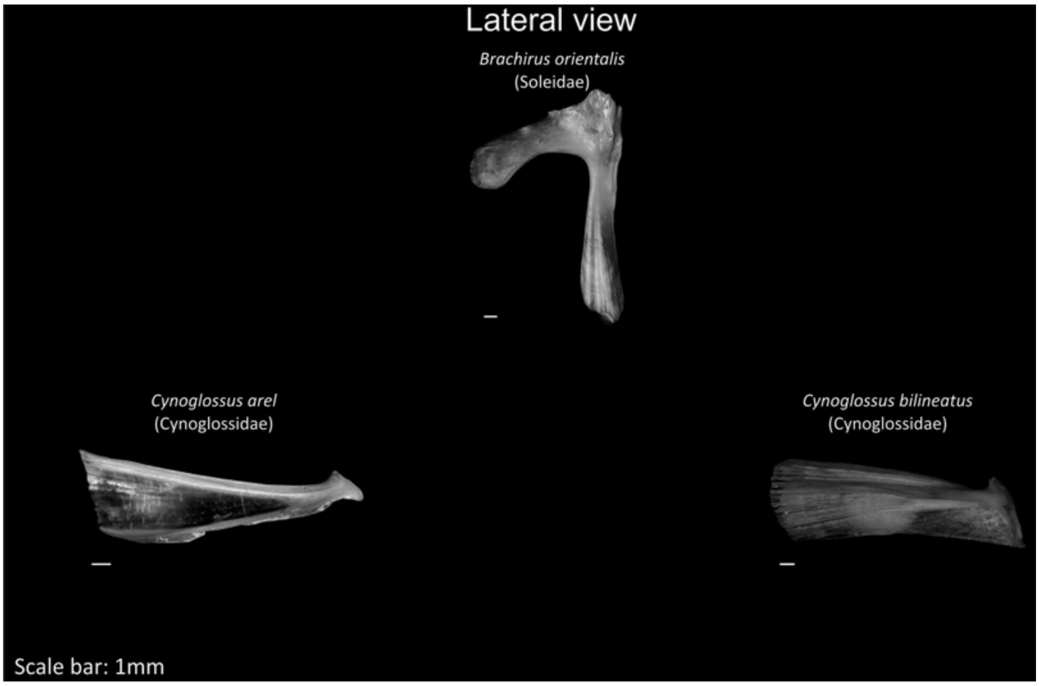

Fig. 18. Lateral view of the urohyal of *Brachirus orientalis* (Soleidae) to *Cynoglossus bilineatus* (Cynoglossidae). Scale bar = 1 mm.

Table 2. Shape of urohyal bone as shown in the dorsal view.

Shape	Species	Shape	Species
Aeroplane	*Drepane punctata* (Figure 7)	Irregular shaft	*Argyrops spinifer* (Figure 6)
	Upeneus sulphureus (Figure 6)		*Cheimerius nufar* (Figure 6)
Elongated arrow	*Tylosurus crocodilus* (Figure 4)		*Secutor insidiator* (Figure 5)
Blade	*Atropus atropus* (Figure 5)		
Comet	*Sphyraena putnamae* (Figure 7)		
Curved broad end	*Cynoglossus arel* (Figure 8)		
Two head ovate	*Eleutheronema tetradactylum* (Figure 6)	Slug	*Pseudorhombus elevatus* (Figure 7)
	Polydactylus sextarius (Figure 6)	Spatula	*Cynoglossus bilineatus* (Figure 8)
Rhombus	*Siganus sutor* (Figure 7)		
Flask			
Tailed flask	*Pomadasys furcatus* (Figure 5)		
	Pomadasys maculatus (Figure 5)	Slender	
Narrow flask	*Pomadasys stridens* (Figure 6)	Slender plate	*Gerres filamentosus* (Figure 5)
	Plectorhinchus schotaf (Figure 5)		
Irregular		Curved sward shape Spindle	*Chirocentrus nudus* (Figure 4)
Irregular triangular	*Anodontostoma chacunda* (Figure 4)	Irregular spindle	*Ephippus orbis* (Figure 7)
	Nematalosa nasus (Figure 4)		*Nemipterus japonicus* (Figure 6)
Irregular rode	*Carangoides malabaricus* (Figure 5)	Elongated spindle	*Brachirus orientalis* (Figure 8)
	Psettodes erumei (Figure 7)		
Penholder		Triangular head	*Lethrinus lentjan* (Figure 5)
Penholder	*Carangoides armatus* (Figure 5)		*Planiliza subviridis* (Figure 7)
	Parastromatus niger (Figure 5)	Wedge	
Curved penholder	*Saurida tumbil* (Figure 4)	Wedge	*Lutjanus fulviflamma* (Figure 5)
	Ilisha megaloptera (Figure 4)		*Nibea maculata* (Figure 6)
Broad penholder	*Ilisha melanostoma* (Figure 4)	Broad wedge	*Otolithes ruber* (Figure 6)
Penshape	*Scomberoides commersonianus* (Figure 7)	Elongated wedge	*Cephalopholis hemistiktos* (Figure 4)
			Epinephelus stoliczkae (Figure 4)
Plunger shape	*Sillago sihama* (Figure 7)	Tailed wedge	*Acanthopagrus arabicus* (Figure 5)
Shaft			*Diplodus sargus kotschyi* (Figure 6)
Proper shaft	*Pampus argenteus* (Figure 7)		
	Scarus ghobban (Figure 7)		
Curved shaft	*Alepes djedaba* (Figure 4)		
	Rastrelliger kanagurta (Figure 7)		
	Scomberomorus guttatus (Figure 7)		
Neck-headed shaft	*Lutjanus lutjanus* (Figure 5)		

Table 3. Shape of urohyal bone as shown in the ventral view.

Shape	Species	Shape	Species
Aeroplane	*Upeneus sulphureus* (Figure 11)	Shaft	
Arrow		Proper shaft	*Gerres filamentosus* (Figure 10)
			Scarus ghobban (Figure 12)
Elongated arrow	*Tylosurus crocodilus* (Figure 9)		*Scomberomorus guttatus* (Figure 12)
Comet arrow	*Sphyraena putnamae* (Figure 12)	Irregular shaft	*Argyrops spinifer* (Figure 11)
			Cheimerius nufar (Figure 11)
			Pampus argenteus (Figure 12)
Elongated		Curved shaft	*Chirocentrus nudus* (Figure 9)
Proper elongated	*Carangoides armatus* (Figure 10)		
	Carangoides malabaricus (Figure 10)		
	Atropus atropus (Figure 10)		
	Alepes djedaba (Figure 9)		
	Parastromatus niger (Figure 10)		
	Scomberoides commersonianus (Figure 10)		
Curved elongated	*Ilisha megaloptera* (Figure 9)		*Rastrelliger kanagurta* (Figure 12)
	Ilisha melanostoma (Figure 9)		
Flask	*Pomadasys furcatus* (Figure 10)	Broadshaft	*Secutor insidiator* (Figure 10)
		Shuttle-cock	*Platycephalus indicus* (Figure 9)
	Pomadasys maculatus (Figure 10)	Slug	*Pseudorhombus elevatus* (Figure 12)
	Pomadasys stridens (Figure 11)	Spade	*Drepane punctata* (Figure 12)
	Plectorhinchus schotaf (Figure 10)		
Lizard	*Ephippus orbis* (Figure 12)	Spindle	
		Irregular spindle	*Nemipterus japonicus* (Figure 11)
		Elongated spindle	*Brachirus orientalis* (Figure 13)
Neck headed	*Lethrinus lentjan* (Figure 10)	Triangular head	*Planiliza subviridis* (Figure 12)
Oblong-elliptical		Wedge	
Broad oblong	*Cynoglossus bilineatus* (Figure 13)	Wedge proper	*Lutjanus fulviflamma* (Figure 10)
Narrow oblong	*Cynoglossus arel* (Figure 13)		
			Lutjanus lutjanus (Figure 10)
Ovate			*Nibea maculata* (Figure 11)
Non-tailed ovate	*Eleutheronema tetradactylum* (Figure 11)	Tailed wedge	*Anodontostoma chacunda* (Figure 9)
			Nematalosa nasus (Figure 9)
Tailed ovate	*Polydactylus sextarius* (Figure 11)		
		Broad wedge	*Otolithes ruber* (Figure 11)
		Elongated wedge	*Cephalopholis hemistiktos* (Figure 9)
			Epinephelus stoliczkae (Figure 9)
Plunger	*Sillago sihama* (Figure 9)	Two-tailed wedge	*Acanthopagrus arabicus* (Figure 10)
Regular rhomboidal	*Siganus sutor* (Figure 12)		*Diplodus sargus kotschyi* (Figure 11)
Rod			
Irregular rod	*Psettodes erumei* (Figure 12)		
Broad pin rod	*Saurida tumbil* (Figure 9)		

prove to be good taxonomic criteria to identify the species, and to solve their taxonomic problems.

The ventral side of the urohyal shows one sub-shape less than what it is observed in the dorsal side. The content of the shapes with subdivisions slightly varies between the dorsal and ventral sides. In the dorsal side, the number of species ranges from three to 10, while in the ventral side the number ranges three to 10. These trivial differences between the two sides might indicate that different species are conservative in the shape of their urohyal.

Looking at the distribution of the studied species, and according to the shape of their urohyal viewed ventrally, *Sphyraena putnamae* and *Tylosurus crocodilus* have the same general ventral shape of the urohyal. These two species belong to two different families, but the similarity in the shape of their urohyal might be due to the food type and feeding habits or similarities in muscle anatomy and function. Both species have fusiform bodies, posteriorly placed dorsal and anal fins, elongate jaws, large, conical teeth and piscivorous feeding habit (Lovejoy *et al.*, 2004; Porter & Motta, 2004). Such adaptation might make the ventral shape of these two species similar. On the other hand, the shape of the urohyal viewed ventrally succeeded in grouping some members of the same family in one shape grouping. For example, the four species of the family Haemulidae all have a flask shape, the six species of the family Carangidae have an elongated shape, and the two species of the family Lutjanidae have a wedge shape (Table 3, Figures 9–13). Members of some genera are grouped in sub-shapes within a similar main shape type, such as in the case of the two species of the genus *Ilisha*. For the four species of the family Sparidae, *Argyrops spinifer* and *Cheimerius nufar* were grouped in the irregular shaft sub-shape criteria, while the other two species, *Acanthopagrus arabicus* and *Diplodus sargus kotschyi* have a two-tailed wedge shape, and the two serranid species *Cephalopholis hemistiktos* and *Epinephelus stoliczkae* have an elongated wedge shape. The two species of the genera *Cynoglossus* and *Scarus* have different sub-shape

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Table 4. Shape of urohyal bone as shown in the lateral view.

Shape	Species	Shape	Species
Aeroplane tail	*Acanthopagrus arabicus* (Figure 15)	Rectangular	
		High side rectangular	*Alepes djedaba* (Figure 15)
	Argyrops spinifer (Figure 16)		*Atropus atropus* (Figure 15)
			Parastromatus niger (Figure 15)
	Cheimerius nufar (Figure 16)	Tailed rectangular	*Plectorhinchus schotaf* (Figure 15)
	Diplodus sargus kotschyi (Figure 16)		
Bat wing		Thin tailed rectangular	*Pomadasys furcatus* (Figure 15)
Bat wing proper	*Ephippus orbis* (Figure 17)	Narrow rectangular	*Pomadasys maculatus* (Figure 15)
			Pomadasys stridens (Figure 16)
	Lutjanus fulviflamma (Figure 15)	Rectangular proper	*Planiliza subviridis* (Figure 17)
	Lutjanus lutjanus (Figure 15)		
	Polydactylus sextarius (Figure 16)		*Upeneus sulphureus* (Figure 16)
Elongated bat wing	*Eleutheronema tetradactylum* (Figure 16)	Incomplete rectangular	*Nibea maculata* (Figure 16)
			Otolithes ruber (Figure 16)
Bird wing	*Psettodes erumei* (Figure 17)	C-shape	*Epinephelus stoliczkae* (Figure 14)
			Cephalopholis hemistiktos (Figure 14)
		Sail	*Nemipterus japonicus* (Figure 16)
	Anodontostoma chacunda (Figure 14)		
	Nematalosa nasus (Figure 14)		
	Ilisha megaloptera (Figure 14)	Spatula	*Chirocentrus nudus* (Figure 14)
	Ilisha melanostoma (Figure 14)	Swift tail	*Scarus ghobban* (Figure 17)
Clever	*Cynoglossus arel* (Figure 18)	Triangular	
	Cynoglossus bilineatus (Figure 18)		
Comet	*Sphyraena putnamae* (Figure 17)	Triangular proper	*Carangoides malabaricus* (Figure 15)
			Carangoides armatus (Figure 15)
			Pampus argenteus (Figure 17)
			Siganus sutor (Figure 14)
Slim elevated	*Sillago sihama* (Figure 14)	Rounded triangular	*Scomberoides commersonianus* (Figure 15)
		Narrow triangular	*Scomberomorus guttatus* (Figure 17)
			Rastrelliger kanagurta (Figure 17)
		Broad triangular	*Secutor insidiator* (Figure 15)
Elongated balloon	*Saurida tumbil* (Figure 14)	Umbrella	*Drepane punctata* (Figure 17)
Hen	*Gerres filamentosus* (Figure 15)		
Hook	*Pseudorhombus elevatus* (Figure 17)	Walking stick	*Tylosurus crocodilus* (Figure 14)
	Brachirus orientalis (Figure 18)		
Elongated			
Proper elongated	*Lethrinus lentjan* (Figure 15)		
Double-tailed elongated	*Platycephalus indicus* (Figure 14)		

types within the main shape division of oblong-elliptical and shaft respectively. Similarly, the two polynemid species *Eleutheronema tetradactylum* and *Polydactylus sextarius*, have non-tailed and tailed-ovate shape respectively. It is unlikely that the different shape groups obtained in the present study have a taxonomic basis as they comprise species belonging to different families; however, feeding and mouth opening mechanisms may have related origins (Chollet-Villalpando *et al.*, 2014).

The lateral profile of the urohyal succeeded in placing the fish species in different shapes (Table 4, Figures 14–18). Some of these shapes contain solely species belonging to the same family as in the case of the four sparid species or to the same genus as seen in the two members of the genus *Cynoglossus*. These shapes can be considered a good taxonomic criterion to identify sparid and cynoglossid fish species. To accept this character as a taxonomic criterion for the families of these species, the morphology of more sparid and cynoglossid species is required. The lutjanid species fall in a sub-shape shared by other species, and the two species of sciaenids are present in a sub-shape not shared by other species (Table 4).

The lateral side of the urohyal shows more main shapes with several sub-shapes than the dorsal and ventral sides (Tables 2–4, Figures 14–18). This indicates that the lateral profile of the urohyal might be the best tool to identify fish species.

All the sides of the urohyal are designed to receive attachments for muscles serving different functions, but mainly for those assisting in the mouth opening mechanism (Kusaka, 1974; Arratia & Schultze, 1990). Therefore, the urohyal exhibits several morphological features that vary with the anatomy of the skull, mouth and the mechanism of feeding. Such morphological variations in the shape of the sides of the urohyal are noticed in some members of the family Gerreidae (Chollet-Villalpando *et al.*, 2014), and they are observed in the urohyal of the fish species considered in the present study and might be related to the anatomy of the skull, mouth and the mechanism of feeding.

Kusaka (1974) suggested that the length of the urohyal relative to head length is between 20–50% for the fish species used in his study and there is a slight increase of 10% for some species. The results obtained in this study do not support the suggestion of Kusaka (1974) and show a range of 30.7–99.6%. As the study of Kusaka (1974) was preliminary, there is a possibility that some of the species examined in the present study that showed relative urohyal length

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Table 5. Features of the urohyal bone with their shapes and variations.

Feature	Shape	Variations
Basibranchial attachment	Short (29 species); long (11 species); not developed (11 species)	Posterior end: rounded (42 species); triangular (*Cynoglossus arel*); pointed (*Pomadasys stridens*); curved down (*Scarus ghobban*); short (three species); covered with bony growth (three species)
Condyle	Short (28 species); long (seven species); undeveloped (16 species); undefined shape (*Platycephalus indicus*) (Linnaeus, 1758)	Anterior end straight (*Polydactylus sextarius*); posterior end: straight (four species); extends to the posterior edge of the bone (*Plectorhinchus schotaf*)
Dorsal edge	Broad (26 species); narrow (25 species); undeveloped (six species)	Uneven (*Ilisha megaloptera*); smooth (25 species); curved (five species); elevated (17 species); straight anterior end (*Saurida tumbil*); posterior end: wide (*Parastromateus niger*); raised (five species)
Dorsal plate	Short (eight species); long (32 species); undeveloped (11 species)	Constricted at the middle (*Carangoides malabaricus*); posterior end: extends to the posterior edge of the bone (18 species); extends only to the middle of the bone (two species); elevated (*Acanthopagrus arabicus*)
Hypohyal attachment	Short (29 species); long (four species); undeveloped (18 species)	Posterior end: pointed (two species); flat (*Tylosurus crocodilus*); extended antero-ventrally (*Ilisha melanostoma*)
Lateral plate	Broad (23 species); narrow (16 species); undeveloped (six species)	Posterior end: curved (*Carangoides armatus*); straight (*Saurida tumbil*)
Postero-dorsal edge	Broad (47 species); narrow (two species)	Posterior end extends to the posterior edge of the bone (*Scomberoides commersonianus*); with uneven surface (*Brachirus orientalis*); undefined shape (two species); elevated (*Nematalosa nasus*); wavy (*Drepane punctata*); posterior end: straight (*Ilisha megaloptera*); rounded (*Ilisha melanostoma*); curved down (*Ephippus orbis*); bifurcated (*Platycephalus indicus*) and hairy (*Sphyraena putnamae*)
Posterior edge	Smooth (25 species); wavy (13 species); undeveloped (three species)	crenulated (*Carangoides armatus*); emarginated (*Polydactylus sextarius*); lunate (four species); with coarse indentations (two species); with fine, irregular indentations (two species); elevated (*Epinephelus stoliczkae*); wavy ventrally (*Pomadasys maculatus*); with notch at the middle (*Eleutheronema tetradactylum*); posterior edge: uneven (*Saurida tumbil*)
Radial band	Narrow (30 species); broad (eight species); undeveloped (21 species)	Posterior end: elevated and extending to the posterior edge of the bone (six species); not reaching the posterior edge of the bone (*Parastromateus niger*)
Ventral extension	Narrow (24 species); broad (17 species); undeveloped (10 species)	With ribs extending through: one rib (*Parastromateus niger*); two ribs (*Plectorhinchus schotaf*); thick rib (two species); ventral extension curved (two species); posterior edge: curved horizontally (three species); extends to the posterior edge of bone (six species)
Ventral plate	Narrow (26 species); broad (23 species); undeveloped (two species), rectangular (one species)	Extending to the posterior edge of the bone (22 species); not extending (five species); Posterior end: tapering (two species); getting thicker posteriorly (*Ilisha melanostoma*); deeply curved (two species); elongated (two species); curved upward (*Cephalopholis hemistiktos*); straight (three species of *Pomadasys*); presence of thick rib (eight species); presence of groove posteriorly (*Ilisha melanostoma*)

values higher than 50–60% are not included in the study of Kusaka (1974). Large urohyal size is usually found in active fish species (Kusaka, 1969a, b, 1974; Kusaka & Thuc, 1972). This criterion is found in the majority of the studied fish species which were active species. The urohyal of *Ilisha megaloptera* and *Ilisha melanostoma* is medium to large, and they are active species, but with their planktonic mode of feeding their urohyal is shown to fall between the medium and large criteria.

The present study shows that the deep bodied fish species, for example, in members of the families Sparidae, Drepanidae, Ephippidae, Haemulidae, Stromateidae and Leiognathidae have a short urohyal, while those with a slender head like members of the families Belonidae, Scombridae and Sphyraenidae have a long urohyal. This result agrees with the suggestion of Kusaka (1974). Moreover, Kusaka (1974) has related the development of the ventral spread of the urohyal to the activity of the fish and ranges from an undeveloped ventral side in the active fish species to well developed in the slow moving species. The urohyal of several species fall in between these two criteria. The present results support this suggestion in having the urohyal of the members of the families Belonidae, Scombridae and Synodontidae with reduced ventral side.

The value of the angles were successfully being used to determine the shapes of fish body structures like the otolith and to identify species accordingly (Chen *et al*., 2011; Annabi *et al*., 2013; Reichenbacher & Reichard, 2014; Teimori *et al*., 2014) and bones (Brainerd & Patek, 1998; Herrell *et al*., 2002). So far, no attempt has been made to use angles between the sides of fish urohyal to establish the characteristic of the urohyal and to separate species accordingly. In the present study, the value of three angles found between the three major sides of the urohyal were measured

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with an aim to evaluate this character as a taxonomic criterion to separate the examined fish species.

The values of angles of the different sides of the urohyal obtained for the fish species examined in the present study coincide with the shape of the urohyal of these species. They can define how the ventral and posterior edges are spread and how they differ in the height of the urohyal. As in other studies that used the values of angles in fish osteology (Brainerd & Patek, 1998; Herrell *et al*., 2002) and as in the morphometry of the fish otolith (Reichenbacher *et al*., 2007; Chen *et al*., 2011; Annabi *et al*., 2013; Reichenbacher & Reichard, 2014; Teimori *et al*., 2014), the angles proved a good support for the shape of the urohyal of the species in the present work.

The shape of the urohyal of the members of the families Clupeidae, Chirocentridae, Belonidae, Serranidae, Carangidae, Leiognathidae, Lutjanidae, Haemulidae, Nemipteridae, Polynemidae, Drepanidae, Siganidae, Sphyraenidae and Stromateidae in the present work looks similar to that shown by Kusaka (1974), with slight differences which are considered related to the species characteristics. These differences are: the shape of the urohyal of *Alepes djedaba* is slightly different from the shape of the other members of this genus; the postero-dorsal edge is elongated and high; the urohyal of *Secutor insidiator* is curved and straight; and the dorsal surface of the urohyal of *Pampus argenteus* is smooth and no broad spine is present.

Rao (1977) described the osteology of *Saurida tumbil* and illustrated the urohyal which looks similar to that obtained in the present study. The exception is slightly notched postero-dorsal edge in the present study *vs* broadly notched in *S. tumbil*, and the ventral plate is narrow in the specimen of the present study *vs* wide in the specimen of *S. tumbil*. Kusaka (1974) illustrated the urohyal of two species of the genus *Saurida* i.e. *S. tumbil* and *S. undosquamis*. Although these two species belong to the same genus, the shape of their urohyal looks completely different, and the shape given to *S. tumbil* is different from that obtained in the present study and from that obtained by Rao (1977). Since the illustrations provided by Kusaka (1974) are only sketches and the study is preliminary in nature, the differences could be due to such reasons.

The urohyal of *Platycephalus indicus* is thin and has not much surface for muscle attachments. This result is also observed by Gosline (1996) who suggested that only few muscles are attached to the urohyal and the majority of muscles are attached to the hypohyal bone.

Kaga (2013) has reviewed the family Sillaginidae and described the urohyal of four species of the genus *Sillago*. The urohyal of *S. sihama* shown by Kaga (2013) is characterized in having low dorsal extension, short basibranchial attachment and straight hypohyal attachment. On the contrary, the urohyal of our specimen showed high dorsal extension, long basibranchial attachment and downward directed hypohyal attachment.

In general, the shape of the urohyal of *Sillago sihama* obtained in the present study looks similar to that of the other members of the genus *Sillago* reported by Kusaka (1974). However, there are some differences that characterize each species. In the present work, the urohyal of *S. sihama* differs from that of *S. japonica* in the length of the elongated basibranchial attachments (long in *S. sihama vs* short in *S. japonica*), dorsal and ventral edges (straight in *S. sihama vs* curved in *S. japonica*), and the posterior edge (broad in *S. sihama vs* broadly pointed in *S. japonica*).

Chollet-Villalpando *et al.* (2014) described the urohyal of six species of the family Gerreidae belonging to four genera. The shape of the urohyal of *Gerres filamentosus* obtained in the present study falls within the shape ranges of the species described by Chollet-Villalpando *et al.* (2014), but it conserves some characters that separate it from the remaining species of the family Gerreidae. Such similarities of the urohyal obtained for *G. filamentosus* are also seen when compared with the shapes shown by Kusaka (1969a, b, 1974) for other gerreid fish species.

Kusaka (1969a, b, 1974) studied and illustrated the urohyal of 16 species of the family Sparidae belonging to nine genera, Bianchi (1984) examined four species belonging to one genus, and the present study gives descriptions for the urohyal of four species belonging to four genera. It is possible to note that the shape of the urohyal of all these sparid species looks similar, and there are only slight differences between them. Such variations belong to the species characteristics which separate these species. Also the close resemblance in the urohyal in these sparid species reflects the success of the shape of the urohyal to recognize fish species.

The general shape of *Nibea maculata* obtained in the present study matches that of *N. mitsukurii* described by Kusaka (1974) except for some differences like the anterior side of the ventral plate narrow and indented and the basibranchial attachment directed upward. As both are members of the family Sciaenidae, the urohyal of *N. maculata* and *Otolithes ruber* look alike and also look similar to those sciaenid species described by Sasaki (1989).

The shape of the urohyal of the two *Upeneus* species described by Kusaka (1974) and that described by Kim (2002) match very well that of *Upeneus sulphureus* given in the present study. The species of the genus *Upeneus* shared with species of other mullid genera the shape of urohyal as shown by Kusaka (1969a, b, 1974) and Kim (2002).

The shape of the urohyal of *Mugil cephalus* L., 1775 given by Kusaka (1974), the shape of those six species of the four mugilid genera described by Antović & Simonović (2006) and the *Mugil* species described by Keivany (2014) look very close to that of *Planiliza subviridis* obtained in the present study. Such similarity indicates that the shape of the urohyal in the members of the family Mugilidae is conservative.

Jahromi *et al.* (2010) studied two species of the genus *Scarus* i.e. *S. persicus* and *S. ghobban*. In the present study, we used the same specimen of urohyal that Jahromi *et al.* (2010) have used. The idea behind using the same specimen is to add more information about the urohyal of this species such as morphometry, measuring angles and giving detailed description of the urohyal that are not provided by Jahromi *et al.* (2010). It was not possible to include the urohyal of *S. persicus* as the bone that was supposed to be a urohyal after close examination was revealed to be an epicleithrum.

Bellwood (1994) described the urohyal of 10 scarid species with one species belonging to the genus *Scarus*. The anterior part of the urohyal of these 10 species showed wide variation, while the posterior end appeared to be more conservative in its shape, and all the 10 species showed a similar general appearance of the posterior end, including *S. ghobban* described in the present work.

Kusaka (1969a, b, 1974) gave descriptions and illustrations of the urohyal of the members of the genera *Rastrelliger* and

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Scomberomorus. Kohno (1984) studied the morphology of one scombrid species of the genus *Gasterochisma*. The shape of the urohyal of these three genera is closely related to that of the two scombrid species obtained in the present work.

From the five flatfish species dealt with in the present work, the urohyal of *Brachirus orientalis* and *Pseudorhombus elevatus* is curved (reversed L-shaped in *Brachirus orientalis* and reversed c-shaped in *P. elevatus*). Such curved shapes are also reported for the 13 flatfish species described by Kusaka (1974), for *Tephrinectes sinensis* and for other flatfish species like *Citharichthys spilopterus* and *Hippoglossina macrops*. The shape of the urohyal of the two cynoglossid species given in the present work looks completely different from that of other flatfish species. Such differences signify the possibility of using the shape of the urohyal in separating very close related species of flatfish.

The results obtained in the present study showed clearly the usefulness of the morphology of the urohyal to separate the fish species. Such findings can serve fish taxonomists as they add a new distinguishing criteria, fish biologists as they help to identify fish in the food of another fish and in aquatic birds and mammals and archaeologists in giving an idea about the feeding habits of humans in ancient gathering centres and their social life. The results of this study will shed light on the possibility of using other osteological parts of the fish body in similar comparison. Also, the present study has a comprehensive comparison of urohyal anatomy for a wide range of fish groups in one place, a coverage that researchers in several fields can be interested in.

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