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Osteological description of Indian lepidophagous catfish *Pachypterus khavalchor* (Siluriformes: Horabagridae) from the Western Ghats of India

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Abstract. The present study provides a comprehensive osteological description of *Pachypterus khavalchor* from the family Horabagridae. Nine individuals of *P. khavalchor* representing both males and females collected from the type locality were cleared and double-stained to provide a description of osteological characteristics. The presence of an almost straight dorsal roof to the cranium, a long and protruding premaxilla with numerous rows of tiny, villiform teeth, a spoon-like lower jaw with villiform teeth projecting outward, and five long and ossified ceratobranchials, with the 5th ceratobranchial containing a set of 80 to 90 conical teeth, sheds light on the ecomorphological adaptation in *P. khavalchor* that may have led to the evolution of lepidophagy. Furthermore, a slight difference in the structure of the complex hypurapophysis was observed between males and females. The information on the osteology of the Khavalchor catfish forms a baseline for taxonomic research of the entire Horabagridae family comprising four genera with ten species distributed in Asia.

Key words: skeletal morphology, lepidophagy, sexual dimorphism, systematics

Introduction

Despite the widespread sequencing of DNA and subsequent reconstruction of phylogenetic relations based on molecular data osteology remains an important source of data for fish systematics because of the structural and functional nature of evolutionary information (Keivany & Nelson 2004, Katwate et al. 2013, Britz et al. 2020). Osteological traits of fishes

not only give vital information on taxonomy and evolutionary relationships of particular species with other taxonomic groups but also shed light on certain key biological and ecological aspects of fish life (Katwate et al. 2013, Gosavi et al. 2018, Britz et al. 2020).

The Khavalchor catfish *Pachypterus khavalchor* (Kulkarni, 1952) (Horabagridae: Siluriformes) is well-known for its feeding behaviour; eating scales

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Fig. 1. *Pachypterus khavalchor* (a) in life, (b) cleared and double stained male, 63.6 mm (lateral view).

of other fishes which is recognised as lepidophagy (Kulkarni 1952, Gosavi et al. 2018). This specific strategy is evolutionarily conserved and expressed by only selected fishes belonging to five freshwater and seven marine families (Sazima 1983).

There exist various specific behaviours related to lepidophagy, of which many are related to particular morphological structures (Peterson & Winemiller 1997). Some species, such as the cichlid fish *Perissodus microlepis*, stealthily approach and suddenly tear off the scales of their prey as it swims past (Nshombo et al. 1985); for that purpose it has evolved dental and craniofacial asymmetries (Stewart & Albertson 2010). In contrast, *P. khavalchor* represents an aggressive type of scale eating behaviour. It chases and attacks prey, dislodging scales, which are eaten when they fall to the substrate (Gosavi et al. 2018).

Although information on several aspects of *P. khavalchor* is available, such as feeding habits (Gosavi et al. 2018), population dynamics (Gosavi et al. 2019a), digestive physiology (Gosavi et al. 2019b), reproductive biology (Gosavi et al. 2020), a detailed osteological description is scarce.

In addition to information on skeletal adaptations in the Khavalchor catfish reflecting its lepidophagy, the use of osteological data also has broader value. These data are essential for comparative studies among representatives of the entire family Horabagridae. Although some attention has recently been given to this neglected family (Ng & Vidthayanon 2011), osteological studies, other than X-ray images of *Horabagrus brachysoma* (Ali et al. 2014), are completely lacking.

For reference, we list the genera in the family Horabagridae, including the number of species in parentheses to clarify to which genera the missing information refers. The family currently consists of ten species *Pseudotropius* (4), *Horabagrus* (2), *Pachypterus* (3) and *Platytropius* (1) (Fricke et al. 2022). The three-species genus of *Pachypterus* has been represented recently by *Pachypterus atherinoides* (Bloch, 1794), *Pachypterus acutirostris* (Day, 1870) and *P. khavalchor*.

This osteological study aims to address the evolution of complex phenomena such as lepidophagy in fishes and provide baseline data for future taxonomic investigation of the family Horabagridae.



Table 1. Morphometric data of *Pachypterus khawitchor* used for osteological description.

Code	BNHS FWF 338	BNHS FWF 339	BNHS FWF 340	BNHS FWF 341	MCZPK1	MCZPK2	MCZPK3	MCZPK4	MCZPK5
Gender	Female	Male	Female	Male	Female	Male	Male	Female	Female
Total length	92.46	89.89	92.37	82.79	80.55	90.12	94.5	92.01	92.35
Standard length	72.7	70.75	72.35	64.17	70.64	75.53	76.95	73.52	74.44
Length of caudal fin	20.33	19.22	20.69	18.01	11.27	17.03	19.7	15.77	18.9
Predorsal length	27.76	24.18	27.56	38.09	24.14	26.98	28.51	28.55	28.56
Pre anal length	42.34	39.23	43.63	39.13	41.45	41.44	42.7	39.02	41.51
Prepelvic length	32.85	31.72	34.46	31.52	32.33	32.24	33.2	31.89	32.43
Prepectoral length	16.89	16.98	15.41		15.92	15.95	16.57	16.37	17.1
Length of head	18.23	17.12	17.15	17.4	17.13	16.9	17.88	17.76	15.49
Length of snout	6.2	6.03	6.65	5.82	6.07	5.52	7.18	6.79	7.17
Eye diameter	4.73	3.74	4.86	4.64	4.46	4.4	4.12	4.89	4.77
Interorbital width	7.2	6.15	6.54	6.54	5.71	5.47	6.8	5.41	6.08
Gape width	7.79	6.53	7.54	6.5	6.21	6.1	6.89	5.51	6.19
Nasal barbel length	8.57	14.37	8.41	13.1	14.1	10.13	12.12	10.21	10.1
Maxillary barbel length	20.54	26.16	18.56	18.65	17.12	25.64	26.03	26.04	26.19
Inner mandibular barbel length	9.15	11.47	10.93	8.19	7.76	11.17	11.29	10.23	10.27
Outer mandibular barbel length	16.3	17.75	12.46	9.89	9.04	16.99	17.26	13.06	17.39
Depth of body at anus	14.2	13.91	14.26	13.99	12.93	14.29	15	15.01	12.61
Length of dorsal fin base	6.69	7.83	7.19	7.95	7.53	7.53	7.9	7.35	7.5
Length of adipose fin base	3.39	2.16	3.03	3.2	3.1	2.17	2.72	2.92	3.12
Post adipose distance	11.49	12.81	14.5	13.08	12.33	15.66	16.51	15.76	17.37
Dorsal to adipose distance (origin both)	30.88	31.42	31.15	33.29	30.88	32.4	31.52	30.82	33.21
Length of caudal peduncle	6.92	13.19	12.93	11.17	7.3	12.69	13.7	13.69	13.6
Depth of caudal peduncle	6.2	6.88	6.38	6.17	5.87	7.06	7.03	7.14	5.86



Material and Methods

Nine individuals of *P. khavalchor* (Fig. 1a) including both males (n = 4) and females (n = 5) were collected using a cast net from the River Panchaganga (type locality; 16.681° N, 74.394° E and 535 m a.s.l.) at Kolhapur, Maharashtra, India with the help of local fishermen. After capture, fish were immediately anaesthetised, preserved in 10% buffered formalin, and transported to the laboratory. Morphometric measurements were taken using a digital calliper (Mitutoyo, Japan) and expressed to the nearest 0.1 mm. Morphometric methods follow Keskar et al. (2015). The digestive system of all specimens was removed and the gut contents were examined under a stereomicroscope. All specimens were cleared and stained differentially for the bone and cartilage following the methodology defined by Potthoff (1984). The osteological description was taken from cleared and stained specimens using a stereomicroscope (Magnus, India). The terminology for skeletal description followed Bockmann & Miquelarena (2008). Four specimens were deposited in the Bombay Natural History Society (BNHS) museum collection, Mumbai, Maharashtra, India, with accession numbers BNHS FWF 338-341 and the others in the collection of the Department of Zoology, Modern College of Arts, Science and Commerce, Ganeshkhind, Pune, India MCZPK 1-5. Scanning Electron Microscopy was used to examine the oral cavity of *P. khavalchor*, following the methodology established by Fishelson et al. (2014). At 10 kV accelerating voltage, samples were inspected and photographed using an analytical scanning electron microscope (JEOL JSM-6360A; JEOL, Akishima, Japan).

Anatomical abbreviations

ac – anterior ceratohyal; acp – articular cleithral process; af – anterior fontanel; ap – autopalatine; an – antorbital; bb2, 3 and 4 – basibranchials 2 to 4; bo – basioccipital; br – branchiostegal rays; bs – basipterygium; cb1-5 – ceratobranchials 1 to 5; cle – cleithrum; cWV – compound Weberian vertebra; de – dentary; dh – dorsal hypohyal; eap – external anterior process (or anterolateral arm); eb1-5 – epibranchials 1 to 5; ep – epioccipital; epu – epural; es – extrascapular; ex – exoccipital; fr – frontal; ha+has – complex hypurapophysis (hypurapophysis and secondary hypurapophysis fused); hb1-3 – hypobranchials 1 to 3; hu1+hu2 – ventral hypural plate formed by coossification of hypurals 1 and 2; hu3+hu4+hu5 – dorsal hypural plate formed by co-ossification of hypurals 3, 4 and 5; hy – hyomandibular; iap – internal anterior process (or anteromedial arm); ic – inter-

ceratohyal cartilage; ih – interhyal; i1 – infraorbital sensory branch 1; i3-6 – infraorbital sensory branches 3 to 6; io – interopercle; le – lateral ethmoid; lp – lateral process; ma – mesocoracoid arch; me – mesethmoid; mx – maxilla; na – nasal; of – optic foramen; op – opercle; os – orbitosphenoid; pa – parasphenoid; pb1, 2, 3, 4 – pharyngobranchials 1, 2, 3 and 4; pcb – posterior complex bone of pectoral girdle (coracoid, mesocoracoid, and scapula fused); pcp – postcleithral process; pc – posterior ceratohyal; pf – posterior fontanel; ph – parhypural; pop – preopercle; ppr – posterior process; pre – premaxilla; pro – prootic; ps – pterosphenoid; pt – pterotic; pu1+u1 – complex centrum composed of preural centrum 1 and ural centrum 1; pu2 – preural centrum; qu – quadrate; rpr1 – rigid part of pectoral-fin ray 1; so – suspensorium; soc – supraoccipital; sp – sphenotic; spr1 – soft part of pectoral-fin ray 1; st1-4 – suborbital tubules 1 to 4; tf – trigeminofacial foramen; tp5 – transverse process 5; tp6 – transverse process 6; trp – tripus; uh – urohyal; ur – uroneural; vh – ventral hypohyal; vo – vomer; W adap – Weberian complex anterodorsal accessory process; W tp4a – anterior limb of Weberian complex transverse process 4; Wtp4b – posterior limb of Weberian complex transverse process 4.

Results

Details of the morphometric measurements are provided in Table 1. Gut content observations of all studied specimens show the presence of multiple stacked scales in the stomach. Insect body parts and larvae were also detected in the digestive system of *P. khavalchor*. No noticeable sexual dimorphism was found except for a slight difference in the structure of the complex hypurapophysis. The representative image of a clear and stained specimen of *P. khavalchor* is shown in Fig. 1b, and detailed osteological representations are shown in Figs. 2 and 5.

Cranium (Fig. 2a, b)

The dorsal roof of the cranium is almost straight, with no apparent fossae/crests and several tiny bones articulated with distinct boundaries. There are two elongated conspicuous cranial fontanels (anterior and posterior) separated by an epiphyseal bar. For ease of description, the neurocranium is divided into rostral, optic and otic regions.

The rostral region is divided into several subregions, including the pre-maxilla and maxilla, mesethmoid, autopalatine, nasals, and vomer. The premaxilla is long and protruding, with numerous rows of tiny, villiform teeth anteriorly directed. Teeth present on

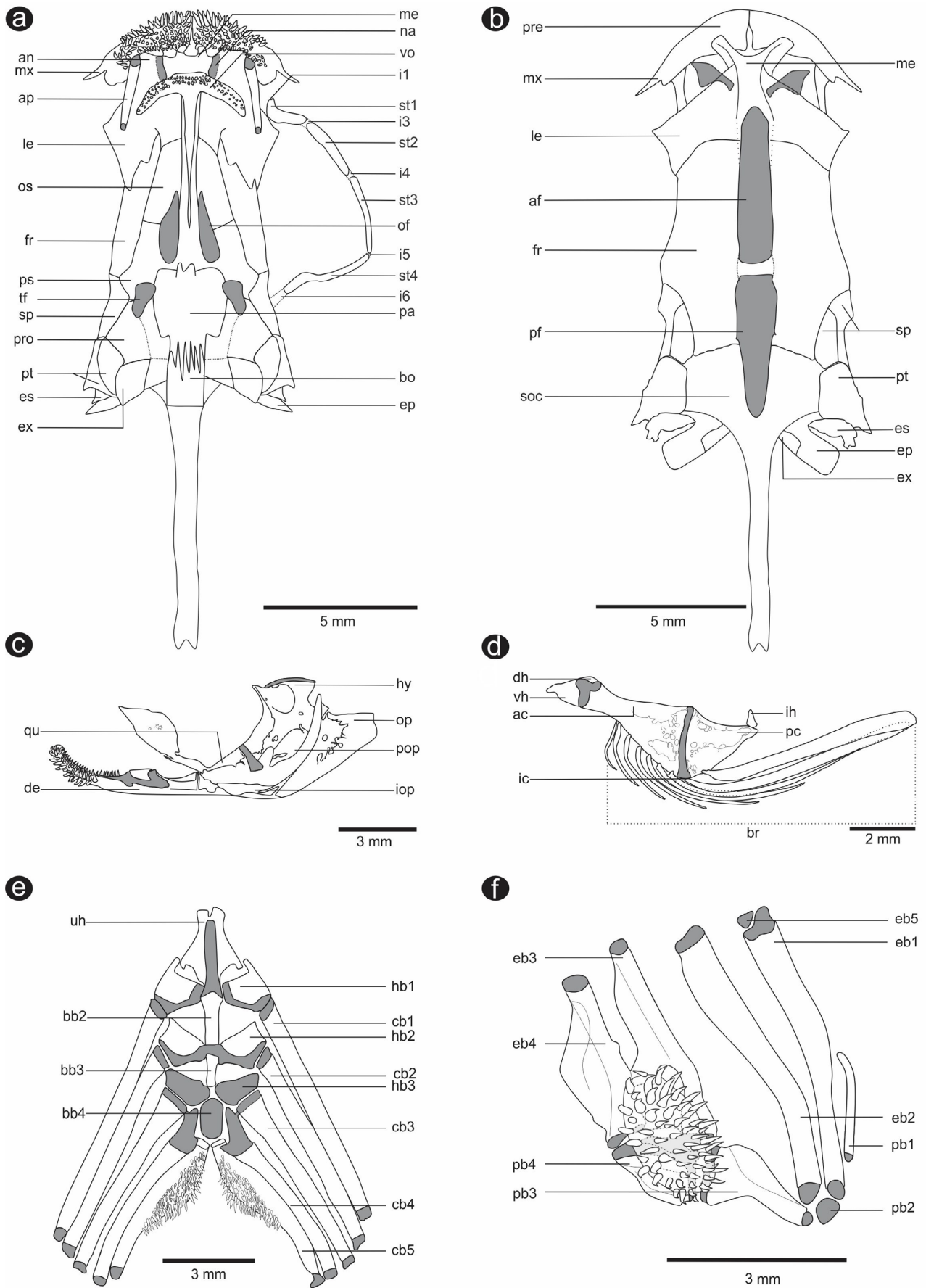


Fig. 2. Osteology of *Pachypterus khavalchor*, specimen BNHS 6032, (a) cranium, ventral view, (b) cranium, dorsal view, (c) lower jaw, (d) hyoid skeleton, (e) gill arch, (f) dorsal gill arch.

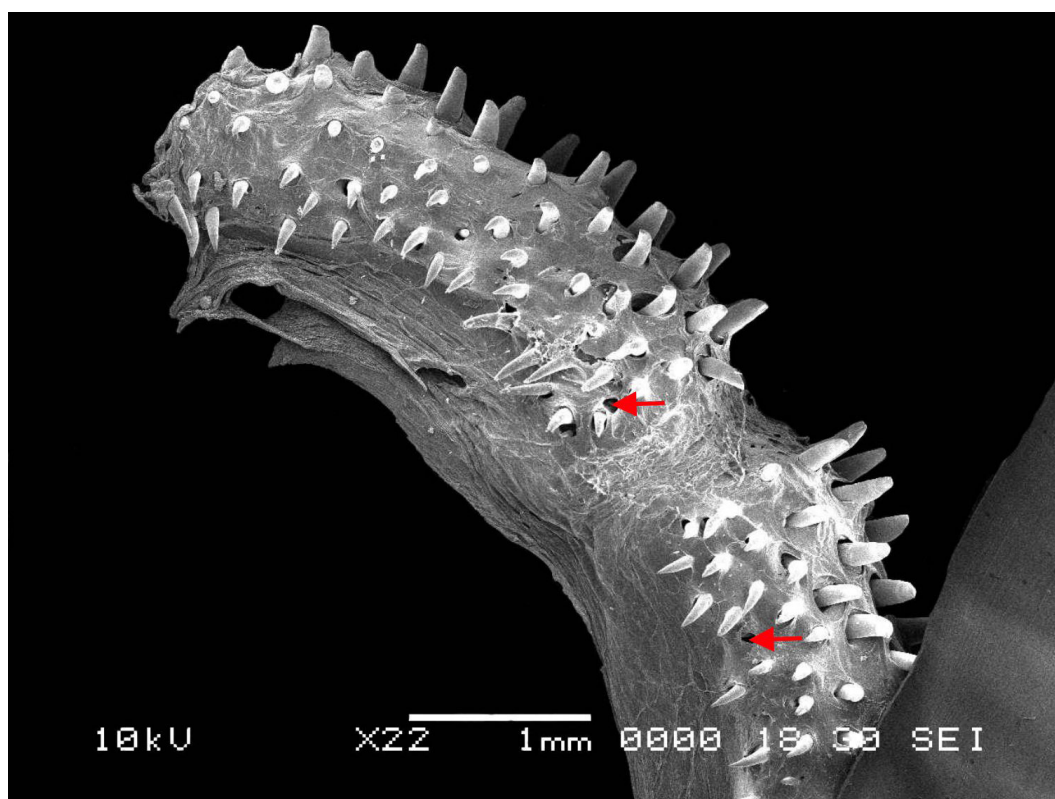


Fig. 3. Scanning electron micrograph of lower jaw of *Pachypterus khavalchor*, dorsal view (arrow heads shows cavities due to dislodged teeth).

the posterior side of the premaxilla are shorter than the anterior, with a few broken or dislodged (Fig. 3). The maxilla is small, entirely ossified, and located distally to the premaxilla. The mesethmoid is a “Y” shaped structure with short, thick, and blunt cornua anterolaterally directed. The autopalatines are paired, tubular, and laterally situated, with tiny, rounded cartilages at their ends. The nasals are ossified and short, with entrance and exit sites for the supraorbital laterosensory canal and antorbital. The vomer is sagittiform in shape, centrally located, partially ossified with laterally curved arms and possessing tiny villiform teeth on the front.

The orbital region is clearly visible in the dorsal view, delimited anteriorly by the lateral ethmoid, laterally by the frontal, and posteriorly by the sphenotic. The inter-orbital width accounts for around 40% of the entire length of the cranium. Lateral ethmoids are paired, entirely ossified, roughly rectangular, bordered anteriorly by autopalatines and located on each side of the vomer. It comprises the posterior section of the olfactory organ and connects to the orbitosphenoid through an unsutured articulation. The frontal bone, the largest in the skull, is entirely ossified and is bordered anteriorly by the lateral ethmoid and posteriorly by the supraoccipital. The sphenotic bones are paired, completely ossified,

approximately triangular, laterally positioned, and bordered anteriorly by frontal, anterolaterally by parasphenoid, and posterolaterally by prootic. It has three laterosensory canal openings: the supraorbital laterosensory canal (anteromesial opening), the infraorbital laterosensory canal (lateral opening) and the otic laterosensory canal (posterior opening). The infraorbital laterosensory canal has six branches (i1-6) connected with suborbital tubules (st1-4). The supraorbital laterosensory canal has eight branches (s1-8). The optic foramen is elongated, roughly twice the length of the trigeminofacial nerves, and is surrounded by orbitosphenoids (anterodorsally and anteroventrally), pterosphenoids (posterodorsally), and parasphenoids (posteroventrally). The trigeminofacial foramen is smaller, oval, and surrounded by pterosphenoid (anteriorly and dorsally) and prootic (posteriorly and posteroventrally).

Prootic, pterotics, supraoccipital, parasphenoid, epiotic, extrascapular, basioccipital, pterosphenoid, and exoccipital bones articulate in the otic area. Pterotics are completely ossified, located posterolaterally to the prootics (on the ventral side), and meet the supraoccipital on the dorsal side, whereas the epiotic, which is elongated and forms the posterior-most border, meets on the posteromedial side. All of their connections are sutured. The



extrascapular is ossified and slightly triangular in the posterolateral corners of the skull. The supraoccipital bone is completely ossified and is long, straight, and forked distally. The width of the pointed tip of the supraoccipital process is constant until its posterior end. The parasphenoid is fully ossified and square in shape, anteriorly bifurcated and merges with the posterior portion of the vomer, with a zig-zag sutured pattern posteriorly. The basioccipital is broad, positioned posterior to the parasphenoid, joins the exoccipital laterally, and tapers posteriorly and articulated with the first abdominal vertebra.

Lower jaw, suspensorium and associated structures (Fig. 2c)

The lower jaw resembles a spoon, having a broad base and a tapering dentigerous area. The dentary is completely ossified and elongated, with several irregular rows of small villiform teeth on the anterior margin and dorsal surface projecting outward and inward respectively. The preopercle is triangular, strong and slightly concave, firmly attached to the hyomandibula. The preopercle is connected to the quadrate anteriorly. Its anterior section extends up to the posterior edge of the dentary and firmly articulates with the preopercle. The inter-opercular is approximately triangular, posteriorly close to the opercle boundary. The hyomandibula bone is roughly rectangular and joins with the quadrate via a cartilaginous sheet. Posteroventrally, the hyomandibula connects the preopercle and sub-triangular opercle.

Hyoid arches (Fig. 2d)

The dorsal and ventral hypohyals differ in size and are divided by a tiny irregular cartilage band. The anterior ceratohyal is longer than the posterior ceratohyal and is divided by a thin cartilaginous strip called the inter-ceratohyal. It is narrower in the centre and broader towards the tip, providing a surface for hypohyal articulation. The posterior ceratohyal, on the other hand, is broader at the base and narrower towards the tip. The nodular and ossified interhyal is located at the tip of the posterior ceratohyal. There are nine branchiostegal rays in all. The first seven connect to the anterior ceratohyal ray, the eighth to the inter-ceratohyal ray, and the ninth to the posterior ceratohyal ray. The length and breadth of the branchiostegal rays increase anteroposteriorly.

Gill arch (Fig. 2e, f)

Basibranchial: basibranchial 1 is absent. Ossified basibranchial 2 and 3 are fused, forming a long

rod. Basibranchial 2 is anteriorly positioned on the dorsal side of the urohyal, whereas the posterior tip of basibranchial 3 is located in the intermediate area of hypobranchial 3. Basibranchial 4 is entirely cartilaginous and bordered anteriorly by hypobranchial 3, laterally by the cartilaginous heads of ceratobranchial 4 and posteriorly by the ossified head of ceratobranchial 5, respectively.

Hypobranchials: three hypobranchials are present. Hypobranchial 1 has an uncinat process on its anterodistal side. Hypobranchials 1 and 2 are entirely ossified, with a cartilage sheet running along their entire posterior border. Hypobranchial 3 is approximately rectangular and totally cartilaginous. Hypobranchial 4 is absent.

Ceratobranchials: there are five long and ossified ceratobranchials. Ceratobranchials 1 to 4 have cartilage at their extremities and are noticeably wider than the middle portion and form a rod-like shape. Ceratobranchial 5 has a set of 80-90 conical teeth of almost the same size. The basal head of ceratobranchial 5 is cartilaginous with its tip ossified.

Epibranchials: there are five epibranchials. Epibranchials 1 to 4 are elongated and completely ossified with cartilage at their extremities. Epibranchial 5 is tiny, knob-like and completely cartilaginous.

Pharyngobranchials: four pharyngobranchials are present. Pharyngobranchial 1 is an ossified rod-like structure with cartilage at the tip of one end. Pharyngobranchial 2 is nodular and completely cartilaginous. Pharyngobranchial 3 is irregular, broad and entirely ossified, except for the presence of cartilage at their extremities. Pharyngobranchial 4 is rod-like, completely ossified with a cartilage sheet at both ends.

Tooth plate: a globular tooth plate is located on the posterior side of pharyngobranchial 3, pharyngobranchial 4, and the terminal ends of epibranchial 3 and 4, bears around sixty-four teeth on each tooth plate.

Urohyal: the urohyal dorsal view is triangular, ossified, and has a greater dorsal keel than the horizontal position. Its posterior boundary approaches the anterior boundary of the basibranchials.

Weberian apparatus (Fig. 4)

The anterior four vertebrae contribute to the Weberian apparatus. The tripus is well developed with hook-

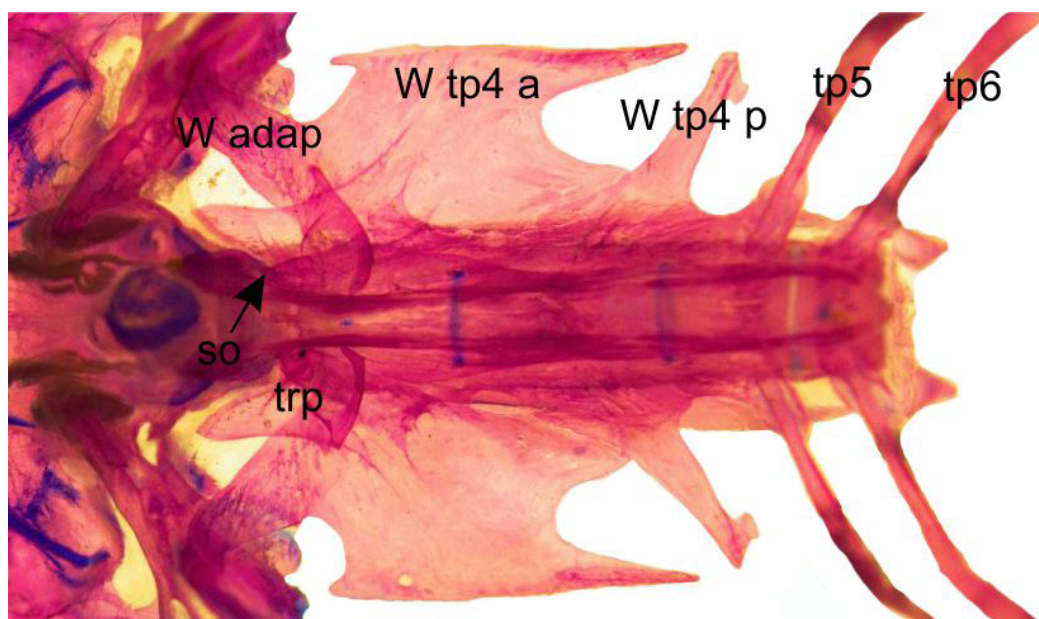


Fig. 4. Weberian apparatus attached to neurocranium in *Pachypterus khavalchor*, ventral view.

like transformator process at the posterior end. The suspensorium is nodule-like in shape and loosely attached to transverse process 4. A broad anterior limb and a rod-like posterior limb of transverse process 4 divides the fourth transverse process, giving a deep U shape. The transverse process of vertebrae 5 and 6 are longer than the posterior limb of the fourth transverse process. The accessory the anterodorsal process of the compound Weberian centrum is fused with anterior limb of transverse process 4 and lies close to the exoccipital.

Vertebral column (Fig. 1b)

There are 39 vertebrae in total, including 13 abdominal (including Weberian vertebrae 1-4) and 26 caudal vertebrae. The distal ends of the ribs are narrow. The neural and haemal spines of the caudal vertebrae are mostly straight, with no apparent projection. The first dorsal fin is supported by seven distal-proximal pterygiophores, one unbranched dorsal fin ray, and seven-branched soft rays are present. The anal fin has three anal spines and the remaining twenty-two are branched soft rays and is supported by the distal-proximal pterygiophores.

Pectoral girdle (Fig. 5a)

The pectoral girdle is formed by the ossification of two long bones, the cleithrum. These two bones are fused, forming the posterior complex bone ventrally, and are joined by four interlocking sutures. The post-cleithral process is pointed and narrow. The anterior cleithral process is curved and about half the length of the post-cleithral process. The mesacoracoid arch is pointed, located about above the anterior cleithral

process. The rigid pectoral ray is ossified and bears serrations, whereas the soft pectoral ray is short, branched, and totally cartilaginous.

Pelvic girdle (Fig. 5b)

The basiptyerygium has a slightly arched and excavated dorsal and ventral surface. External and internal anterior processes (anterolateral and anteromedial arms, respectively) are very long anteriorly oriented processes. The basal arm of the anterolateral is consistently thick but narrow at the tip and devoid of cartilage. The basal portion of the anteromedial arm is wider than the tip that meets its counterparts. The anteromedial arm is slightly shorter than the anterolateral arm. The basiptyerygium has a slight lateral process and a prominent posterior process. Both the lateral and posterior basiptyerygium cartilages are clearly separated from one another. The bony section of the posterior process is curved and shorter than the majority of the basiptyerygium. Each branched cartilaginous part of the posterior process is longer than the bony portion of the posterior process. The cartilaginous middle portion of basiptyerygium is separated from each other. The basiptyerygium has six segmented pelvic fin-rays. One ray is unbranched, while the following five are branched.

Caudal skeleton (Fig. 5c)

The ossified hypural 1 and 2 are merged, resulting in a single ventral caudal plate. The parhypural runs near to the ventral caudal plate, distinctly separated from the margin of the ventral caudal plate. The rod-like, entirely ossified uroneural, is located above the dorsal hypural plate.

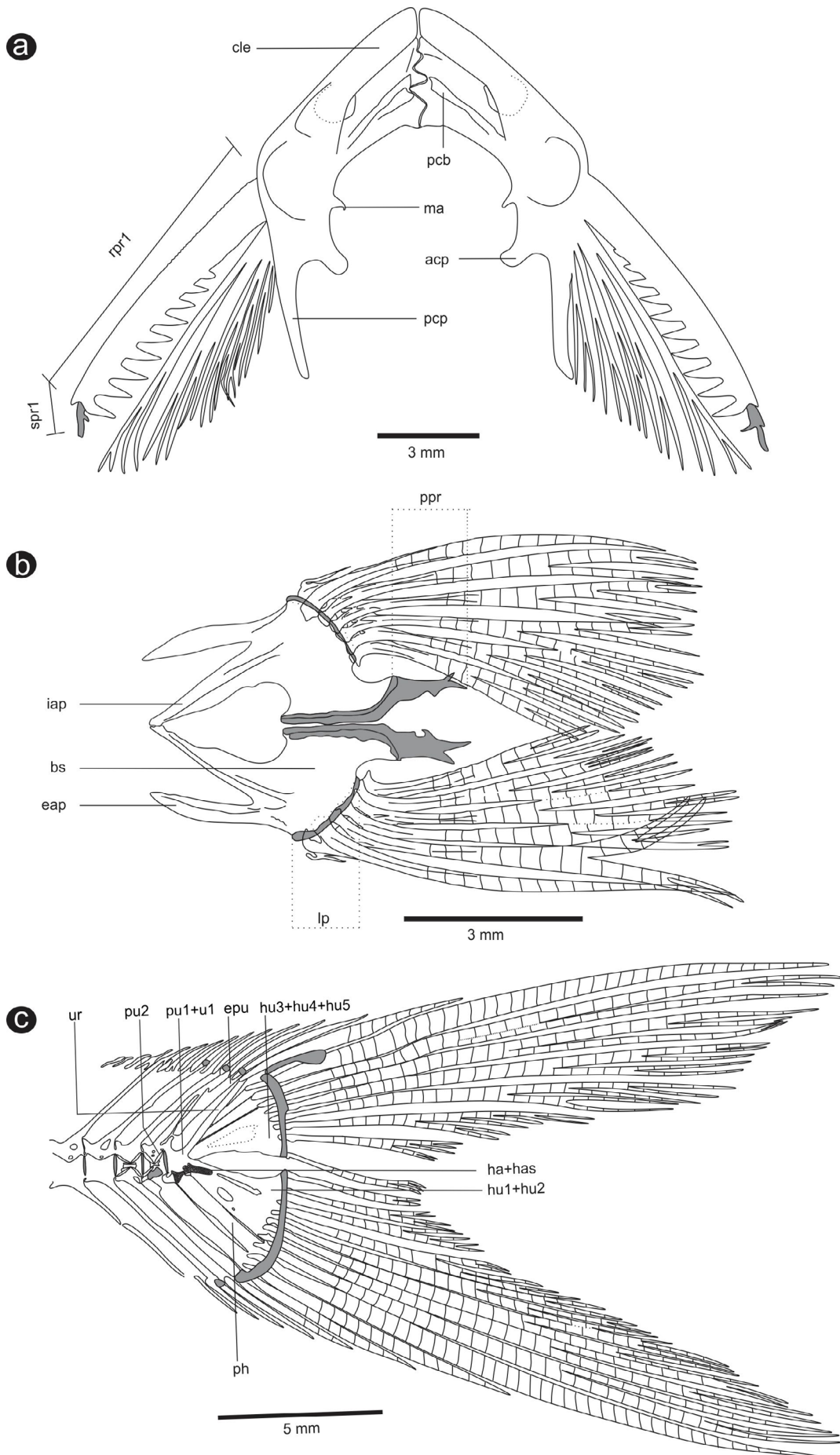


Fig. 5. (a) pectoral girdle, (b) pelvic girdle, (c) caudal skeleton of *Pachypterus khavalchor*.



The dorsal and ventral hypural plates are distinct from one another except for their base. The hypural three, four, and five plates are merged and ossified to create a single dorsal, caudal plate. The hypurapophysis and secondary hypurapophysis are fused, forming a complex hypurapophysis, a wide horizontal plate, that reaches the base of hypural 2 (hypurapophysis “type C” of Lundberg & Baskin 1969). There is a slight difference in the structure of the complex hypurapophysis between males and females. The hypurapophysis and secondary hypurapophysis are more robust and pointed in females than males. The caudal artery foramen is located on the ventral caudal plate. The dorsal, caudal plate comprises a uroneural and complex dorsal hypural plate (including hypurals 3, 4 and 5), bears seven branched rays and two unbranched rays with one dorsal most attached to the uroneural. The ventral caudal plate is made up of a parhypural and complex ventral hypural plate (including hypurals 1 and 2) that bears eight branched and two unbranched rays. The epural is a broad region located near the neural spine of preural centrum 2. The intricate centrum is made up of two parts: preural centrum 1 and ural centrum 1, which is made up of the haemal spine and neural spine.

Discussion

We present a thorough osteological description of *P. khavalchor* in this work. However, due to the lack of information about the osteological aspects of the Horabagridae family, our comparative analysis is limited. Thus, the osteology of *P. khavalchor* was compared to that of *H. brachysoma* (family Horabagridae) and its close relatives of the family Bagridae (Kaatz et al. 2010) as well as other fishes belonging to the order Siluriformes.

Lepidophagy in fish is known to have evolved as a derived, highly specialised habit supported by behavioural and morphological modifications (Sazima 1980, 1983). Gosavi et al. (2018) provided empirical evidence for scale-eating behaviour in the catfish *P. khavalchor*, as well as limited data on the significance of the oral anatomy in the lepidophagous behaviour of this species. The peculiar form and arrangement of teeth in the upper and lower jaws together with behaviour and digestive physiology have been reported to assist *P. khavalchor* in efficiently using the scales of live fish as food (Gosavi et al. 2018).

According to Gosavi et al. (2018), the pre-maxilla of *P. khavalchor* is protruding, with many rows of tiny, molariform teeth extending outward, indicating

that the mouth cavity is suited for hard food, such as scales. However, our study shows that the teeth present on the pre-maxilla are directed outward but villiform in shape. Similar villiform shaped pre-maxillary teeth were shown in carnivorous catfishes such as *Bagrus bajad*, *Pseudobagrus aurantiacus* (*Tachysurus aurantiacus*) and *Pseudobagrus tokiensis* (*Tachysurus tokiensis*) (Watanabe & Maeda 1995, Eshra & El Asely 2014).

Generally, premaxillary teeth are directed inward in catfishes, such as *Pangasius macronema*, *Pareiorhaphis miranda*, *Hypostomus pantherinus* and *Horaglanis krishnai* (Mercy & Pillai 1985, Diogo & Diogo 2007, Pereira & Zanata 2014, Zawadzki et al. 2021), but our investigation shows the orientation of the premaxillary teeth is outward, which was also supported by Gosavi et al. (2018). Orientation of teeth observed in *P. khavalchor* may be among the most important adaptations in support of lepidophagous behaviour.

The dietary patterns of *H. brachysoma* are unspecialised and opportunistic (reviewed in Raghavan et al. 2016). There have been no reports of lepidophagy in this species, suggesting it is likely to have generic oral morphology, as no specific oral structural description is available to make concrete statements.

Both the upper and lower pharyngeal jaws have conical pharyngeal teeth, which could be utilized for crushing hard food materials, such as scales, insect body parts and molluscs. Other non-lepidophagous Siluriformes fishes, such as *Rita rita*, *Kryptoglanis shajii* and *Erethistes pussilus*, have a similar arrangement and structure of the pharyngeal teeth (Khanna 1962, Gauba 1967, Lundberg et al. 2014). This observation demonstrates that the structure of pharyngeal teeth is not designed for lepidophagy, but rather for crushing hard objects.

The anal fin ray count of *P. khavalchor* is three unbranched rays and the remaining twenty-two are branched soft rays, while *H. brachysoma* has three unbranched rays and twenty-nine branched fin rays in some specimens. There is one unbranched dorsal fin ray and seven-branched soft rays in *P. khavalchor*, and one unbranched dorsal-fin ray, and six to seven branched rays in *H. brachysoma* (Ali et al. 2014). The supraoccipital process is long and distally forked in *P. khavalchor*, which is identical to *Pseudobagrus adiposalis* valid as *Tachysurus adiposalis*, while it is short and distally not forked in *Pseudobagrus gracilis* valid as *Tachysurus gracilis*, and *Pseudobagrus brachyrhaddon*

valid as *Tachysurus brachyrhabdion* (Li et al. 2005, Cheng et al. 2008). *Tachysurus lani* has a slender supraoccipital process with uniformly converging sides and a forked apex (Cheng et al. 2021). The pterotics are completely ossified and are positioned postero-laterally to the prootics (on the ventral side) and medially to the supraoccipital on the dorsal side. In *P. khavalchor*, all connections between them are sutured, but in *B. bajad*, the pterotics constitute the posterolateral portion of the otic capsule and are sutured with parieto-supraoccipital.

The osteology described in this study serves as a reference for further study of lepidophagous behaviour in catfishes, as well as a species-specific osteological investigation.

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