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Research Article

Taxonomic insights into groupers (Perciformes: Epinephelidae) of the Persian Gulf and Oman Sea: A combined traditional and geometric morphometric approach

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Abstract

Taxonomic identification of commercially important but relatively understudied groupers (Epinephelidae) inhabiting various habitats has traditionally relied on morphological characteristics, particularly meristic counts and morphometric measurements. However, these approaches are often constrained by high morphological similarity among closely related species and the presence of cryptic diversity within the family. To evaluate both traditional and geometric morphometric approaches to the taxonomy of epinephelids, 99 specimens from eight species in the Persian Gulf and the Oman Sea were analyzed for shape variation and taxonomic characters. Traditional morphometric and meristic analyses revealed that traits including dorsal-fin length, prepelvic length, gill-raker count, and tubed lateral-line scale count were identified as the most discriminatory characters. These traits yielded high classification success rates of 92.1% for meristic analyses and 88.5% for morphometric analyses. Geometric morphometric analyses further distinguished taxa based on shape variation in the head, the position of the dorsal fin and the dimensions of the pectoral and caudal fins, and body depth, identifying subtle but consistent interspecific differences. The findings demonstrated that shape variation exceeded size variation and effectively differentiated closely related species. The classification success of the geometric morphometric data derived from the 15 landmarks was also established. Morphological clustering is largely consistent with habitat types and divides species into soft-bottom and hard-bottom groups, and it is largely consistent with previous molecular phylogenies. These findings demonstrate that the combination of meristic, geometric morphometric and ecological data provides a powerful framework for resolving species boundaries in morphologically conservative groupers. In addition, detailed descriptions of eight grouper species are provided to cover their morphological characteristics, geographic distributions, habitats, and a diagnostic identification key.

Introduction

Accurate taxonomic identification is essential for the assessment of fish biodiversity (Traldi *et al.,* 2020; McCord *et al.,* 2021). Recent in-depth morphological studies have led to substantial revisions of fish taxonomy (Chollet-Villalpando *et al.,* 2019; Damadi *et al.,* 2020; Damadi *et al.,* 2024a; Yazdani Moghaddam *et al.,* 2025). Such revisions are essential for reliable documentation of biodiversity and effective conservation strategies, as accurate taxonomy reflects both the evolutionary relationships and ecological role of species (Giangrande, 2003; Freitas *et al.,* 2020; Damadi *et al.,* 2023). These findings illustrate why ongoing biodiversity monitoring is essential for clarifying taxonomic uncertainties, assessing conservation needs and supporting sustainable management, especially as new species discoveries and distributional changes continue to emerge. The Persian Gulf and the Oman Sea are dynamic marine ecosystems characterized by complex oceanographic processes, unique ecological features and distinct physiological adaptations (Coles, 2003; Burt *et al.,* 2011; Maghsoudlou *et al.,* 2019). These semi-enclosed basins exhibit exceptional environmental gradients, ranging from extreme temperature and salinity fluctuations in the Persian Gulf to the more stable conditions of the Oman Sea (Feary *et al.,* 2010; Vaughan *et al.,* 2019). Although the broader Northwest Indian Ocean (NIO) is recognized as a biodiversity hotspot with high endemism and species richness (DiBattista *et al.,* 2017; Torquato *et al.,* 2019; Damadi *et al.,* 2020; Damadi *et al.,* 2026), the Persian Gulf itself displays considerably lower levels of both species richness and endemism relative to most other marginal seas of the Indian Ocean. The unique biogeographical location and ecological heterogeneity make the region an ideal model system for studying the connectivity, evolutionary adaptation and the ecological effects of habitat fragmentation of marine populations (DiBattista *et al.,* 2017; Torquato *et al.,* 2019). The Epinephelidae Bleeker, 1874 are commonly known as groupers and are mainly found in shallow water habitats such as coral reefs, estuaries, mangroves and seagrasses in the tropical and subtropical areas of the Indo–West Pacific (IWP). This family represents a diverse taxonomic group comprising 16 genera and 176 species currently recognized worldwide (Fricke *et al.,* 2025). Within this wide distribution, the Persian Gulf and Oman Sea region harbors part of this diversity with the documented occurrence of five genera (*Aethaloperca, Chelidoperca, Dermatolepis*, *Cephalopholis* and *Epinephelus*) and 36 species (Eagderi *et al.,* 2026). However, molecular studies have challenged the taxonomic validity of some of these genera, revealing that *Aethaloperca* nests within *Cephalopholis* and that the traditionally defined *Epinephelus* is polyphyletic (Ma *et al.,* 2016; Ma and Craig, 2018). This represents about 3.4% of the 1,047 species considered here (36 species), with these species concentrated in these semi-enclosed marine ecosystems (Eagderi *et al.,* 2026). Although Epinephelus is one of the most extensively studied genera within Epinephelidae, it still suffers from persistent taxonomic ambiguities (Craig and Hastings, 2007;

Zhuang *et al.,* 2013; Ma *et al.,* 2016). The genus has a broad distributional range, extending from the tropics and subtropics globally . These commercially vital fish often have a remarkably biogeographical distribution, with the ranges of related species overlapping considerably (Fricke *et al.,* 2025). Their evolutionary biology has long attracted the interest of scientists, not only because of their extraordinary phenotypic and ecological diversity, but also because of their propensity for rapid sympatric speciation a phenomenon that has made them a compelling model system for investigating the drivers of marine diversification (Hodge and Bellwood, 2016). Taxonomic delineation of *Epinephelus* groupers has historically relied heavily on two primary diagnostic characters: colour pattern and geographical distribution (Craig *et al.,* 2001). However, this traditional approach has proven problematic due to several biological complexities: First, the genus exhibits morphological conservatism, with many species showing minimal morphological differentiation. Furthermore, both pigmentation and morphometric features exhibit significant ontogenetic variation and environmental lability, making these traits unreliable for consistent species identification across different life stages (Condini *et al.,* 2014; Renán *et al.,* 2015).

Previous molecular studies have identified multiple cryptic species complexes in groupers from the Persian Gulf and the Sea of Oman (Tavakoli-Kolour *et al.,* 2022; Damadi *et al.,* 2026).

These findings highlight the limitations of traditional morphological identification methods due to overlapping meristic counts, ontogenetic phenotypic plasticity, and habitat-driven convergent evolution, all of which necessitate taxonomic revisions and have critical implications for biodiversity assessments and conservation management in this ecologically unique marine basin. However, taxonomic interpretations in this region must also consider the influence of environmental stressors. The Persian Gulf and Oman Sea are not only biodiversity hotspots but are increasingly subjected to anthropogenic pollutants, including heavy metals (e.g., arsenic, cadmium, chromium, lead, and copper) and pesticides (Orun *et al.,* 2008; Ateş *et al.,* 2008; Gulhan *et al.,* 2012; Talas *et al.,* 2014; Caglar *et al.,* 2019). Furthermore, maritime transport and port activities add additional ecological pressure on these aquatic ecosystems (Mesut, 2021; Selamoglu, 2021). Previous ecotoxicological studies have demonstrated that such contaminants can induce oxidative stress, disrupt hematological and biochemical parameters, and alter physiological functions in fish (Orun *et al.,* 2008). These physiological disruptions can, in turn, influence phenotypic plasticity and potentially obscure or confound the morphological characters traditionally used for species identification. Therefore, integrating morphological assessments with an awareness of environmental quality is essential for accurate taxonomic delineation and sustainable biodiversity management. Therefore, an integrated morphological approach combining geometric morphometrics with univariate and multivariate statistical analyses can help address these taxonomic challenges by (a) identifying diagnostic morphological

traits and thresholds among eight grouper species, while considering their biological characteristics and geographic distributions, and (b) determining whether observed morphological variation reflects taxonomic differentiation among species.

Materials and methods

Study area and collection of specimens

Sampling was carried out taking into account the geographical diversity, including the type of substrate and geographic distances, at four stations in the Oman Sea (Beris, Tis, Pozm, and Jask) and four stations in the Persian Gulf (Qeshm, Kangan, Bushehr, and Hendijan) (Fig. 1).

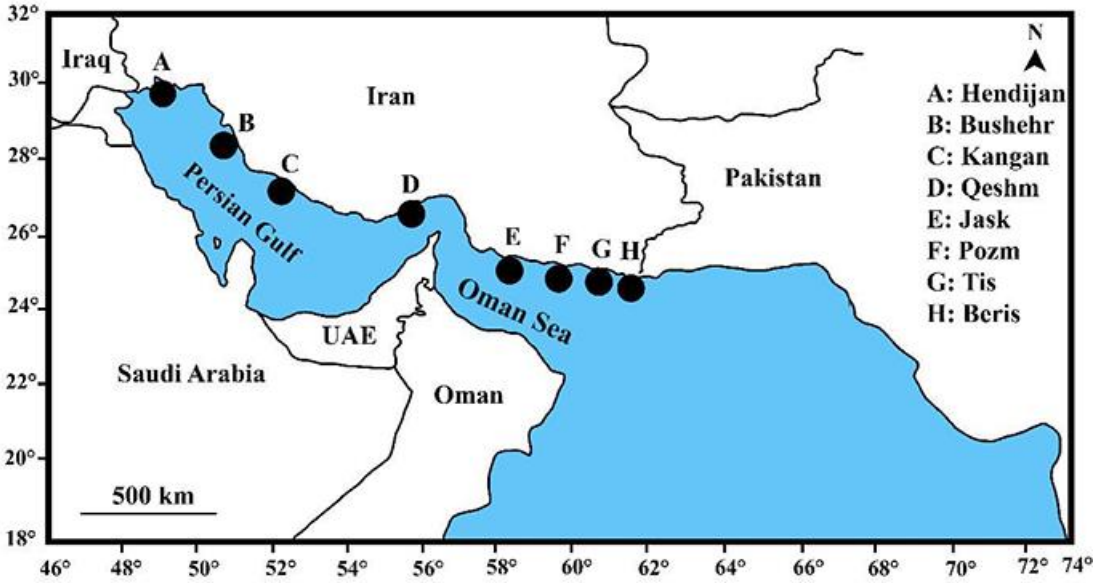


Figure 1: Sampling stations for grouper fishes in the Persian Gulf and the Oman Sea (Damadi *et al*., 2021).

Collection data for each species are listed in Table 1. The stations were selected in locations with different substrates. A total of 99 specimens of this family were collected between August 2019 and October 2021 with the help of local fishermen using nets, hooks, and spears. The specimens were identified using validated taxonomic descriptions and keys (Randall, 1995; Heemstra *et al.,* 2022). The collected samples were examined for diagnostic morphological characteristics, including coloration patterns and body shape. The specimens were photographed from the left side under fresh conditions after they were brought to the laboratory. After identification, the specimens were placed in a freezer at −4°C for storage. The voucher specimens are deposited in the Zoological Museum of Ferdowsi University of Mashhad (ZMFUM), Iran.

Morphological analysis

The study evaluated 16 morphometric measurements and six meristic counts. For brevity, the following abbreviations will be used for specific characters: Counts: NDF=dorsal-fin rays, NAF=anal-fin rays, NPF=pectoral-fin rays, NLLTS=lateral-line scales, Gill rakers=NGR (NGRU-NGRL); Measurements: BD=body depth, HL=head length, OD=orbit diameter,

SNL=snout length, UJL=upper-jaw length, CPD=caudal-peduncle depth, CPL=caudal-peduncle length, PAL=preanal length, PPL=prepelvic length, DFB=length of dorsal-fin base, DFL=dorsal-fin length, AFB=length of anal-fin base, PFL=length of pelvic fin, LDFR=Longest dorsal-fin ray, and LAFR=Longest anal-fin ray.

Table 1: Collection data of grouper specimens from the Persian Gulf and the Oman Sea.

Species	Location	Museum number	Date	Geographic coordinates
Cephalopholis hemistiktos (n=5)	Oman Sea: Tis	ZMFUM-EP-111	10.09.2020	25°17'N; 60°35'E
	Persian Gulf: Qeshm	ZMFUM-EP-32	01.09.2020	26°28'N; 55°22'E
	Oman Sea: Beris	ZMFUM-EP-140	05.08.2020	25°07'N; 61°10'E
	Persian Gulf: Bushehr	ZMFUM-EP-141	08.11.2020	28°56'N; 50°47'E
Epinephelus areolatus (n=15)	Oman Sea: Pozm	ZMFUM-EP-3	07.12.2020	25°41'N; 57°43'E
	Persian Gulf: Qeshm	ZMFUM-EP-121-124	01.09.2020	26°28'N; 55°22'E
	Oman Sea: Beris	ZMFUM-EP-127-128	05.08.2020	25°07'N; 61°10'E
	Persian Gulf: Bushehr	ZMFUM-EP-125-126	08.11.2020	28°56'N; 50°47'E
	Oman Sea: Tis	ZMFUM-EP-3,5	10.09.2020	25°17'N; 60°35'E
	Persian Gulf: Kangan	ZMFUM-EP-192-197	13.04.2021	27°49'N; 52°20'E
	Oman Sea: Pozm	ZMFUM-EP-114, 118	12.10.2020	25°41'N; 57°43E
E. bleekeri (n=12)	Persian Gulf: Qeshm	ZMFUM-EP-13 (n=6)	01.09.2020	26°28'N; 55°22'E
	Oman Sea: Beris	ZMFUM-EP-155-156 (n=2)	05.08.2020	25°07'N; 61°10'E
	Oman Sea: Pozm	ZMFUM-EP-157-158	12.10.2020	25°41'N; 57°43E
E. coioides (n=12)	Oman Sea: Tis	ZMFUM-EP-144 (n=4)	10.09.2020	25°17'N; 60°35'E
	Persian Gulf: Kangan	ZMFUM-EP-145-146	13.04.2021	27°49'N; 52°20'E
	Persian Gulf: Hendijan	ZMFUM-EP-147 (n=4)	05.06.2021	29°58'N; 49°13'E
E. diacanthus (n=12)	Oman Sea: Pozm	ZMFUM-EP-104	07.12.2020	25°41'N; 57°43'E
	Persian Gulf: Qeshm	ZMFUM-EP-16 (n=2)	01.09.2020	26°28'N; 55°22'E
	Oman Sea: Beris	ZMFUM-EP-159-160	05.08.2020	25°07'N; 61°10'E
	Persian Gulf: Bushehr	ZMFUM-EP-162 (n=3)	08.11.2020	28°56'N; 50°47'E
	Oman Sea: Tis	ZMFUM-EP-163	10.09.2020	25°17'N; 60°35'E
	Persian Gulf: Kangan	ZMFUM-EP-164	13.04.2021	27°49'N; 52°20'E
	Oman Sea: Pozm	ZMFUM-EP-165-166	12.10.2020	25°41'N; 57°43E
E. latifasciatus (n=11)	Persian Gulf: Qeshm	ZMFUM-EP-19 (n=4)	01.09.2020	26°28'N; 55°22'E
	Oman Sea: Beris	ZMFUM-EP-167-168 (n=4)	05.08.2020	25°07'N; 61°10'E
	Oman Sea: Pozm	ZMFUM-EP-169-170	07.12.2020	25°41'N; 57°43'E
E. polylepis (n=10)	Persian Gulf: Qeshm	ZMFUM-EP-135 (n=2)	01.09.2020	26°28'N; 55°22'E
	Oman Sea: Beris	ZMFUM-EP-109 (n=5) -110	05.08.2020	25°07'N; 61°10'E
	Persian Gulf: Kangan	ZMFUM-EP-171-172	13.04.2021	27°49'N; 52°20'E
E. stoliczkae (n=22)	Oman Sea: Pozm	ZMFUM-EP-105-107	07.12.2020	25°41'N; 57°43'E
	Persian Gulf: Qeshm	ZMFUM-EP-121-124	01.09.2020	26°28'N; 55°22'E
	Oman Sea: Tis	ZMFUM-EP-102-103	05.08.2020	25°07'N; 61°10'E
	Persian Gulf: Bushehr	ZMFUM-EP-6	08.11.2020	28°56'N; 50°47'E
	Oman Sea: Tis	ZMFUM-EP-115-117	10.09.2020	25°17'N; 60°35'E
	Persian Gulf: Kangan	ZMFUM-EP-142-143	13.04.2021	27°49'N; 52°20'E
	Oman Sea: Pozm	ZMFUM-EP-113,145,134,14	12.10.2020	25°41'N; 57°43E
	Persian Gulf: Hendijan	ZMFUM-EP-173-180	05.06.2021	29°58'N; 49°13'E

Since morphometric variations could result from size differences, all measurements were size-corrected (traits divided by standard length) prior to analysis (Johnson and Worthington Wilmer, 2019). Data normality and homogeneity of variance were verified using Shapiro-Wilk and Levene's tests (p=0.05), respectively. To confirm the adequacy of the sample size, a power analysis was conducted to evaluate

the effect size and confidence intervals. Sex determination was based on the gonads, following the methodology of Peng *et al*. (2020). Multivariate analysis of variance (MANOVA) assessed sexual dimorphism, and sampling location effects on morphometric traits. Confidence intervals, means, and standard deviations were calculated, with significance set at $p<0.05$. Analyses were performed in PAST v.4.03 (Hammer, 2020) and SPSS v.23 (SPSS Inc., Chicago, IL). One-way ANOVA evaluated interspecific variations, followed by Tukey's HSD post-hoc tests (when variances were equal) for pairwise comparisons (P=0.05). Normalized data were analyzed using multivariate methods including group difference analysis, the principal component analysis (PCA), and discriminant function analysis (DFA) for trait discrimination, with group separation assessed by Wilks' Lambda statistic (Cruz-Castillo *et al.,* 1994). Cross-validation (holdout leave-one-out) was performed to calculate the percentage of correct classification for the species groups.

Geometric morphometrics

Left-lateral images were captured under standardized conditions (Canon PowerShot SX150 IS; fixed lens/focus/distance/magnification/lighting) . Fifteen homologous landmarks (Fig. 2) (Damadi *et al.,* 2024a) were digitized using tpsDig v.2.16, aligned via Generalized Procrustes Analysis (Rohlf, 1999), and analyzed using covariance matrices. Canonical variance analysis (CVA) (MorphoJ v.1.04a; Klingenberg, 2011) evaluated group separation based on within-/between-group covariance, unlike PCA.

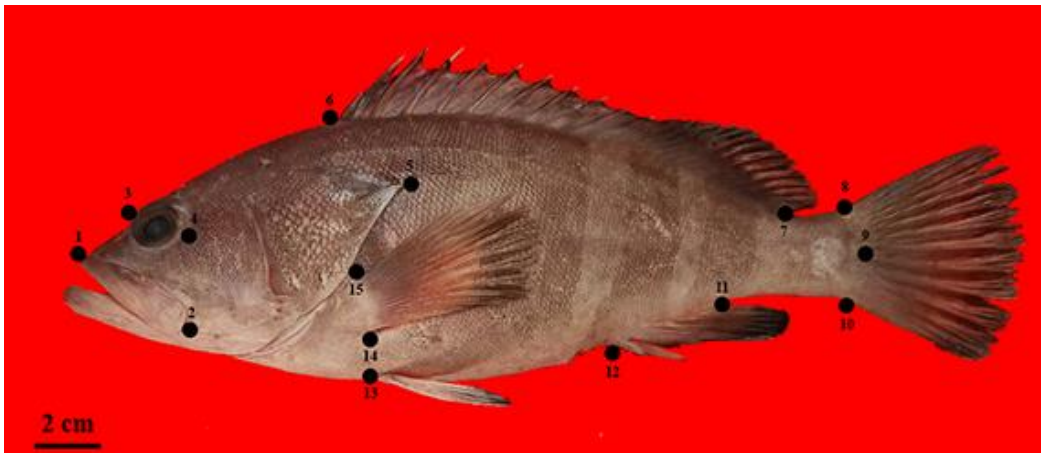


Figure 2: The locations of morphometric landmarks are illustrated on the left lateral view of Epinephelus diacanthus. The digitized landmarks are as follows: (1) anterior tip of the premaxilla, (2) posteroventral tip of the maxilla, (3) anterior edge of the eye, (4) posterior edge of the eye, (5) anterior extent of the opercular opening, (6) dorsal extent of the pectoral fin base, (7) ventral extent of the pectoral fin base, (8) anterior extent of the pelvic fins, (9) base of the anteriormost dorsal spine in the first dorsal fin, (10) base of the posteriormost dorsal ray of the second dorsal fin, (11) dorsal tip of the caudal fin hypurals, (12) center of the caudal fin hypurals, (13) ventral tip of the caudal fin hypurals, (14) base of the posteriormost anal fin ray, and (15) base of the first anal spine.

Results

Based on morphological analyses, including traditional morphometrics and geometric morphometrics, two genera and eight species of Epinephelidae were identified in the Persian Gulf and the Oman Sea. Diagnostic characteristics, distribution, and habitat information for each species in these regions are provided (Figs. 1 to 14; Table 2).

Table 2: Descriptive statistics for morphometric and meristic traits of grouper species. Morphometric data are presented as a ratio of standard length (%SL).

Characters	Species	N	Mean± Std.Deviation	Lower-Upper	Mean Square	F	*P*-value
	C. hemistiktos	5	35.9 ± 2.87	32.3-39.5			
	E. areolatus	15	29.8 ± 2.79	28.3-34.4			
	E. bleekeri	12	29.5 ± 1.64	27.8-31.2			
	E. coioides	12	28.3 ± 1.62	26.8-29.8			
BD	*E. diacanthus*	12	32.3 ± 2.62	30.3-34.3			
	E. latifasciatus	11	32.1 ± 2.25	29.8-34.5			
	E. polylepis	10	31.7 ± 1.50	29.8-33.5			
	E. stoliczkae	22	31.2 ± 1.89	30.4-32.1			
	Among Species				33.1	6.631	0.001
	C. hemistiktos	5	38.9 ± 1.76	36.7-41.1			
	E. areolatus	15	37.2 ± 2.30	35.9-38.4			
	E. bleekeri	12	35.3 ± 2.86	32.3-38.3			
	E. coioides	12	35.9 ± 1.73	34.3-37.5			
HL	*E. diacanthus*	12	41.4 ± 1.48	40.3-42.5			
	E. latifasciatus	11	38.2 ± 1.05	37.1-39.3			
	E. polylepis	10	36.3 ± 2.23	33.5-39.0			
	E. stoliczkae	22	38.8 ± 2.29	37.8-39.8			
	Among Species				31.5	7.056	0.001
	C. hemistiktos	5	8.3 ± 0.68	7.4-9.1			
	E. areolatus	15	6.9 ± 0.79	6.4-7.3			
	E. bleekeri	12	7.6 ± 0.66	6.9-8.3			
	E. coioides	12	6.7 ± 0.37	6.4-7.1			
SNL	*E. diacanthus*	12	6.6 ± 0.94	5.9-7.3			
	E. latifasciatus	11	7.0 ± 0.45	6.5-7.5			
	E. polylepis	10	7.5 ± 0.59	6.8-8.3			
	E. stoliczkae	22	6.4 ± 0.84	6.0-6.8			
	Among Species				3.0	5.350	0.001
	C. hemistiktos	5	4.7 ± 0.85	3.7-5.8			
	E. areolatus	15	6.8 ± 1.36	6.1-7.6			
	E. bleekeri	12	5.6 ± 0.88	4.7-6.5			
OD	*E. coioides*	12	5.6 ± 1.34	4.4-6.8			
	E. diacanthus	12	7.4 ± 0.97	6.6-8.1			
	E. latifasciatus	11	5.7 ± 0.59	5.1-6.4			
	E. polylepis	10	5.1 ± 0.73	4.1-6.0			
	E. stoliczkae	22	6.6 ± 1.14	6.0-7.1			
	Among Species				6.3	5.127	0.001
	C. hemistiktos	5	15.2 ± 1.65	13.1-17.2			
	E. areolatus	15	15.0 ± 1.77	14.1-16.0			
	E. bleekeri	12	14.6 ± 1.61	12.9-16.3			
	E. coioides	12	14.9 ± 1.66	13.4-16.4			
	E. diacanthus	12	14.4 ± 1.43	13.3-15.5			
UJL	*E. latifasciatus*	11	13.2 ± 1.24	11.8-14.5			
	E. polylepis	10	15.3 ± 2.11	12.7-17.9			
	E. stoliczkae	22	16.8 ± 1.62	16.0-17.5			
	Among Species				12.4	4.601	0.001

Table 2 (continued):

Characters	Species	N	Mean± Std.Deviation	Lower-Upper	Mean Square	F	*P*-value
CPD	*C. hemistiktos*	5	14.2 ± 1.03	12.9-15.5			
	E. areolatus	15	10.1 ± 0.69	9.8-10.5			
	E. bleekeri	12	10.5 ± 0.63	9.8-11.1			
	E. coioides	12	10.3 ± 0.63	9.7-10.9			
	E. diacanthus	12	9.1 ± 0.65	8.6-9.6			
	E. latifasciatus	11	10.2 ± 0.43	9.7-10.6			
	E. polylepis	10	9.6 ± 0.66	8.7-10.4			
	E. stoliczkae	22	10.8 ± 0.54	10.6-11.1			
	Among Species				13.7	33.524	0.001
CPL	*C. hemistiktos*	5	14.7 ± 1.69	12.6-16.8			
	E. areolatus	15	18.3 ± 2.02	17.2-19.5			
	E. bleekeri	12	19.5 ± 1.15	18.2-20.7			
	E. coioides	12	20.4 ± 0.71	19.8-21.1			
	E. diacanthus	12	19.1 ± 1.78	17.7-20.4			
	E. latifasciatus	11	21.2 ± 0.83	20.3-22.1			
	E. polylepis	10	20.0 ± 2.00	17.6-22.5			
	E. stoliczkae	22	17.7 ± 2.16	16.8-18.7			
	Among Species				25.0	7.556	0.001
PAL	*C. hemistiktos*	5	6.5 ± 0.40	6.0-7.0			
	E. areolatus	15	6.4 ± 0.29	6.2-6.6			
	E. bleekeri	12	6.2 ± 0.34	5.9-6.6			
	E. coioides	12	6.4 ± 0.11	6.3-6.5			
	E. diacanthus	12	6.5 ± 0.28	6.3-6.7			
	E. latifasciatus	11	6.3 ± 0.19	6.1-6.5			
	E. polylepis	10	6.6 ± 0.15	6.4-6.7			
	E. stoliczkae	22	6.4 ± 0.28	6.3-6.5			
	Among Species				0.1	0.970	0.460
PPL	*C. hemistiktos*	5	36.6 ± 2.17	33.9-39.3			
	E. areolatus	15	36.8 ± 2.77	35.2-38.3			
	E. bleekeri	12	35.9 ± 2.78	33.0-38.8			
	E. coioides	12	33.4 ± 1.59	31.9-34.8			
	E. diacanthus	12	36.8 ± 2.07	35.2-38.4			
	E. latifasciatus	11	29.3 ± 2.89	26.3-32.4			
	E. polylepis	10	34.9 ± 2.70	31.5-38.2			
	E. stoliczkae	22	34.7 ± 2.42	33.6-35.7			
	Among Species				43.7	7.185	0.001
DFB	*C. hemistiktos*	5	46.2 ± 0.56	45.5-46.9			
	E. areolatus	15	51.9 ± 2.09	50.7-53.0			
	E. bleekeri	12	53.1 ± 1.58	51.4-54.7			
	E. coioides	12	50.07 ± 1.30	49.5-51.9			
	E. diacanthus	12	52.7 ± 1.69	51.4-54.0			
	E. latifasciatus	11	49.5 ± 1.40	48.0-51.0			
	E. polylepis	10	51.7 ± 2.20	48.9-54.4			
	E. stoliczkae	22	55.2 ± 3.27	53.7-56.6			
	Among Species				62.9	11.642	0.001

Table 2 (continued):

Characters	Species	N	Mean± Std.Deviation	Lower-Upper	Mean Square	F	*P*-value
DFL	*C. hemistiktos*	5	16.1 ± 1.55	14.2-18.0			
	E. areolatus	15	16.0 ± 1.99	14.9-17.1			
	E. bleekeri	12	15.5 ± 1.89	13.5-17.4			
	E. coioides	12	14.0 ± 1.46	12.7-15.4			
	E. diacanthus	12	15.0 ± 1.10	14.2-15.8			
	E. latifasciatus	11	14.1 ± 1.65	12.4-15.8			
	E. polylepis	10	14.3 ± 1.27	12.7-15.9			
	E. stoliczkae	22	14.3 ± 2.64	13.1-15.5			
	Among Species				6.7	1.659	0.134
AFB	*C. hemistiktos*	5	16.9 ± 0.84	1.59-18.0			
	E. areolatus	15	14.1 ± 1.85	13.1-15.1			
	E. bleekeri	12	15.1 ± 3.93	11.0-19.2			
	E. coioides	12	15.6 ± 2.38	13.4-17.8			
	E. diacanthus	12	15.3 ± 1.50	14.1-16.4			
	E. latifasciatus	11	13.5 ± 0.79	12.7-14.3			
	E. polylepis	10	14.5 ± 2.97	10.8-18.2			
	E. stoliczkae	22	15.2 ± 2.88	13.9-16.5			
	Among Species				7.2	1.228	0.300
CFL	*C. hemistiktos*	5	17.1 ± 2.75	13.7-20.5			
	E. areolatus	15	15.3 ± 2.39	13.9-16.2			
	E. bleekeri	12	17.8 ± 2.16	15.6-20.1			
	E. coioides	12	16.2 ± 1.30	15.0-17.4			
	E. diacanthus	12	17.5 ± 0.56	17.0-17.9			
	E. latifasciatus	11	15.1 ± 1.93	13.1-17.2			
	E. polylepis	10	14.6 ± 1.37	12.9-16.3			
	E. stoliczkae	22	17.9 ± 1.59	17.2-18.6			
	Among Species				16.5	4.891	0.001
PFL	*C. hemistiktos*	5	24.5 ± 1.49	22.7-26.4			
	E. areolatus	15	21.4 ± 3.46	19.5-23.3			
	E. bleekeri	12	20.3 ± 1.50	18.8-21.9			
	E. coioides	12	20.8 ± 2.42	18.5-23.0			
	E. diacanthus	12	22.4 ± 1.71	21.1-23.8			
	E. latifasciatus	11	19.4 ± 0.89	18.5-20.4			
	E. polylepis	10	19.1 ± 1.20	17.6-20.6			
	E. stoliczkae	22	22.3 ± 1.83	21.5-23.1			
	Among Species				19.3	3.949	0.001
LDFR	*C. hemistiktos*	5	8.6 ± 0.80	7.6-9.6			
	E. areolatus	15	12.1 ± 1.79	11.1-13.1			
	E. bleekeri	12	10.2 ± 1.21	9.0-11.5			
	E. coioides	12	10.4 ± 0.74	9.7-11.1			
	E. diacanthus	12	11.6 ± 1.05	10.8-12.4			
	E. latifasciatus	11	10.9 ± 1.49	9.3-12.5			
	E. polylepis	10	13.0 ± 1.05	11.7-14.3			
	E. stoliczkae	22	11.5 ± 1.72	10.8-12.3			
	Among Species				11.1	5.158	0.001

Table 2 (continued):

Characters	Species	N	Mean± Std.Deviation	Lower-Upper	Mean Square	F	*P*-value
LAFR	*C. hemistiktos*	5	8.5 ± 1.76	6.3-10.7			
	E. areolatus	15	7.0 ± 2.21	5.8-8.2			
	E. bleekeri	12	7.8 ± 2.00	5.7-9.9			
	E. coioides	12	7.1 ± 1.99	5.2-8.9			
	E. diacanthus	12	7.4 ± 2.28	5.7-9.2			
	E. latifasciatus	11	8.0 ± 1.40	6.5-9.4			
	E. polylepis	10	5.5 ± 0.61	4.8-6.3			
	E. stoliczkae	22	7.2 ± 2.11	6.2-8.0			
	Among Species				4.2	1.048	0.407
NDF	*C. hemistiktos*	5	14 ± 0.45	14-15			
	E. areolatus	15	16 ± 0.72	15-17			
	E. bleekeri	12	17 ± 0.52	16-17			
	E. coioides	12	16 ± 0.38	15-16			
	E. diacanthus	12	17 ± 0.97	15-17			
	E. latifasciatus	11	12 ± 1.21	12-15			
	E. polylepis	10	17 ± 0.00	17-17			
	E. stoliczkae	22	17 ± 0.71	16-18			
	Among Species				17.3	32.396	0.001
NAF	*C. hemistiktos*	5	9 ± 0.45	8-9			
	E. areolatus	15	8 ± 0.6	7-8			
	E. bleekeri	12	8 ± 0.00	8-8			
	E. coioides	12	8 ± 0.00	8-8			
	E. diacanthus	12	8 ± 0.00	8-8			
	E. latifasciatus	11	8 ± 0.00	8-8			
	E. polylepis	10	8 ± 0.00	8-8			
	E. stoliczkae	22	8 ± 0.00	8-8			
	Among Species				0.4	17.376	0.001
NLLTS	*C. hemistiktos*	5	48 ± 1.14	47-50			
	E. areolatus	15	51 ± 0.64	50-52			
	E. bleekeri	12	51 ± 0.75	50-52			
	E. coioides	12	56 ± 2.21	52-58			
	E. diacanthus	12	55 ± 2.00	53-59			
	E. latifasciatus	11	61 ± 1.51	58-61			
	E. polylepis	10	67 ± 1.82	66-70			
	E. stoliczkae	22	51 ± 0.80	50-52			
	Among Species				244.5	144.966	0.000
NPF	*C. hemistiktos*	5	16 ± 0.39	16-17			
	E. areolatus	15	17 ± 0.36	17-18			
	E. bleekeri	12	18 ± 0.61	18-19			
	E. coioides	12	19 ± 0.52	19-20			
	E. diacanthus	12	19 ± 0.51	18-20			
	E. latifasciatus	11	8 ± 0.39	18-19			
	E. polylepis	10	9 ± 0.00	18-18			
	E. stoliczkae	22	7 ± 0.73	17-18			
	Among Species				8.1	25.863	0.000

Table 2 (continued):

Characters	Species	N	Mean± Std.Deviation	Lower-Upper	Mean Square	F	*P*-value
NGRU	*C. hemistiktos*	5	13 ± 0.55	6-7			
	E. areolatus	15	15 ± 0.51	8-9			
	E. bleekeri	12	10 ± 0.55	9-10			
	E. coioides	12	9 ± 0.69	8-10			
	E. diacanthus	12	8 ± 0.50	8-9			
	E. latifasciatus	11	8 ± 0.82	8-10			
	E. polylepis	10	9 ± 0.55	9-10			
	E. stoliczkae	22	7 ± 0.77	6-8			
	Among Species				9.3	22.034	0.001
NGRL	*C. hemistiktos*	5	13 ± 0.89	13-15			
	E. areolatus	15	15 ± 0.70	14-16			
	E. bleekeri	12	16 ± 0.55	16-17			
	E. coioides	12	15 ± 1.11	14-17			
	E. diacanthus	12	15 ± 1.20	15-18			
	E. latifasciatus	11	17 ± 0.82	15-17			
	E. polylepis	10	17 ± 0.55	17-18			
	E. stoliczkae	22	20 ± 0.73	19-22			
	Among Species				60.2	86.825	0.001

Morphological analyses

The geographical separation and sexual dimorphism of 99 specimens belonging to eight species of the genera *Cephalopholis* and *Epinephelus* showed no significant differences (p>0.05). Therefore, male and female specimens were pooled for the subsequent analyses. The analysis confirmed that this sample size was adequate for meristic and morphometric analyses to yield reliable results (Effect Size>0.5; Power>0.8; p<0.05).

Univariate analyses

A one-way analysis of variance (ANOVA) was performed for 22 morphological traits (16 morphometric and six meristic) in the eight *Cephalopholis* and *Epinephelus* species. Of these 22 traits, 12 morphometric and six meristic traits showed significant differences among species (p<0.05). Post-hoc Tukey tests were then performed to compare the variables between the different species of these two genera. The results showed that *Cephalopholis hemistiktos*, *Epinephelus latifasciatus* and *E. areolatus* exhibited the most significant differences in meristic traits, while *C. hemistiktos* and *E. latifasciatus* showed the greatest divergence in morphometric traits. With the exception of length of anal fin spine, length of anal fin base, and length of longest anal fin spine and length of pelvic fin, all other morphometric traits differed significantly between species (p<0.05). All meristic traits were significantly different (p<0.05) between species of these genera (Table 2).

Multivariate analyses

In multivariate analyses, DFA results showed considerable morphometric divergence between the two genera *Cephalopholis* and *Epinephelus*, with distinct clustering along DF1 (Fig. 3a). In

contrast to morphometric traits, meristic traits failed to confirm the distinction between these two genera (Fig. 3b).

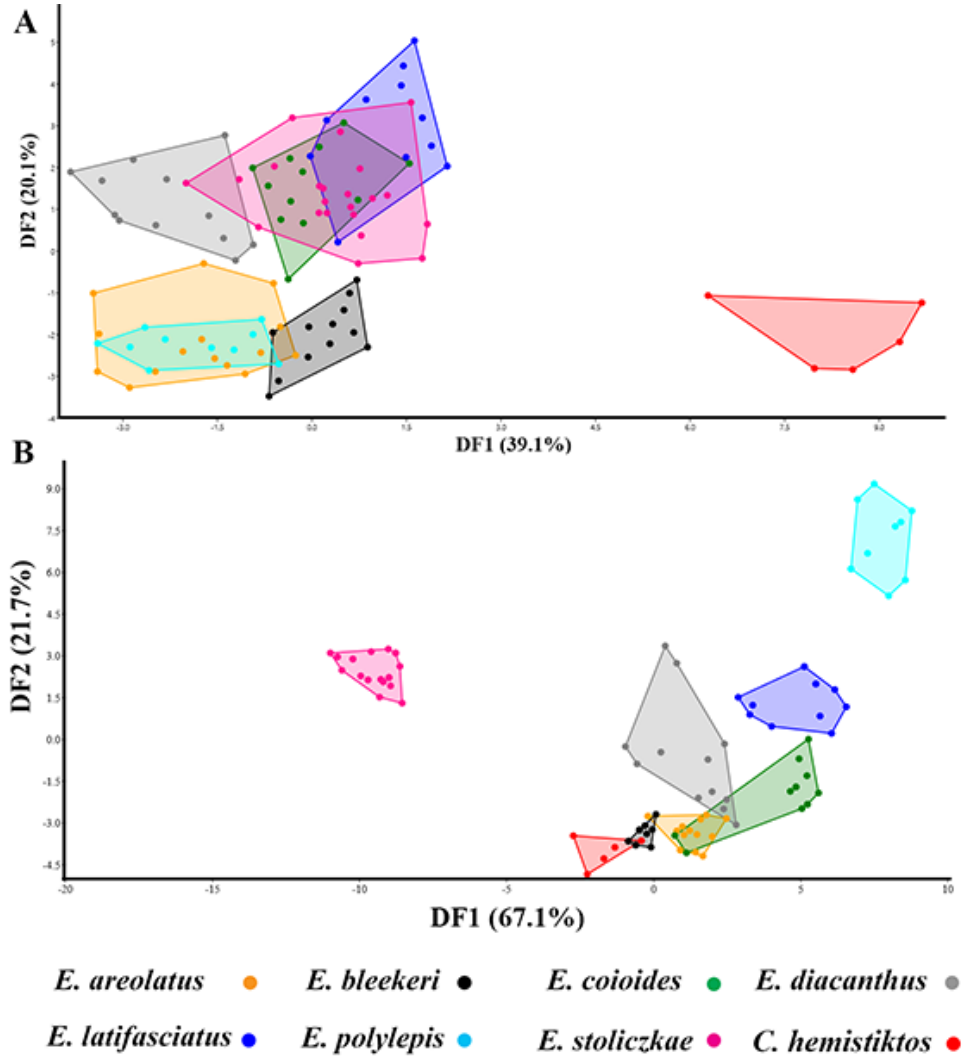


Figure 3: Results of the discriminant function analysis (DFA) for morphometric (a) and meristic (b) characteristics of grouper fish from the Persian Gulf and Oman Sea.

Multivariate analyses revealed that the first two principal components (PCs), based on morphometric traits and accounting for 46% of the total variance, showed no separation between *Epinephelus* species (data not shown). Discriminant function (DF) analysis based on meristic features (DF1:72.4%; DF2:19.7%) resulted in a classification accuracy of 92.1%, while morphometric features (DF1: 34.5%; DF2: 31%) resulted in a correct classification rate of 88.5% across all species (Fig. 4). Significant species segregation was observed for both meristic traits (Wilk's lambda=0.000, approximately F=51.652, p<0.001) and morphometric traits (Wilk's lambda=0.001, approximately F=6.134, p<0.001). In the Epinephelus-specific meristic DF analysis, *E. stoliczkae* showed a complete separation from the other species along DF1, mainly due to more gill rakers, while DF2 separated *E. polylepis*

mainly by more lateral line tubed scales (Fig. 4a). Along DF1, *E. latifasciatus* and *E. polylepis* were separated from other species by the caudal-peduncle length and snout length, while DF2 showed a complete separation of *E. areolatus*, *E. diacanthus* and *E. polylepis* from congeners, with the prepelvic length being the most influential factor (Fig. 4b).

The UPGMA phenogram based on meristic characteristics indicated three distinct groups, group I (*E. areolatus*, *E. bleekeri*, and *E. stoliczkae*), group II (*E. diacanthus*, *E. latifasciatus* and *E. coioides*) and group III (*E. polylepis*) (Fig. 4c).

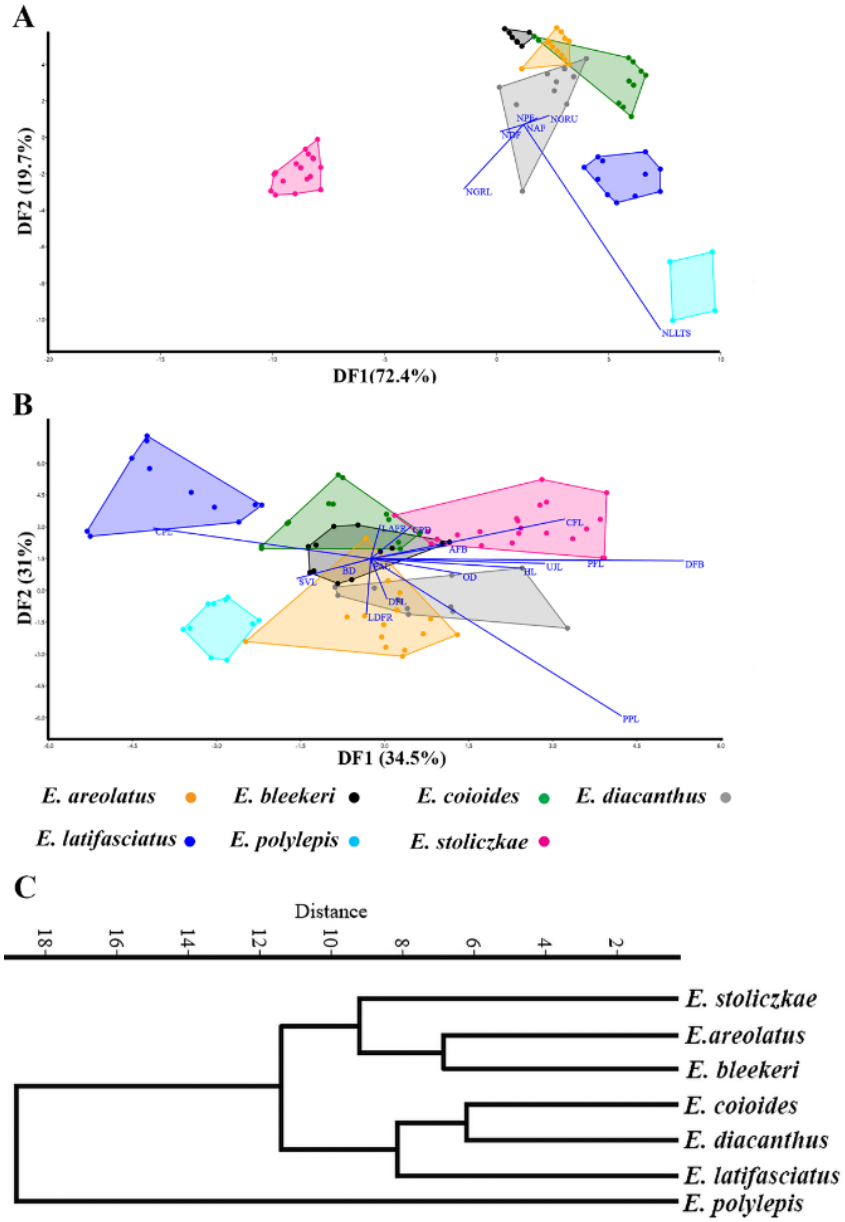


Figure 4: Results of the discriminant function analysis (DFA) based on meristic characteristics (a), morphometric characteristics (b), and the UPGMA phenogram generated from morphometric characteristics of *Epinephelus* species from the Persian Gulf and Oman Sea (c).

Geometric morphometric analysis

Geometric morphometric analysis revealed considerable shape variation between the two genera, underscoring a significant morphological divergence (Fig. 5). This analysis revealed that the first two canonical axes accounted for 50.6% and 19.5% of the total variance (cumulative 70.1%). The first canonical axis primarily captured variation in the positions of the median fins and the anterior placement of the lateral line, while the second axis primarily reflected variation in the position of the caudal fin, pectoral fin and dorsal fin. Along the first canonical axis, *E. areolatus* and *E. stoliczkae* showed complete separation from the other species. Along the second canonical axis, *E. diacanthus* was clearly separated from the other species (Fig. 6).

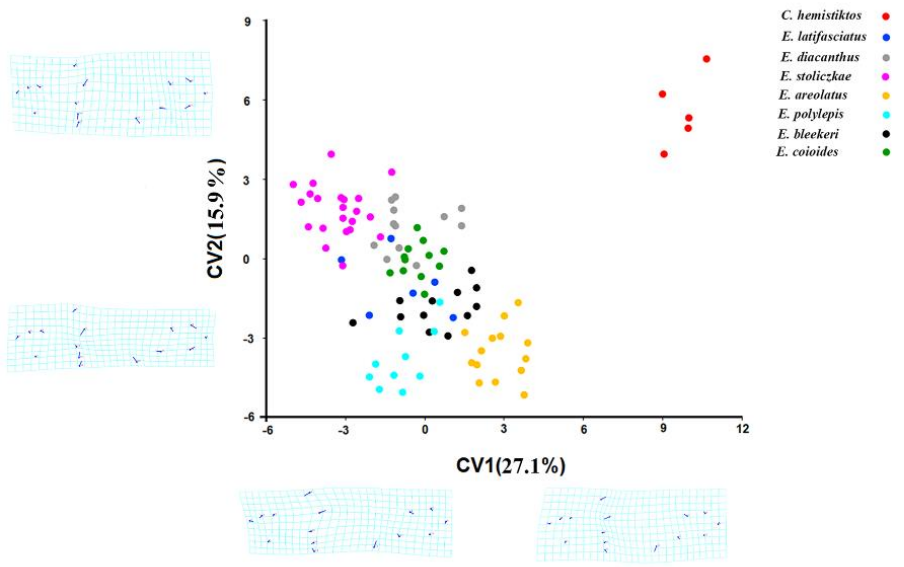


Figure 5: CVA illustrating the differences in body shapes among the ellipses of grouper species from the Persian Gulf and Oman Sea.

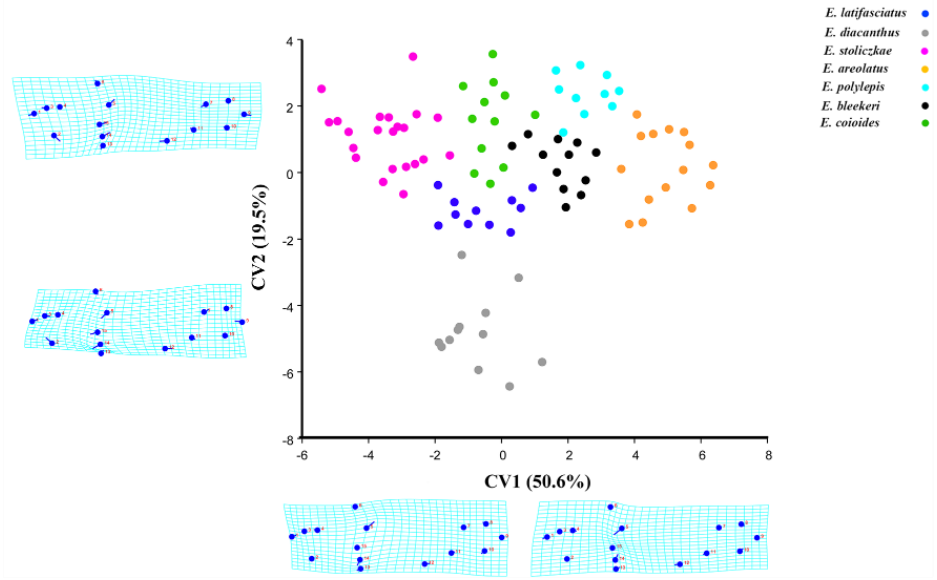


Figure 6: CVA showing the body shape differences with the ellipses of Epinephelus species from the Persian Gulf and Oman Sea.

***Cephalopholis hemistiktos* (Rüppell, 1830)**

Common name: Yellowfin Hind

***Serranus hemistiktos* Rüppell 1830, Type locality: Red Sea, Massawa, Eritrea.**

Diagnostic Characters: This species is characterized by a dorsal fin featuring 9 spines and 14–15 soft rays, along with 6–8 upper gill rakers and 13–15 lower gill rakers (for a total of 19–23 gill rakers). It has 47–50 lateral line pores, 16–19 pectoral fin rays, a rounded caudal fin, and typically rounded posterior sections of the dorsal and anal fins, while the pectoral fins are pointed.

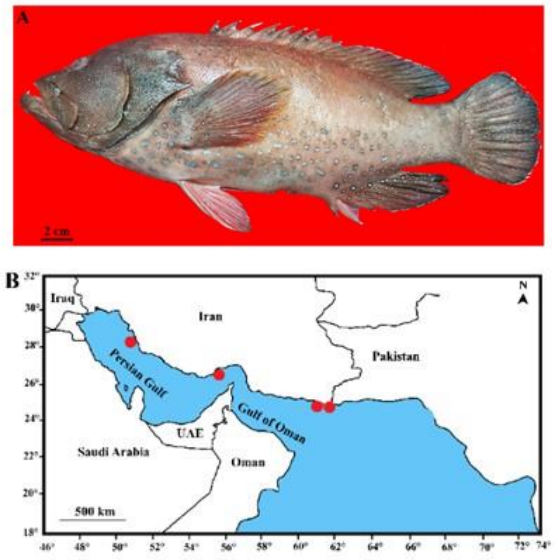


Figure 7: *Cephalopholis hemistiktos*, Persian Gulf: Qeshm. Photo by E. Damadi.

Coloration: The body displays significant color variability, ranging from red to brown, adorned with numerous small blue spots on the lower head and body, and fewer on the dorsal fin. The caudal fin and the soft portions of the dorsal and anal fins are darker than the body and also covered with small blue spots. Orange tips of spinous dorsal-fin membranes. The pectoral fins are brown to reddish-brown, featuring a few small blue spots near the base (Fig. 7a).

Distribution and Habitat: This species is observed throughout coral reef areas in the Oman Sea and the Persian Gulf at depths of 5–30 m (Fig. 7b).

Taxonomic Accounts of the Genus *Epinephelus* (Bloch, 1793): This genus is distinguished from others by possessing 7 to 10 soft anal-fin rays, a body depth that is greater at the dorsal fin origin than at the anal fin origin, and typically rounded or emarginated caudal fins.

***Epinephelus areolatus* (Forsskål, 1775)**

Common name: Yellowspotted Rockcod

Perca areolata Forsskål in *Niebuhr 1775,* **type locality:** *Red Sea: Saudi Arabia, Jeddah.*

Bodianus melanurus Geoffroy Saint-Hilaire 1817, **type locality:** *Red Sea: Egypt, Suez.*

Serranus angularis Valenciennes in *Cuv. and Val. 1828,* **type locality***: Indian Ocean: Sri Lanka.*

Serranus glaucus Day 1871, **type locality***: Indian Ocean: Andaman.*

Diagnostic Characters: This species is characterized by a dorsal fin featuring 11 spines and 15-17 soft rays, along with 8-10 upper gill rakers and 14-16 lower gill rakers (for a total of 22-26 gill rakers). It has 50-52 lateral line pores and 17-19 pectoral fin rays. The caudal fin is slightly truncated. The head, mid-body, and pelvic fins appear whitish and are covered with numerous yellowish-brown spots, further distinguishing this species from others.

Coloration: The body is light gray, adorned with large brown spots arranged longitudinally along its length, white posterior margin (Fig. 8a).

Distribution and Habitat: This species is typically found in seagrass beds near coral reefs, at depths ranging from 3 to 100 meters in the Persian Gulf and Oman Sea (Fig. 8b).

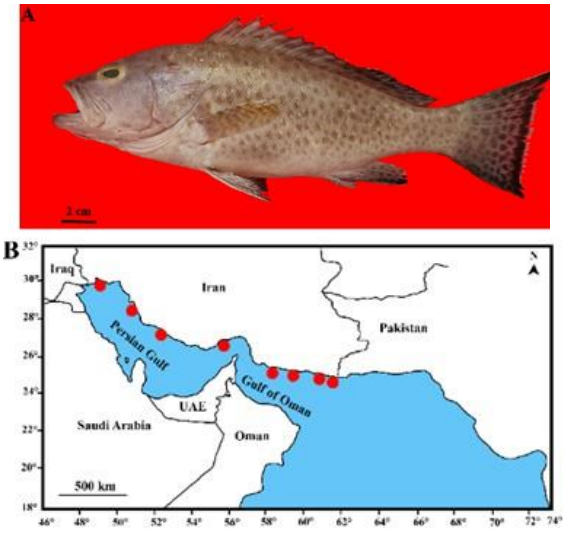


Figure 8: ***Epinephelus areolatus*****, Oman Sea: Pozm. Photo by E. Damadi.**

Epinephelus bleekeri **(Vaillant, 1878)**

Common name: Blacktail Grouper

Serranus bleekeri Vaillant in *Vaillant and Bocourt 1878,* **type locality:** *Indonesia: Java, Jakarta.*

Diagnostic characters: The species is identified by a dorsal fin containing 11 spines and 16-18 soft rays, 9-11 upper gill rakers, and 16-18 lower gill rakers (totaling 25-29 gill rakers), as well as 50-52 lateral line pores and 17-19 pectoral fin rays. The caudal fin has an emarginate margin, and its lower half is dark grey to black.

Coloration: The body displays hues ranging from brown to purplish-gray, adorned with numerous yellowish-orange spots distributed across the head, body, dorsal fin, and upper third of the caudal fin (Fig. 9a).

Distribution and habitat: This species has been exclusively recorded in the eastern Persian Gulf and the Sea of Oman, inhabiting coastal waters near coral reef areas at depths of 10-50 meters (Fig. 9b).

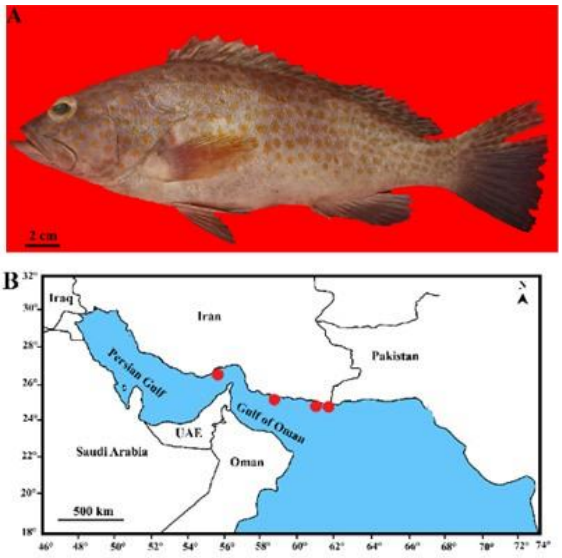


Figure 9: ***Epinephelus bleekeri*****, Oman Sea: Tis. Photo by E. Damadi.**

Epinephelus coioides **(Hamilton, 1822)**

Common name: Orange-spotted Grouper

Bola coioides Hamilton 1822, **type locality:** India, Ganges River mouth.

Serranus nebulosus Valenciennes 1828, **type locality:** no locality given

Serranus suillus Valenciennes 1828, **type locality:** India: Coromandel coast.

Diagnostic Characters: Distinguished by a dorsal fin with 11 spines and 13-16 soft rays, 8-10 upper gill rakers, and 14-17 lower gill rakers (total gill rakers 22-27). It has 52-58 lateral line pores and 18-20 pectoral fin rays. The head, body, and median fins are marked by numerous orange, orange-brown, or reddish-brown spots. Two dark spots on interopercle. The body also displays five faint, irregular grayish bars that bifurcate ventrally (Fig. 10a).

Distribution and Habitat: Collected from stations in the eastern Oman Sea and the western Persian Gulf, this species is typically found near estuaries at depths of 20-30 meters (Fig. 10b).

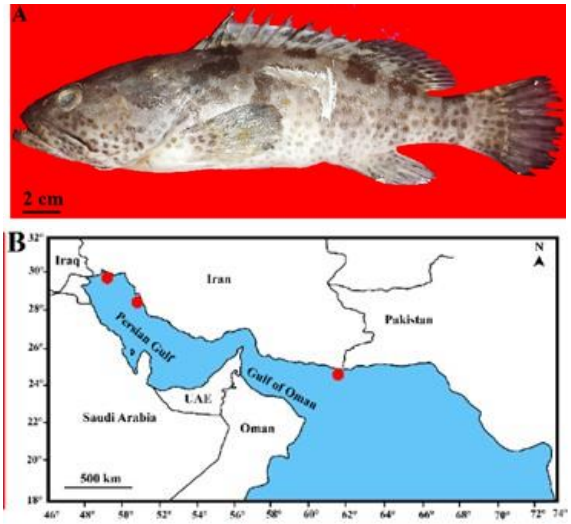


Figure 10: ***Epinephelus coioides*****, Oman Sea: Beris. Photo by E. Damadi.**

Epinephelus diacanthus **(Valenciennes, 1828)**

Common name: Five-banded Grouper

Serranus diacanthus Valenciennes in *Cuv. and Val. 1828,* **type locality:** *India, Malabar coast, Kerala.*

Epinephelus dayi Bleeker 1874, **type locality:** *India, Cochin.*

Diagnostic Characters: This species is characterized by a dorsal fin featuring 11 spines and 15-17 soft rays, along with 8-10 upper gill rakers and 15-18 lower gill rakers (totaling 23-28 gill rakers). It also has 53-59 lateral line pores and five distinct vertical bands along the ventral surface, which help differentiate it from other congeners.

Coloration: The body displays a pale grayish-brown coloration, typically featuring five broad dark vertical bands that are wider than the spaces between them (Fig. 11a).

Distribution and Habitat: This species is distributed throughout the Persian Gulf and Sea of Oman, where it is commonly found on muddy substrates or within silty sand habitats (Fig. 11b).

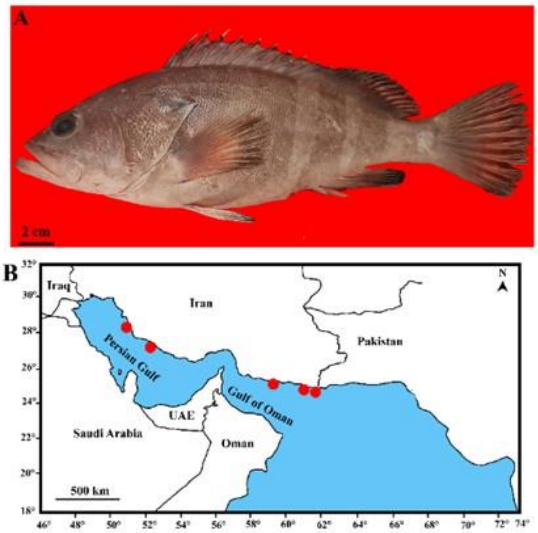


Figure 11: ***Epinephelus diacanthus*****, Persian Gulf: Bushehr. Photo by E. Damadi.**

Epinephelus latifasciatus **(Temminck and Schlegel, 1843)**

Common name: Striped Grouper

Serranus latifasciatus Temminck and Schlegel 1843, **type locality:** *Japan, Nagasaki.*

Serranus grammicus Day 1868, **type locality:** *India, Chennai.*

Priacanthichthys maderaspatensis Day 1868, **type locality** *India, Chennai.*

Diagnostic Characters: Characterized by a dorsal fin featuring 11 spines and 12-14 soft rays, 8-11 upper gill rakers, and 15-18 lower gill rakers (totaling 23-29 gill rakers), as well as 58-61 lateral line pores, 17-19 pectoral fin rays, and three distinct narrow longitudinal stripes along the body.

Coloration: Large adult specimens exhibit uniformly gray heads and bodies, with

dark, broken stripes that appear as discontinuous lines and spots (Fig. 12a).

Distribution and Habitat: This species is widely distributed throughout most areas of the Oman Sea and eastern Persian Gulf, commonly found near coral reefs and rocky substrates at depths of 10-35 meters (Fig. 12b).

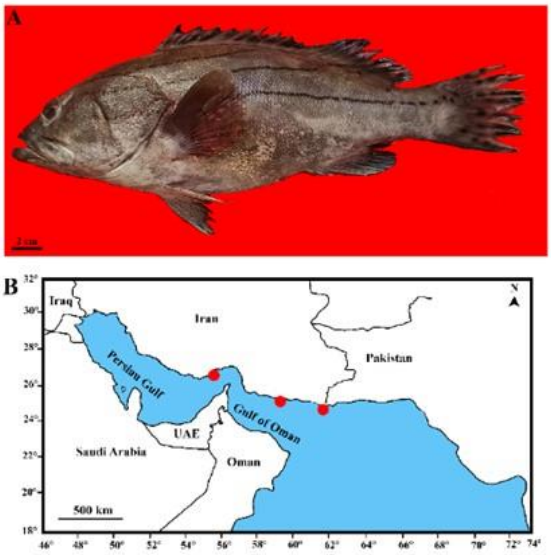


Figure 12: ***Epinephelus latifasciatus*****, Oman Sea: Beris. Photo by E. Damadi.**

Epinephelus polylepis **Randall and Heemstra, 1991**

Common name: Small-scaled Grouper

Type locality: Persian Gulf, Bahrain.

Diagnostic characters: Distinguished by a dorsal fin with 11 spines and 16-17 soft rays, 9-10 upper gill rakers, and 17-18 lower gill rakers (total gill rakers: 26-28), 66-70 lateral line pores, and 18 pectoral fin rays. The head, body, and fins are pale with numerous small, closely spaced dark brown spots; those on the fins and dorsal portions are smaller and more densely distributed than those on the lateral and ventral surfaces. The dorsal edge of the caudal fin displays a white margin with a row of dark brownish-black spots. The preopercle is angular, featuring a distinct notch on its upper margin (Fig. 13a).

Distribution and habitat: Recorded from single stations in both the Persian Gulf and Oman Sea (Fig. 13b), this species inhabits rocky areas at depths of 15-50 meters.

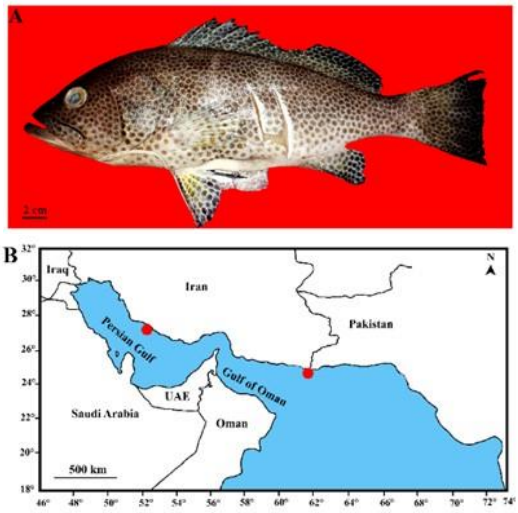


Figure 13: ***Epinephelus polylepis*****, Oman Sea: Tis. Photo by E. Damadi.**

Epinephelus stoliczkae **(Day, 1875)**

Common name: Olive-spotted Grouper

Type locality: Arabian Sea: Pakistan, coast of Sindh.

Diagnostic characters: The species has a dorsal fin with 11 spines and 16-18 soft rays, 50-52 lateral line pores, 6-7 upper gill rakers, and 13-15 lower gill rakers (totaling 19-22 gill rakers), as well as 17-19 pectoral fin rays. Its body features smooth scales, except in the pectoral fin region, and has a rounded caudal fin. The coloration includes a dark greenish-brown anterior head and body that gradually transitions to pale greenish-gray or white towards the posterior, with three dark greenish-brown bands on the posterior body. Additionally, the head and anterior body (including the

first dark band) display reddish-brown spots and a prominent dark spot behind the eye (Fig. 14a).

Distribution and habitat: The species is found in shallow sandy bottoms near small coral formations in both the Persian Gulf and Oman Sea (Fig. 14b).

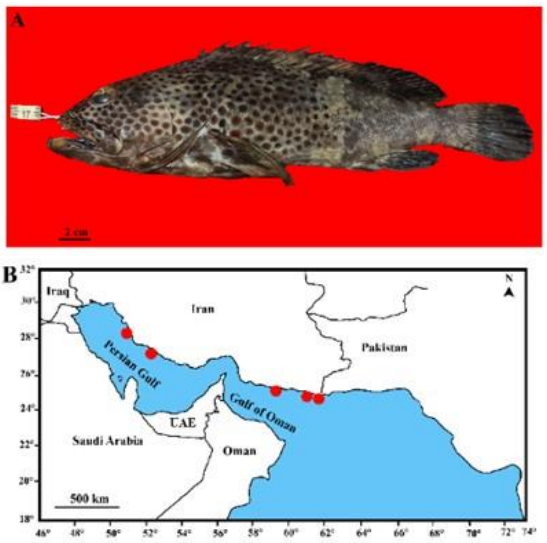


Figure 14: *Epinephelus stoliczkae*, Oman Sea: Pozm. Photo by E. Damadi.

Discussion

In the present study, we investigated morphological variation in body shape and size among groupers using geometric morphometric, univariate, and multivariate techniques. Our main finding is that both approaches provided strong statistical support for effectively differentiating *Cephalopholis hemistiktos* and *Epinephelus* species, especially in challenging cases where confirmatory analyses apply. These morphometric methods yielded more accurate identifications than traditional subjective visual assessments of morphological traits. This is because traditional identification methods, which rely on subjective visual assessments of traits like color patterns, are generally confounded by the significant changes these diagnostic characters undergo during ontogenetic stages. However, we emphasize that this does not imply morphometrics should be used primarily or exclusively for species identification. Previous molecular studies distinguishing epinephelid species in the Persian Gulf and the Sea of Oman support our findings (Ketchum *et al*., 2016; Tavakoli-Kolour *et al.,* 2022; Gholipour Gilak *et al.,* 2024). The genera *Cephalopholis* and *Epinephelus* exhibited high morphological variation, consistent with previous molecular studies (Craig and Hastings, 2007) (Fig. 3).

Traditional morphometric analyses revealed clear distinctions between morphotypes, particularly for meristic traits. Specifically, meristic traits such as the number of gill rakers and lateral-line tubed scales were diagnostic at the species level. These characters, along with color patterns, have historically been the most important features for distinguishing epinepheline species (Randall, 1995; Heemstra *et al.,* 2022). Lateral-line pored scales exhibit significant phenotypic divergence, resulting in a clear separation (p<0.01) of *E. polylepis* from other congeners (*E. polylepis*, 66-70 vs. <59 in sister taxa) in univariate and multivariate analyses (Fig. 4a; Table 2). Previous studies have shown that interspecific morphological variation in the lateral line system of teleost fishes is typically correlated with ecological differences, particularly habitat characteristics and behavioral adaptations. For example, species inhabiting turbid or high-flow environments often exhibit an increased

number of superficial neuromasts as a sensory adaptation (Piotrowski and Baker, 2014; Webb, 2014). Similarly, reef-dwelling species, such as *E. polylepis*, frequently demonstrate enhanced development of both canal and superficial neuromasts as an evolutionary adaptation that improves hydrodynamic detection capabilities in complex benthic environments, facilitating prey localization and predator avoidance in structurally rich coral reef habitats. *Epinephelus stoliczkae* has a significantly higher number of gill rakers (19-22) compared to its congeners (13-18) (p<0.01). This adaptation is likely driven by its specialized planktivorous feeding strategy in shallow sandy habitats near coral heads, where seasonal variations in plankton availability are similar to those observed in marine fishes (Liem, 1980; Sanderson *et al.,* 2001; Gajdzik *et al.,* 2016; Kiljunen *et al.,* 2020).The results of traditional morphometrics, including meristic traits, grouped the species into three clusters (Fig. 4c), which largely align with substrate type (Randall, 1995; our data) and molecular data (Ma and Craig, 2018). Group I included species primarily inhabiting soft-substrate habitats (grass beds, sand, mud/muddy substrates), while group II consisted of species associated with hard-substrate habitats (rocky areas and coral reefs). Previous molecular studies demonstrated that the genus *Epinephelus* is not monophyletic and comprises four distinct genetic clades (Ma and Craig, 2018). Our results (Fig. 4c) are consistent with prior molecular data (Craig and Hastings, 2007; Ma *et al.,* 2016) and support the hypothesis that groups I and II represent separate sister lineages within *Epinephelus*. Our study reveals that *E. polylepis* clusters in a distinct clade (Group III) (Fig. 4c), which is inconsistent with previous molecular and morphological data (Randall, 1995; Craig and Hastings, 2007; Ma *et al.,* 2016; Heemstra *et al.,* 2022). This divergence likely arises from accumulated genetic differences, unique ecological adaptations to rocky habitats, and a separate evolutionary history due to early divergence or limited gene flow with other congeneric species.

In this case, subtle habitat specializations, such as preferences for rocky substrates, along with limited dispersal in the northwest Indian Ocean, have driven genetic differentiation despite conserved morphology (Rocha *et al.,* 2007; Tavakoli-Kolour *et al.,* 2022; Damadi *et al.,* 2026).

The pattern of morphometric diversification among *Epinephelus* species in the Persian Gulf and the Oman Sea is complex and may be influenced by the characteristics of their microhabitats (Coles, 2003; Burt *et al.,* 2011; Maghsoudlou *et al.,* 2019). This influence may be attributed to interspecific phenotypic plasticity, which can be affected more by environmental factors, such as water temperature and salinity. This pattern is consistently observed in *Epinephelus* studies demonstrating significant intraspecific plasticity (Russo *et al.,* 2009; Mujar *et al.,* 2025). While the morphometric differentiation observed in this study effectively delineates the examined grouper species, it is important to interpret these findings in the context of environmental health. Previous studies have shown that exposure to heavy metals

and pesticides causes significant alterations in biochemical markers, including increased malondialdehyde (MDA) levels, elevated liver enzymes, and changes in hematological indices such as red blood cell counts and hemoglobin (Ateş *et al.,* 2008; Gulhan *et al.,* 2012; Talas *et al.,* 2014). Moreover, natural antioxidants like propolis and selenium have been found to mitigate these toxic effects by enhancing antioxidant enzyme activities (e.g., catalase and glutathione peroxidase) and reducing lipid peroxidation (Orun *et al.,* 2008; Talas *et al.,* 2014). Given that heavy metal bioaccumulation has been recorded in fish from similar environments (Caglar *et al.,* 2019), the observed morphological variations might not solely reflect phylogenetic divergence but could also incorporate adaptive phenotypic responses to localized pollution gradients. Consequently, future research should combine high-resolution geometric morphometrics with systematic ecotoxicological monitoring to disentangle the effects of evolutionary history from environmental stressors. Such integrative approaches will enhance the accuracy of taxonomic assessments and support effective conservation strategies for these ecologically and commercially valuable species in the Persian Gulf and Oman Sea.

Morphometric traits had a minimal effect on the separation of *Epinephelus* species compared to meristic traits (Fig. 4b). Meristic traits are generally more reliable for species discrimination in systematic studies of fish due to their greater stability and lower susceptibility to environmental factors. In contrast, morphometric traits tend to show higher variability, which reduces their diagnostic power. This distinction is especially apparent in regions like the Persian Gulf and the Oman Sea, where environmental gradients such as the Persian Gulf's extreme salinity (>40 ppt) and significant temperature fluctuations can greatly impact morphometric plasticity (e.g., body shape or fin proportions) while leaving meristic counts (e.g., fin rays or vertebrae) largely unaffected. Consequently, researchers should exercise caution when using these traits for taxonomic identification in these biogeographic regions. DFA based on morphometric characters, including the length of the caudal peduncle, length of the snout, length of the dorsal fin, length of the caudal fin, and length of the prepelvic region, consistently identified these factors as the most significant contributors to the morphometric distinction between the species (Fig. 4b). Previous morphometric studies have identified the length of the pectoral-fin and body depth as diagnostic traits for species discrimination (Randall, 1995; Heemstra *et al.,* 2022).

Geometric morphometric analysis provides a comprehensive assessment of comparative shape change and effectively reveals subtle shifts in organismal morphology (Thacker, 2017). Among the *Epinephelus* species examined, the expressions of morphological change are varied, lacking a consistent pattern (Fig. 6). CV1 revealed the most morphological variation in the positions of the median fins and the anterior placement of the lateral line between *E. stoliczkae* and *E. areolatus* (Fig. 6). Given the habitat of *E. areolatus* in seagrass beds, these changes are likely related to the intensity of the water current.

In these areas, the faster water current results in slender and flexible fins, enabling the fish to maneuver in crowded environments and adapt to these conditions, as documented in marine fish (Nauen and Lauder, 2000; Wang *et al.,* 2020). In CV2, the most significant changes involve the positions of the caudal and pectoral fins, as well as the shape of the head, particularly around the mouth (Fig. 6). These changes are especially evident in *E. diacanthus*, likely due to adaptations related to feeding and locomotion. As a species that inhabits muddy or muddy-sand bottoms, *E. diacanthus* has a ventrally positioned mouth adapted for suction feeding on benthic invertebrates and organic detritus (Randall, 1995). In these habitats, fish develop distinctive fin adaptations: broad pectoral fins that function like paddles for maneuvering through sediment, compact rounded caudal fins for sudden directional changes, and forward-positioned pelvic fins that help anchor them while foraging in the substrate (Blake, 2004; Helfman *et al.,* 2009; Damadi *et al.,* 2021; Damadi *et al.,* 2024b; Günther, 2025). Shape variation analysis has been enhanced as an effective method to distinguish representatives of marine fish families, such as Gobiidae (Polgar *et al.,* 2017), Haemulidae (Damadi *et al.,* 2020; Damadi *et al.,* 2021; Damadi *et al.,* 2024a), Lethrinidae (Damadi *et al.,* 2024b), and Blenniidae (Sharifiniya *et al.,* 2025) from the Persian Gulf and the Oman Sea. This study underscores the value of these methods for taxonomic classification and for assessing environmental influences on marine organisms.

The results suggest that integrating comprehensive morphological analyses with molecular techniques could further enhance our understanding of grouper diversity and adaptation in various marine ecosystems.

Identification Key for the Persian Gulf and Oman Sea Groupers:

1a. Head, body, and fins with small blue ocelli spots; tips of spinous dorsal-fin membranes orange.....*Cephalopholis hemistiktos*

1b. Lacks blue ocelli spots on head/body/fins; spinous dorsal-fin membranes blackish/darker.....2

2a. Lateral line pores 66–70; fins with small dark black spots .....*Epinephelus polylepis*

2b. Lateral line pores <66; lacks small dark spots on fins.....3

3a. Body with three narrow longitudinal stripes (breaking into dashes/spots on head); nostrils subequal.....*Epinephelus latifasciatus*

3b. Lacks longitudinal stripes; nostrils unequal.....4

4a. Body with five dark vertical bars (wider than pale interspaces); ventrally positioned mouth.....*Epinephelus diacanthus*

4b. Lacks five dark bars; terminal mouth..... 5

5a. Lateral line pores 52–58; two dark spots on interopercle; body with irregular vertical bars..... *Epinephelus coioides*

5b. Lateral line pores <52; no dark spots on interopercle..... 6

6a. 19–22 lower-limb gill rakers; head with dark reddish-brown spots and dark blotch behind eye; two or more dark bars on body; caudal fin rounded..... *Epinephelus stoliczkae*

6b. 14–17 lower-limb gill rakers; lacks reddish spots, a dark blotch, and bars; caudal fin emarginated.....7
7a. Lower caudal fin dark; body with orange-yellow spots……..……*Epinephelus bleekeri*
7b. Caudal fin with white posterior margin; head, body, and fins with brown spots……....*Epinephelus areolatus*

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Conflict of interest
The authors declare that they have no conflict of interest.

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