

Research Article

Phylogeny of Leiognathidae based on the osteological characters in the northern Persian Gulf and Oman Sea

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Abstract

Six species of the Ponyfish species (Leiognathidae) from five genera were investigated for osteological phylogeny analysis from coastal marine waters of the Northern Persian Gulf and Oman Sea. Five specimens of each species were cleared and stained for detailed osteological examination. Additionally, *Diapterus auratus* was selected as an out-group for comparative analysis. The resulting data matrix was analyzed to reconstruct the phylogenetic tree. Through parsimony analysis, the studied species were classified into two main clades. The first clade comprised *Nuchequula gerreoides* + (*Aurigequula fasciata* + *Karalla daura*). The second clade included (*Deveximentum mekranense*+*Deveximentum ruconiu*)+in *Photopectoralis bindus*. Results were congruent with previously reported molecular phylogenetic analysis and underscored the significance of osteological features in distinguishing taxonomic groups within the Leiognathidae family.

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Introduction

The Ponyfishes (Leiognathidae) encompasses demersal fishes found in tropical and subtropical habitats (Nelson, 1994; Sparks *et al.*, 2005) across a wide geographic range from the Red Sea and the eastern coast of Africa to India, Indonesia, Australia, Japan, and the Pacific Islands, extending as far as Tahiti and Hawaii (Jones, 1985). These fish are characterized by their protractible mouth (Giat *et al.*, 2008), small to medium-sized laterally compressed body and silver coloration (Banu *et al.*, 2020). The family includes 53 known species distributed among nine genera: *Leiognathus*, *Deveximentum*, *Gazza*, *Nuclenchius*, *Karalla*, *Equulites*, *Aurigequla*, *Eubleekeria* and *Photopectoralis* (Abraham *et al.*, 2011; Banu *et al.*, 2020; Fricke *et al.*, 2024). The Leiognathidae family presents a rich diversity that holds promise for commercial exploitation (James, 2008). Twelve species from eight genera (except *Eubleekeria*) have been documented in the Iranian coastal waters of the Persian Gulf and Oman Sea (Valinassab, 2013; Alavi-Yeganeh and Deyrestani, 2016a,b; Alavi-Yeganeh and Bahmani, 2018; Khajavi and Alavi-Yeganeh, 2020; Alavi-Yeganeh *et al.*, 2021).

Accurate species identification is crucial for scientific research (Fontanilla *et al.*, 2014) as relying solely on morphological traits may not always be sufficient due to variability and overlap in morphometric characteristics among ponyfish species (Bickford *et al.*, 2007; James, 2008). While molecular methods are valuable tools for species identification, they may not always be practical for field work or the

development of identification keys. Therefore, integrating multiple types of data simultaneously is advisable to enhance species identification accuracy. The skeletal structure of fishes is a significant characteristic that provides valuable ecological information and plays a crucial role in taxonomic studies. Understanding the skeletal structure of fishes is essential for advancing our knowledge of fish biology (Helfman *et al.*, 2009).

Taxonomic uncertainties persist within the Leiognathidae family, as highlighted by taxonomic revisions (Giat *et al.*, 2008). Despite some research efforts focusing on the biology and fishery of various species across their distribution range, a comprehensive osteological examination of this family is not considered. While the genera *Leiognathus*, *Deveximentum* and *Gazza* exhibit distinct skeletal characteristics (James, 2008, 2011), the skeletal differences among the newly identified genera within this family have not been thoroughly explored. Particularly, structures such as urohyal, hypural, and neurocranium elements demonstrate significant variability, providing valuable insights for taxonomic classification within the family (James, 2008; De La Cruz-Agüero, 2013; Chollet-Villalpando *et al.*, 2014). Given that phylogenetic analysis at the family level has improved our understanding of the interrelationships among Leiognathidae genera and species (Sparks and Dunlap, 2004; Banu *et al.*, 2020), this study aims to elucidate the phylogenetic relationships among some members of this family in the Persian Gulf and Oman Sea, by identifying and analyzing key skeletal features. The

outcomes of this research are expected to contribute to the development of robust identification keys for this group of fish.

Materials and methods

A total of six species representing five genera belonging to the Leiognathidae were collected from three stations along the Oman Sea including the Gwatr Bay, Chabahar Bay and Jask coastal waters and three stations along the Persian Gulf including Hormuz Island, Bandar Lengeh and Bushehr coastal waters of Persian Gulf using fishing methods of beach seine, cast net and trawl nets. The collected specimens were identified based on available regional identification keys (Alavi-Yeganeh and Deyrestani, 2016a, b; Alavi-Yeganeh and Bahmani, 2018; Khajavi and Alavi-Yeganeh, 2020; Alavi-Yeganeh *et al.*, 2021).

The species examined in this study were *Aurigequula fasciata*, *Deveximentum mekranense*, *Deveximentum ruconius*, *Karalla daura*, *Nuchequula gerreoides* and *Photopectoralis bindus*. Five specimens of each species were collected and subjected to anesthesia using 1% clove solution and then fixed in 10% buffered formalin. Subsequently, specimens were cleared and stained based on a modified protocol derived from Taylor and Van Dyke (1985). An additional species, *Diapterus auratus* was utilized as an out-group for comparative analysis. Morphological structures including the urohyal from the hyoid arch, hypural from the caudal skeleton and vomer from the neurocranium were meticulously examined. High-resolution scans of these structures were obtained using a Scanner (Epson v700) and

analyzed under a stereomicroscope. The obtained images were drawn using CorelDrawX6 software.

In this study, the phylogenetic relationships were hypothesized using the cladistic method (Swofford *et al.*, 1996). The polarity of these characters was determined following the guidelines of Watrous and Wheeler (1981). In our analysis, a total of 16 morphological characters were extracted to construct a robust data matrix for subsequent phylogenetic analysis. Unspecified data were denoted as "?". Phylogenetic reconstruction was carried out employing the maximum parsimony criterion using PAUP4 (Swofford, 1998) software package. The bootstrap analysis with 1000 iterations was performed utilizing a Heuristic search algorithm.

Results

Vomer

The vomer, an unpaired element situated at the antero-ventral aspect of the ethmoid region, features two antero-ventral processes and bilateral ascending wings on its anterior half (Fig. 1). The posterior section of the vomer tapers gradually towards its distal end which overlaps with the anterior portion of the parasphenoid bone and lies in its groove.

Character states

The antero-ventral processes of the vomer exhibit four distinct states: (0) distinct, round and completely prominent, (1) distinct, round, and stumpy, (2) distinct, pointed, and tending backward, (3) indistinct wide plate-shaped extending on the ventral side of the bone. In *A. fasciata*

and *N. gerreiodes* similar to the out-group these processes are prominence and thick (Fig. 1 e and f). In contrast, in species such as *P. bindus* and *K. daura*, these processes are smaller and less prominent (Fig. 1. b and g). Notably, the structure differs in the genus *Deveximentum*; In *D. mekranense*, these processes are distinct, pointed and inclined backward (Fig.1 c), while in *D. ruconius*, they are plate-shaped with no distinct projection (Fig. 1d). The outer margin of the wings can be classified as either (0) straight or (1) crinkled. The ancestral state was exclusively observed in *Diapterus auratus*, and this character remains consistent across all studied species. The presence or absence of a groove in the margin of wings is described by two states: (0) no groove and (1) a deep groove in the anterior margin of wings dividing it into two parts. This groove is visible in species such as *A. fasciata*, *K. daura* and *D. ruconius*. While *D. ruconius* exhibits a small depression (Fig.1 d), the groove is deeper and more distinct in the other two species. The orientation of the wings can be characterized as either (0) inclining backward or (1) inclining upward. The derived state, observed in *D. ruconius*, shows an upward inclination of the wings (Fig.1 d), while the remaining species exhibit a similar orientation to the ancestral species.

Regarding the presence of pores on the anterior part of the vomer, two states are identified: (0) no pores and (1) numerous pores. The presence of pores is specific to species such as *A. fasciata* and *K. daura* (Fig. 1 f and g) and is not observed in other species examined. The configuration of the right and left anterior parts of the vomer can

be (0) fused together anteriorly, (1) reaching each other without fusion, and (2) not reaching each other. In most studied species, except for *A. fasciata* and *K. daura*, these portions are fused together, forming an integrated structure. In *A. fasciata*, they are seen as reaching each other (Fig. 1 f), while in *K. daura*, these two parts are completely separate (Fig. 1 g). The end of the vomer can be either (0) straight or (1) forked. Species belonging to the genus *Deveximentum* and *K. daura* (Figs. 1 c, d, and g) exhibit a forked end of the vomer.

Urohyal

The urohyal, a component of the hyoid arch situated at the posterior aspect of the basihyal beneath the branchial arches, comprises two distinct horizontal and ventral segments exhibiting shape variations across species (Fig. 2).

Character states

(0) Urohyal possesses a ventral plate, (1) has a ventral pointed process from a lateral view, or (2) lacks a ventral plate or process. The shape of the urohyal is distinctly different in the out-group. Despite having vertical and horizontal plates, a more extended ventral plate is observed, reaching the posterior border of the vertical part (Fig 2 a). The posterior margin of the vertical segment can be diagonally (0) with the shorter dorsal edge, (1) with the longer dorsal edge, and (2) straight. In species like *P. bindus*, *D. mekranense*, *D. ruconius* and the out-group, the vertical part exhibits a shorter dorsal edge (Fig. 2 a, b, d). State 1 is uniquely observed in *A. fasciata*, where the vertical part extends past the horizontal end (Fig. 2 f). Conversely, in two other

species, the posterior margin of the vertical segment is straight and extends to the distal end of the horizontal segment (Fig. 2 e, g).

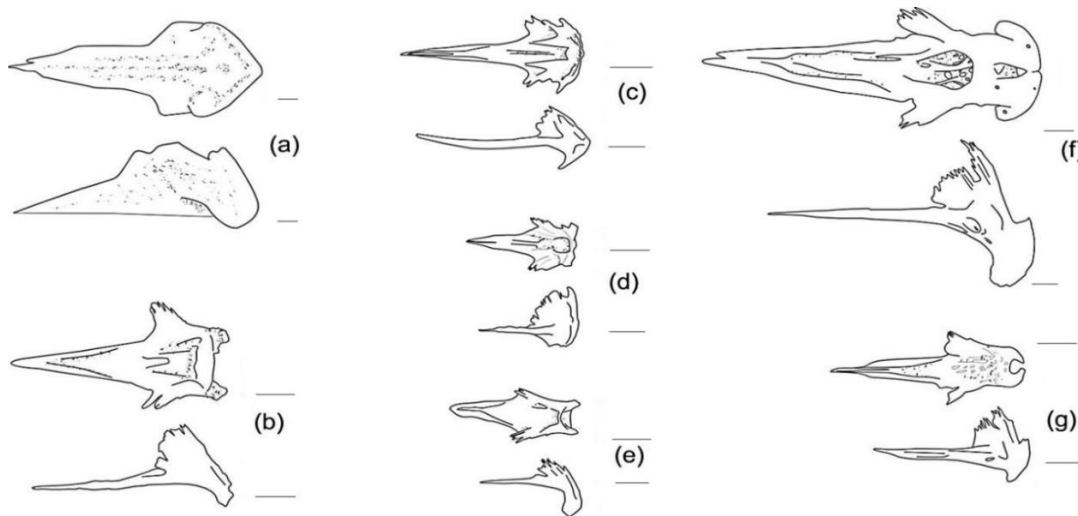


Figure 1: Dorsal and lateral views of Vomer in *Diapterus auratus* (a) (adapted by Kobelkowsky, 2004), *Photopectoralis bindus* (b), *Deveximentum mekranense* (c), *Deveximentum ruconius* (d), *Nuchequula gerreoides* (e), *Aurigequula fasciata* (f) and *Karalla daura* (g). The scale bar demonstrates 1 mm.

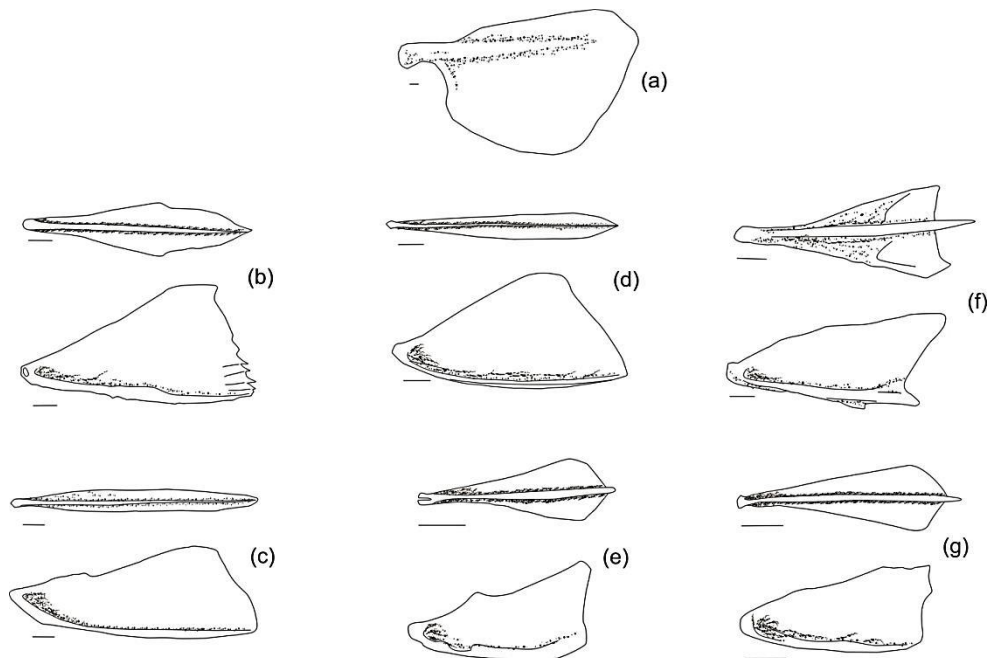


Figure 2: Lateral view of Urohyal in *Diapterus auratus* (a) (adapted by Chollet-Villalpando et al., 2014), *Photopectoralis bindus* (b), *Deveximentum mekranense* (c), *Deveximentum ruconius* (d), *Nuchequula gerreoides* (e), *Aurigequula fasciata* (f) and *Karalla daura* (g). The scale bar demonstrates 1 mm.

The vertical portion is either (0) separate from the tip of the bone or (1) connected to the tip of the urohyal, with the ancestral

state observed in the out-group. The dorsal margin of the vertical part is either (0) straight without projection or (1) with a

pointed or squarish anterior projection. *A. fasciata* displays both states, while the out-group, *D. ruconius* and *P. bindus* have a straight margin. *N. gerreoides*, *K. daura* and *D. mekranense* exhibit projections (Figs. 2 c, e and g). The shape of the horizontal part can have (0) a pear-like shape (with the posterior part wider than the anterior part), (1) a uniform width throughout, or (2) an elongated rhombus shape with a wider middle part. Genus *Deveximentum* shows consistent width in the horizontal part (Figs. 2 c and d), while the *P. bindus* displays state 2 (Fig. 2 b). In the rest of studied species, the ancestral state was observed. The posterior margin of the vertical part can be (0) straight throughout or (1) zigzag at the ventral part, with the derived state observed only in *P. bindus* (Fig. 2b). The tip of the bone can be (0) without a groove or (1) have a narrow groove or tiny hole, with this derived character seen in *N. gerreoides* (Fig. 2e).

Hypural

In the investigated taxa, there are five hypurals. A pair of large triangular plates is discernible within the caudal complex, originating from the fusion of hypural elements. The lower and upper plates correspond to the 1st + 2nd and 3rd-4th hypurals, respectively. The fifth single hypural is rod-like and located on the dorsal part of upper plate. These plates can be conjoined at their anterior ends and exhibit separation towards the posterior aspect, resulting in an interstitial gap between the plates (Fig. 3).

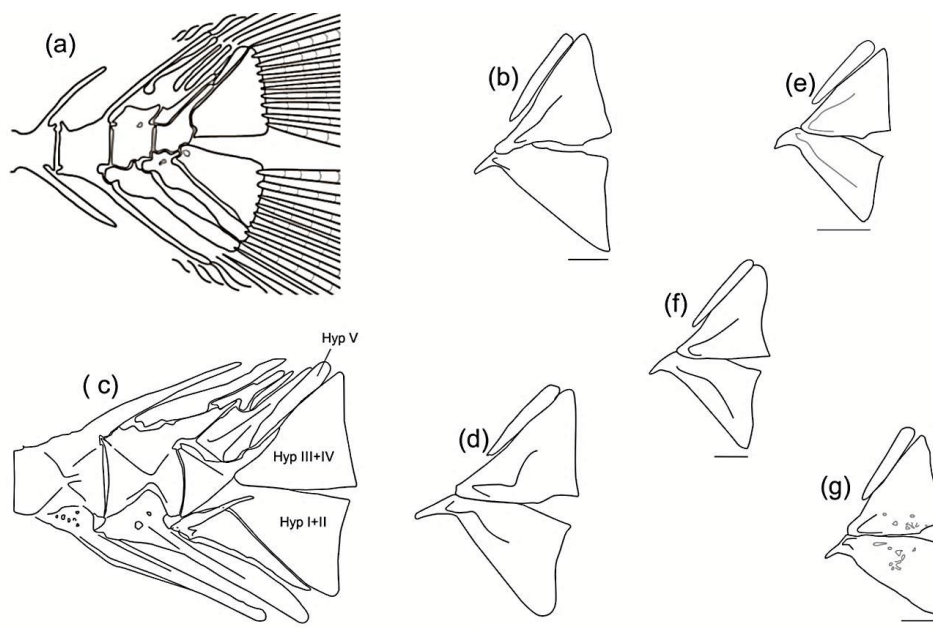


Figure 3: Lateral view of caudal skeletal in *Diapterus auratus* (a) (adapted by Kobelkowsky, 2004), urohyal element of *Photopectoralis bindus* (b), *Deveximentum mekranense* (c), *Deveximentum ruconius* (d), *Nuchequula gerreoides* (e), *Aurigequula fasciata* (f) and *Karalla daura* (g). The scale bar demonstrates 1 mm.

Character states

The hypural plates can be characterized by three distinct states: (0) lacking any connection, resulting in a long and wide diastema between them, (1) having a short anterior connection, and (2) having a wide connection that reaches or exceeds the middle portion of the plates. In the out-group, both plates remain unconnected (Fig. 3a), while in the in-group species, there is a clear conjunction between them. Within the genus *Deveximentum*, this connection is typically short and limited to the anterior part of the plates (Figs. 3 c and d). However, in other species, this connection may extend to the middle or even surpass it.

Regarding the upper plate, it can exhibit two states: (0) lacking a projection or (1)

featuring a ventral projection. This ventral process was observed in species such as *P. bindus*, *D. ruconius* and *K. daura*, while the ancestral character was predominant in other groups (Fig 3 b, d and g).

The data matrix was constructed using 16 extracted characters from six in-groups and one out-group (Table 1). The results of the parsimony analysis based on data matrix had the *most* parsimony trees with a length of 28, consistency index (CI) of 0.82 and retention index (RI) of 0.68.

The consensus majority tree was derived by aggregating results from 1000 replicates, ensuring robustness and reliability in the phylogenetic analysis (Fig. 4).

Table 1: Data matrix for seven studied taxa including six in-groups and one out-group (0=Plesimorphic, 1,2,3 =Apomorph)

Taxon	Character															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>Diapterus auratus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Photopectoralis bindus</i>	1	1	0	0	0	0	0	2	0	1	0	2	1	0	2	1
<i>Deveximentum mekranense</i>	2	1	0	0	0	0	1	2	0	1	1	1	0	0	1	0
<i>Deveximentum ruconius</i>	3	1	?	1	0	0	1	2	0	1	0	1	0	0	1	1
<i>Aurigequula fasciata</i>	0	1	1	0	1	1	0	1	1	1	?	0	0	?	2	0
<i>Karalla daura</i>	1	1	1	0	1	2	1	2	2	1	1	0	0	0	2	1
<i>Nuchequula gerreoides</i>	0	1	0	0	0	0	0	2	2	1	1	0	0	1	2	?

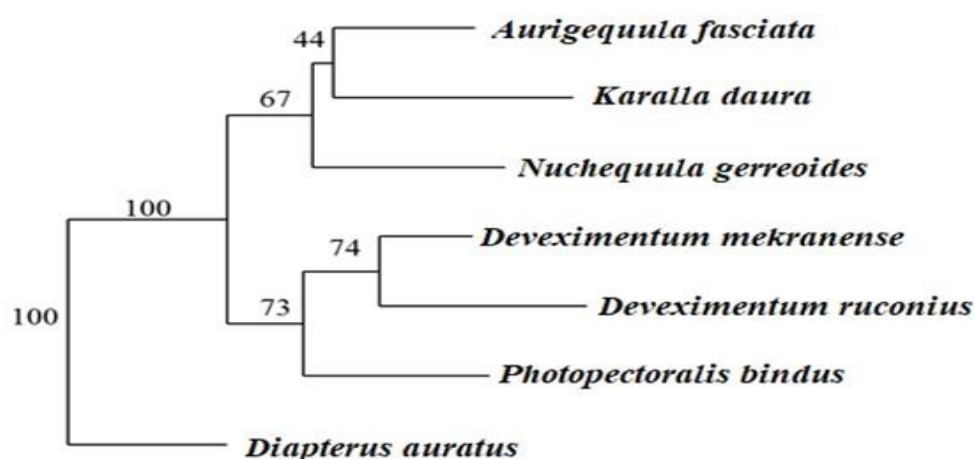


Figure 4: Phylogenetic tree resulting from Parsimony analysis for six in-groups and one out-group using osteological characteristics.

Discussion

Based on parsimony analysis, the studied species were classified into two distinct main clades. The first clade contains *N. gerreoides* + (*A. fasciata* + *K. daura*) and the second clade includes the members of genus *Deveximentum* in the same subclade and *P. bindus* specimens. The ponyfish species from Iranian coastal marine waters were clustered in the same clade by having synapomorphy traits such as a crinkled outer margin of the wings in the vomer, the absence of a ventral plate in the urohyal, and the structural integrity of the vertical portion of the bone extending to its tip in the urohyal. The two species of *Deveximentum* were clustered within a subclade due to characteristics such as the shape of the horizontal part of urohyal and the anterior connection of hypural plates. Molecular studies have provided varied results for some of these fishes, for example, *P. bindus* placed in close relationships with the clade of *Deveximentum* species (Sparks and Chakrabarty, 2015). However, data of species from all genera within Leiognathidae is necessary for a complete and accurate phylogenetic relationship reconstruction.

The vomer exhibits a remarkable diversity across studied genera. The antero-ventral process of the vomer displays a robust and thickened structure in some species, while in others *e.g.* *D. ruconius* this structure is comparatively weaker. Importantly, the articulation of this bone with the maxillae at its anterior end, suggests a potential role in the feeding mechanism. The anterior wings of this bone are Permanently curved upwards in *Deveximentum* (James, 2008,

2011) similar to the studied species. In contrast, *Gazza* and *Leiognathus* show a nearly straight configuration (James, 2008). Furthermore, the posterior segment of the vomer appears elongated in *Deveximentum* and *Gazza* (James, 2011) as well as in studied species like *P. bindus*, *D. mekranense*, *A. fasciata* and *K. daura*, in contrast to the shorter length observed in *D. ruconius* and *N. gerreoides*.

In addition, the urohyal apparatus plays a crucial role in the feeding mechanism of fish, as noted by Chollet-Villalpando *et al.*, (2014). The shape and structure of urohyal is closely linked to the ecological habitat of different fish species: fish with slender head, have an elongated urohyal while deep-bodied fish exhibit vertically expanded urohyals (Kusaka, 1974) like *P. bindus* and the members of *Deveximentum*. The morphology of the urohyal bone can be utilized to distinguish between various families, genera and even species as highlighted by Arratia and Schultze (1990), and may also provide insights into phylogenetic relationships of these family members. It has been suggested that the variability in urohyal morphology could be a valuable tool in fish classification (Kusaka, 1974; Esmaili and Teymouri, 2006).

The caudal skeleton of teleost fish has been useful in their taxonomic and plays a pivotal role in swimming ability of fish. Variability in the shape, quantity, and size of components such as hypurals has been instrumental in distinguishing between different genera and species (De La Cruz Agüero, 2013; Grünbaum and Cloutier, 2010; Kendall, 1976; Greenwood *et al.*, 1966). The fusion of the hypural plates

exhibits variability across analyzed genera. In the genus *Leiognathus* a distinct thickening of the lower margin of hypural I+II has been observed (Yabumoto and Uyeno, 1994), consistent with the characteristics found in the studied species. Additionally, the upper edge of hypural III+IV in all in-group species shows a similar thickening pattern.

Conclusions

This study represents the first comprehensive comparative analysis of the urohyal, hypural, and vomer bones within ponyfishes, significantly advancing our understanding of the osteological structure in this fish group. Within the Leiognathidae family, significant variation exists in osteological features that facilitate the taxonomic differentiation of examined taxa. These distinctions are valuable for elucidating phylogenetic relationships within the family and provide important insights into the evolutionary history of these fish species.

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Conflicts of interest

The authors declare no conflicts of interest.

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