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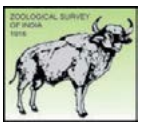

Comparative Cranial Osteology of *Hydrophis schistosus* Daudin, 1803 and *Hydrophis platurus* (Linnaeus, 1766) (Elapidae: Hydrophiinae)

Sonia Mondal*, Souradeepa Kundu, Pratyush P. Mohapatra and C. Raghunathan
Zoological Survey of India, M-Block,
New Alipore, Kolkata 700053

Abstract

The viviparous sea snakes of the subfamily Hydrophiinae are morphologically and ecologically diverse and distributed throughout the Indo-Pacific. Earlier works on the cranial morphology of the Hydrophiinae were mostly on the description of teeth-bearing bones and schematic diagrams of skulls. The present study aims to provide a detailed description of the cranium and mandibular structure of two commonly distributed sea snake species in India, namely *Hydrophis schistosus* and *H. platurus.* This study analyzes the variations in the cranial morphology between these two species using thirty-two allometric characters. This study also reveals that various components of the skull vary in shape as compared to their terrestrial Elapid cousins. On comparison among these two species, it was found that there are considerable morphological variations in the length of major bones like ectopterygoid, frontal, mandible, maxilla, nasal, parietal, premaxilla, pterygoid and quadrate. In addition, structural variation in the frontal, parietal, premaxillary, and basisphenoid bones along with variation in all the teeth-bearing structures including maxilla, palatine, pterygoid and dentine have also been noticed. Further, the basisphenoid process which is present in *H. schistosus* and absent in *H. platurus* which may have a functional role associated with the dietary specialization in the former species to capture the catfishes that constitute their major prey.

Keywords: Basisphenoid process, Cranial morphology, Hydrophiinae, Piscivorous, *Hydrophis,*

Introduction

The skull or the cranium in vertebrates is the protective casing of the brain and is the most complex skeletal structure involving several highly integrated structural and functional units (Hanken and Hall, 1993). The skull and the associated bones are also involved in feeding, protection of the central nervous system and accommodation of sense organs, along with locomotion, social interaction, mate competition, courtship and optionally defence mechanism (Smith, 1993; Cundall 2000; Cundall and Greene 2000; Shine *et al.*, 2000; Herrel *et al.*, 2007). The cranium of a snake is composed of a number of mobile and articulated elements involved in cranial kinetics (Smith, 1993; Herrel *et al.*, 2007). Taxonomic comparison in snakes involves a great deal of the skull (Kramer, 1980; Gloyd and Conant, 1990). Owen (1866) was possibly the first to describe osteology and myology of species such as *Crotalus horridus*, *Python tigris*, *Boa constrictor*, *Naja tripudians* and *Deirodon scaber*. Later, works by Huxley (1871), Gegenbaur (1878), Hoffman (1890), Sedwick (1905), Wiedershiem and Parker (1907), Williston (1925), Kingsley (1917), Goodrich (1930), Versluys (1937) and the classical book on "Osteology of Reptiles" by Romer (1956) have dealt with serpent skeletal systems.

The viviparous sea snakes of the subfamily Hydrophiinae distributed throughout the Indo- Pacific, originated 8-17 million years ago, and about 60% of species richness in this

*Author for correspondence : researchwild.ophidia@gmail.com
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group is accounted for by the exceptionally rapid speciation of the *Hydrophis* clade dated around 1.5-7.5 million years old (Dunson, 1982; Mozzotti and Dunson, 1984). In the Indian Ocean, most of the sea snakes have been colonized within the last 3 million years and have allopatrically speciated from source lineages in the West Pacific (Ukuwela *et al.*, 2017). Earlier work on the cranial morphology of the species under this subfamily was restricted to a few points mentioned about maxilla bone by Gunther (1864) and a short description of some of the cranial bones was mentioned by Smith (1926) along with schematic diagram of the skull without detailed description. Kharin (2007) provided some information on the osteology of *Hydrophis platurus* collected from Russia. In the review of the genus *Hydrophis*, Kharin (2004) mentioned a few osteological characters of the genus. In recent times, only a few works have been done on osteological aspects of sea snakes involving a few Australian and South-east Asian species (Borczyk *et al.*, 2021; Sherratt *et al.*, 2019). There is a lack of literature on the osteological aspects of sea snakes from the Indian subcontinent. To address the gap, here we provide a detailed description and comparative analysis of various components of the cranium and the lower jaw bones in two widespread species, *Hydrophis schistosus* Daudin, 1803 and *H. platurus* (Linnaeus, 1766) in India. The hook-nosed sea snake (*Hydrophis schistosus*) and the yellow-bellied sea snake (*Hydrophis platurus*) are viviparous, of which the former is specialized to feed on spiny catfishes and puffer fishes (Voris and Voris, 1983), whereas the latter is more of a generalist and surface feeder which preys on small pelagic fishes (Klauber, 1935; Kropach, 1975).

Materials and Methods

We examined one adult specimen each of *Hydrophis schitosus* (Registration No. ZSI-K-23476) and *H. platurus* (Unregistered: collected by SKD & PPM from Puri coast, Odisha), housed in the collection of the Zoological Survey of India, Kolkata. These formaldehyde-preserved specimens were utilized in the preparation of skeletal material. The head portion was skinned and kept in boiling water for varying lengths of time, the time determined by the type of skeletal muscle attachment, then the muscles were removed manually using forceps under a stereoscopic microscope (LEICA EZ4). The skeletal material prepared in the aforesaid manner was then photographed using Nikon D7000 digital camera and thereafter the skull was disarticulated to describe various components of the skull bones. For each skull, 30 characters were observed (Bullock and Tanner, 1966), 32 measurements were taken (Borczyk *et al.*, 2021). Based on the overall skull shape and proportions of the skull elements involved in feeding these distances were chosen (Borczyk *et al.*, 2021). All measurements were taken with a digital Mututoyo Absolute calliper (to the nearest 0.1mm) directly from the skull.

Abbreviations: CQL: Quadrate crest length; QL: Quadrate length; ECT: Ectopterygoid length; FL: Frontal length; FW1: Frontal width taken at fronto-parietal contact; FWA: Frontal width at anterior point; FWM: Frontal width at mid-point; FWP: Frontal width at posterior point; FMDB: Mandibular fossa length; MXL: Maxilla length; NL: Nasal length; NW: Nasal width; NCL: Nasal component length taken at naso-frontal articulation to the most rostral tip of premaxilla; PAR: Parietal length; PW1: Parietal width at postorbital process; PWM: Parietal width at midpoint; PWP: Parietal width at posterior point; PFH: Prefrontal height; PFL: Prefrontal length; PML: Premaxilla length; PMW: Premaxilla width; PLL: Palatine length; PRETR: Retroarticular process length; PTL: Pterygoid length; PTTL: Length of tooth row on pterygoid; MDL: Mandible length taken from its rostral tip to the caudal tip; MD2L: Mandible length taken from the rostral tip of the mandible to the mandible joint; DENT: Dentary length; LCM: Length of compound bone of maxilla; STP: Supratemporal length; SL: Skull length; SW: Skull width; SH: Skull height; A: Angular; AR: Articular; BO: Basioccipital; BS: Basisphenoid; D: Dentary; DF: Dental foramen; EC: Ectopterygoid; EO: Exoccipital; FR: Frontal; M: Maxilla; NAS: Nasal; PAL: Palatine; PARA: Parasphenoid; PFR: Prefrontal; PM: Premaxilla; PO: Postorbital; PR: Prootic; PRA: Prearticular; PT: Pterygoid; QU: Quadrate; SA: Surangular; SM: Septomaxilla; SOC: Supraoccipital; SP: Splenial; SUP: Supratemporal; MT: Maxillary teeth; PT: Palatine teeth; PTT: Pterygoid teeth; DT: Dentine teeth.

Results and Discussion

The two species considered in this study (*H. schistosus* and *H. platurus*) show similar components of the cranium, however, they show variations in shape and size in some of the major components of the skull (Figure 1). A comparative measurement of various components of the cranium in these two species is provided in Table 1.

The premaxilla is a single median bone that terminates the snout. Its anterior surface is an inverted Y-shaped ridge, the prongs of which extend in a dorso-lateral direction; it is wider than its length in both the species but is much larger

in *H. platurus* than *H. schistosus*. The postero-dorsal process extends dorsally to connect with the anterior part of the nasal in *H. platurus*, whereas the postero-dorsal process is very short and not in contact with the nasal in *H. schistosus*. The elongate, horizontal, plate-like structure called septomaxillae form the floor of the internal nares. The wing-like structure of the septomaxilla is much wider in *H. schistosus* than *H. platurus*. In the case of *H. schistosus* the edge is much rounded in comparison to the short rectangular edge in *H. platurus*. From a dorsal view, the articulated nasals appear as a pear-shaped structure between the septomaxilla and the frontals and are loosely connected to them by connective tissues. The nasal is not connected to the premaxilla; anteriorly it is connected with the posterior process of the septomaxilla and the posterior end which is oval shaped is articulated in between the two frontals. The nasal is much longer in *H. platurus* than *H. schistosus*. Although it is pear-shaped in both species, in the case of *H. schistosus* each nasal bone is dorsally distinctively separated by a suture, whereas in *H. platurus* this suture is less distinct. The frontals are highly developed and form a complete enclosure for the anterior portion of the skull. Anteriorly the frontal contacts with nasals and septomaxillae, and posteriorly with the parietal. Frontal is longer than wide in both species. It is longer and wider in *H. platurus* in comparison with *H. schistosus*. In the latter, the anterior width and the posterior width are equal having a wider middle region, whereas in the former have a wider middle region and posterior region and a much narrower anterior end. From a lateral view, each prefrontal is an irregular cone-shaped structure with a laterally compressed anterior process (forming the apex of the cone) extending laterally to the posterior portion of the nasal, septomaxilla. The prefrontal height is higher in *H. schistosus* than *H. platurus*. The prefrontal is constricted in the middle region with an elongated posterolateral process in *H. schistosa* as compared to *H. platurus*, the prefrontal is not constricted in the middle and has a wider middle and postero-lateral process. The largest element of the cranium is the parietal and forms the greater part of the braincase, but like frontals, it extends far down on either side of the brain reaching ventrally to the basisphenoid and forming the posterior of each orbit. The parietal is much longer in *H. platurus* and is wider at the point of the postorbital process. The width of the parietal in the middle is narrow in both species, however, the width of the parietal at the posterior region, where it is connected with the supraoccipital is much wider in *H. schistosus* than in *H. platurus*. Each maxilla is a short curved bar that conforms to the shape of the head on the medial border; about mid-way, there is a small horizontal dorso-posteriorly pointing process that articulates with the ventral surface of the prefrontal and does not extend beyond palatine. The maxilla is proportionately longer (MXL/SL) in *H. platurus* than *H. schistosus*. In both species, the venom-delivering poison fang is situated at tip of the maxilla bone followed by a diastema. The number of maxillary teeth after the fang is 3 in *H. schistosus* and 5-6 in *H. platurus*. The pterygoid and palatine are structurally similar in both species but differ in length and number of teeth on those two tooth-bearing structures. The length of the pterygoid is longer in *H. schistosus* than *H. platurus* having 13 and 23 teeth respectively. The percentage of PTTL to the length of the pterygoid is 71% in *H. schistosus*, whereas it is 83.5% in *H. platurus*. The palatine bone attached to the pterygoid also bears teeth which are different in both species, in *H. schistosus* the count is four, and in case of *H. platurus* it is 5-7. The ectopterygoid is a small club- shaped, flat bone in between the maxillae and the pterygoid, overlying on each side at its ends and connects with the pterygoid at the 10th teeth in *H. schistosus* and at 12th in *H. platurus*. The structure of ectopterygoid is similar in both species but is longer in *H. schistosus* than *H. platurus*. The quadrate in both species is rectangular in shape; proximally connected with the postero-lateral border of the supratemporal and distally with the condylar surface of the mandible. The quadrate bone is longer in *H. schistosus* than *H. platurus*, and has a longer crest length in the former. In the case of *H. schistosus,* the anterior end of the quadrate attached to the supratemporal is wider and gradually tapering as it extends down towards its posterior end where it articulates with the mandible, as compared to *H. platurus* which is of equal width along the length of the bone from anterior to the posterior end. The basisphenoid is present without a suture anteriorly to the elongated parasphenoid, forming a single bone. The basisphenoidal portion of the bone is a flat hexagonal plate, bounded dorsally at its margins by prootic and parietal walls and posteriorly by the basioccipital. The basisphenoid is a flat structure with a feeble keel medially in case of *H. platurus*, this structure has a distinct, wide shaft-like process medially in *H. schistosus* which we termed as "basisphenoid process" extending between 2nd -6th pterygoid teeth. The mandible is composed of two bones: the longer posterior part of each jaw is composed of angular, prearticular, articular, surangular and splenial aspects and is without teeth, the dentary forms the anterolateral portion of the jaw.

The Mandible or the lower jaw is 1.7 times longer than the skull length in *H. schistosus* and is 1.3 times in *H. platurus*. In *H. platurus* the compound bone of the maxilla at its anterior-most end is upwardly directed at the juncture to the dentine but is straight in *H. schistosus.* Further, the postero-lateral end of the dentine at the exterior side is longer and gradually slanting in *H. platurus* in comparison to *H. schistosus.* The ratio of dentine bone vs. mandibular length in *H. schistosus* is 0.47 as compared to *H. platurus,* which is 0.51. The dentine in *H. schistosus* has a knob-like process at its anterior free end which is absent in *H. platurus* and is much wider. The number of teeth present on the dentine is almost equal in both species with 15 rows of teeth in *H. schistosus* and 15-17 rows in *H. platurus*. The mandibular fossa is longer in *H. schistosus,* whereas in *H. platurus* the retroarticular process is longer.

Our results show that the overall length of the skull of *H. schistosus* is slightly longer than the *H. platurus*, whereas the skull height and skull width is 1.3 times and 1.2 times respectively than the *H. platurus*. The presence of a strong, wide basisphenoid process in *H. schistosus* and its absence in *H. platurus* indicates that this structure is associated with crushing the hard skull of the spiny catfish which is the predominant prey species in *H. schistosus*.

Table 1. Comparative skull measurement of *Hydrophis schistosus* and *Hydrophis platurus*

Characters	Measurements (mm)	
	Hydrophis schistosus	***Hydrophis platurus***
CQL	6.16	5.08
QL	15.03	10.37
ECT	12.31	7.87
FL	5.94	7.53
FW1	1.30	3.19
FWA	2.84	3.23
FWM	3.33	7.31
FWP	2.84	6.13
FMDB	7.24	5.51
MXL	10.88	13.36
NL	4.88	7.23
NW	1.36	1.81
NCL	9.08	8.95
PAR	9.64	11.38
PW1	6.86	10.08
PWM	3.63	4.89
PWP	5.17	1.99
PFH	6.58	5.26
PFL	3.48	4.36
PML	1.12	2.59
PMW	4.2	5.16
PLL	8.62	9.28
PRETR	3.46	4.76
PTL	27.84	24.46
PTTL	19.80	20.43
MDL	42.32	38.15
MD2L	36.85	32.59
DENT	20.14	19.78
LCM	32.67	26.64
STP	7.41	7.42
SL	30.93	29.00
SW	9.58	7.12
SH	19.17	15.74

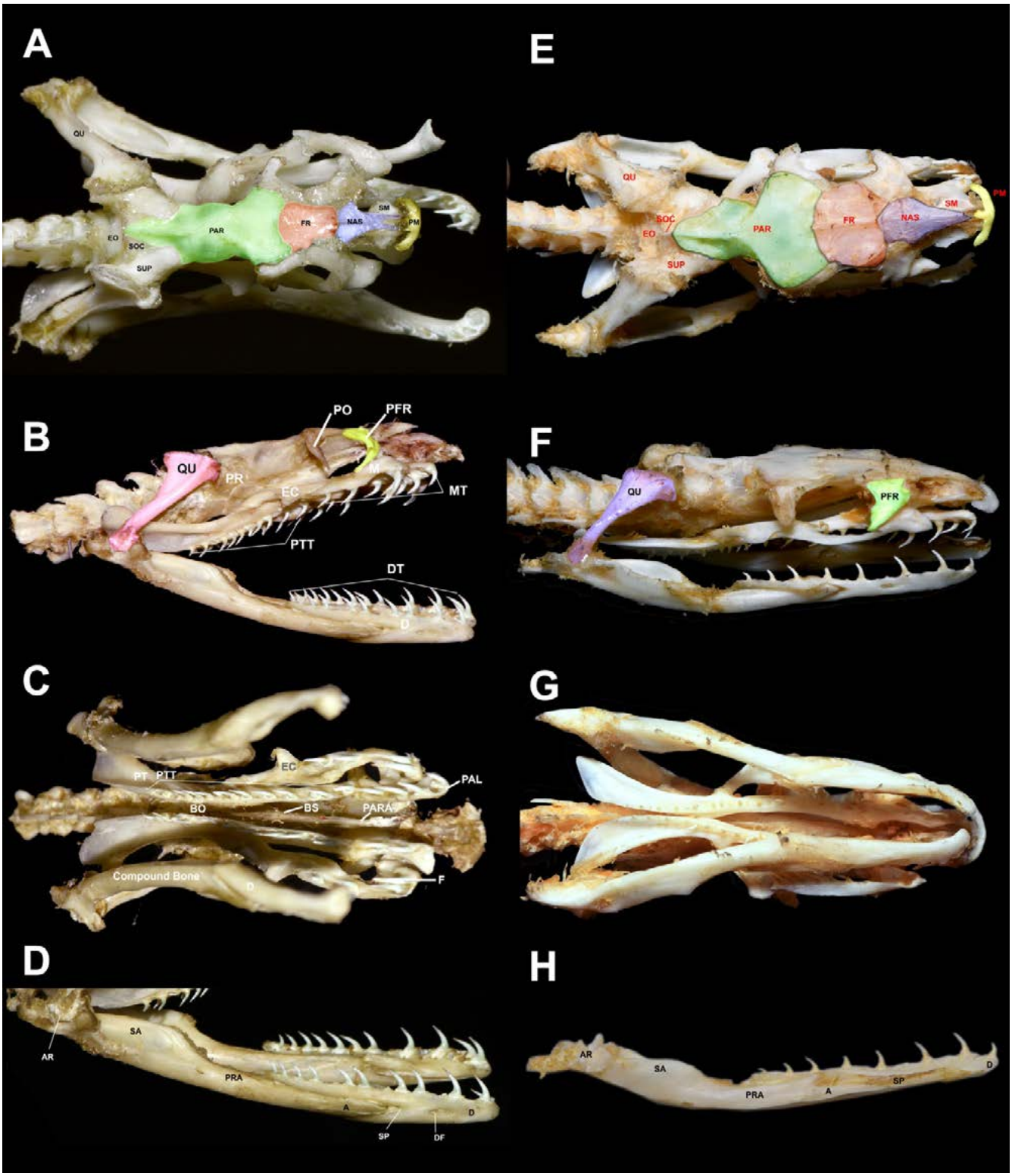

Figure 1: A-D Skull and Mandible of *Hydrophis schistosus*: A. Dorsal View, B. Lateral view, C. Ventral View, D. Mandible; and E-H Skull and Mandible of *Hydrophis platurus*: E. Dorsal View, F. Lateral view, G. Ventral View, H. Mandible.

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