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Research paper

Some aspects of morphometry, systematics and biogeography of the freshwater turtles, *Pangshura* (testudines: Geoemydidae) of Pakistan

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Abstract

The present paper based on multivariate morpho-metry, systematics and biogeographically analyses of the hard-shell freshwater turtles of genus *Pangshura* found in Pakistan. Allo-metric changes in the size of body were examined in the live collected specimens. The morphometric measurements and comparative study of *Pangshura* clearly revealed sexual di-morphism and both the sexes can easily be differentiated. Females are larger in size than males in of this texon. The present study revealed that *P. tecta* are less common in distribution than *P. smithii* in in the studied area of Pakistan. The current study presents a morpho-metric relationship between extant and extinct species of *Pangshura* taxon for the first time. A holotype of this taxon, *Pangshura tatrotia* is described here, which is also considered a sister to P. tecta and a fifth species so far of this texon.

Keywords: Biogeography; Morphometry; Systematics; Pangshura; Pakistan.

1. Introduction

The family Geoemydidae comprises highly endangered species of Southeast Asian countries (Van Dijk et al., 2000). The texon Pangshura comprises medium to small-sized turtles and represented by four extant species (Pangshura smithii, P. tecta, P. tentoria and P. sylhetensis), and a fifth species P. tatrotia is described here, which is considered as a sister to P. tecta taxon by Walter and Tyler (2010) and TEWG (2015). All these species are indigenously found in Sub-continent. Pangshura smithii and P. tecta were recorded by various researchers in Pakistan like (Safi & Khan, 2014; Khan, 2015; Khan et al., 2015 & 2016) but the other two species are not recorded from any localities within Pakistan. A fifth species of this taxon, Pangshura tatrotia was discovered from the Pliocene Siwaliks hills near Padhri village, Dina of Jhelum district of Pakistan, which was suggested a new clade name, Palatochelydia, for the mono-phyletic assemblage to which it belongs but a combined analysis using recent molecular data and an updated morphological data set confidently places this holotype as sister to P. tecta, the extant turtle of this taxon by Walter and Tyler (2010) and TEWG (2015). The holotype of this fossil species was discovered from Tatrot formation in 1932, about two miles north-east of Padhri village of district Jhelum, Pakistan. This specimen is best-preserved and one of the oldest representatives of *Pangshura* and also one among few testudinoids from the Indian sub-continent with well detailed locality data. This specimen was described as a new species of *Pangshura* for the first time by Walter and Tyler (2010). The southern Himalayan Mountains extending from south-west of Kashmir into southern part of Nepal is known as the Siwalik group. This is the hub of extensive fossil remains of Indian Sub-continent in Himalayan foreland form a continuous belt ranging from northern Pakistan to Eastern India. It has an average width of 20 km and elevation of 1000 m. This is associated to the most active Himalayan thrust across Himalayas, which is the main frontal thrust of this region (Dubille and Lave, 2007). (Fig. 1 & Plate

Morpho-metry and its variation play a very important role in evolutionary, physiological, ecological and geographical implication. Empirical data have relationships with chelonian body morpho-metry. They have been established several properties like body's temperature, growth rate and physiology (Spotila and Standora, 1985; Bjorndal and Bolten, 1988). Morpho-metric analysis and Morpho-metric variational data has been documented in many chelonian species so far and for several other vertebrate groups such as fishes (Claude et al., 2003; Walker et al., 1997). Scarce data and information on morpho-metric and geographical distribution range of the texon *Pangshura* are available so far. The main objective of current study and research is to investigate the morpho-metric variation of different *pangshura* species found n Pakistan, an attempt to reveal the bio-geographical distribution and related information and the size related data for identification of sex as well as age of these species in Pakistan. This comparative study will generate necessary information about the systematics, biogeography and natural history of this texon and will be helpful for other researchers.



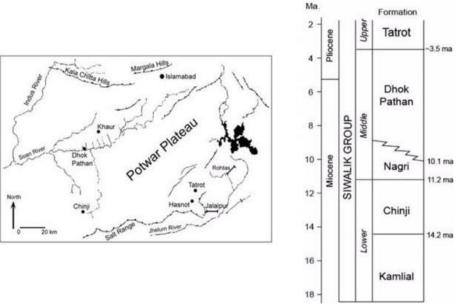


Fig. 1: Siwalik Sequence in Pakistan Indicating Important Points and Chrono-Stratigraphy (Courtesy by: Khan Et Al., 2012).



Plate 1: Photograph of the Discovery Area of P. Tatrotia, Siwalik Hills (Padhri Village) of Pakistan.

2. Materials and methods

The present study has been conducted in KPK and Sindh provinces of Pakistan. The study was carried out in different seasons and in different water bodies with the aim to record the morpho-metric variation, distribution and some other biological features of the genus Pangshura in Pakistan. Surveys were carried out randomly throughout the selected water bodies in different seasons and in different spots (Table 1: Fig. 2). The turtles were searched out in riverine areas and in different habitat conditions such as bushes, under leaf litters, logs, Hill stream beds, in crevices, In gaps of rocks and trees, in gaps in roots of large trees, in sun basking spots, in swimming condition and in hibernating form. Turtles under sun basking and swimming were observed from a distance by using binoculars from boat or by walking along the river/water bodies sides. The local fishermen, farmers and other local communities of studied areas were interviewed using standard photos of Pangshura species. We have followed the identifications protocols of several previous workers for recording morphological measurements and identification standard guidelines (Smith, 1933; Pritchard, 1979; Daniel, 1983; Das, 1985, 1995; Hanfee, 1999; Baruah et al. 2010). Turtles were collected from the Indus river systems and the tributaries along with other wetlands (Table 1; Fig 2) Measurements were taken using the dial-Vernier callipers: CL= straight line of carapace length, CW= carapace width, PL= plastron length, PW= plastron width and SH= shell height for all the collected specimens, which were later released in same water bodies from where they have been captured. Sex determinations were done using the standard techniques and methodology adopted by Ernst et al., 1994. Sexual di-morphism is not found in Juveniles because turtles are not sexually di-morphic before the maturity and hence sex determination was not clear in juvenile specimens. Relative lengths of the plastral-scutes along the midline of adults were calculated by the plastral formula. Measures scute abbreviations are: Gular (g), Humeral (h), Pectoral (p), Abdominal (Ab), Femoral (f) and Anal (a). >, < and >< signs are allotted for greater than, less than and for either may be larger than respectively. Allo-metric changes in the body size of the collected live specimens were examined. Sexual di-morphisms were observed in both the studied extant species.

Table 1: Collection Sites and Population Status of Pangshura Species of Pakistan.

S. No.	District	Water body	P. smithii	P. tectum	Total
1.	Charsadda, KPK	Jindi River	15	10	25
2.	Charsadda, KPK	Swat River	10	05	15
3.	Peshawar, KPK	Kabul River	13	08	21

4.	Peshawar, KPK	Budhni River	3	-	3
5.	Nowshehra, KPK	Kabul River	27	13	40
6.	D.I.Khan, KPK	Indus River	21	07	28
7.	Sukkur, Sindh	Indus River	12	8	20
8.	Sanghar, Sindh	Gujri Lake	6	12	18
9.	Badin, Sindh	Matchary Dhand	12	5	17
10.	Thatta, Sindh	Haleji Lake	3	33	36
11.	Thatta, Sindh	Kinijar Lake	21	8	29
12.	Thatta, Sindh	Karo Lake	12	13	25
			155	122	277

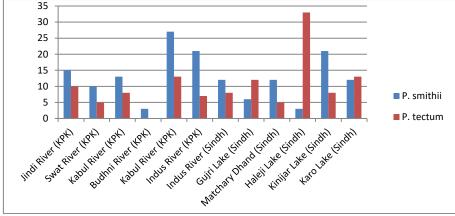


Fig. 2: Collection sites and Population Density of Pangshura Species of Pakistan.

3. Geological settings

YPM4127 is a holotype of an extinct species of *Pangshura* texon, It was collected in a locality of Punjab during the 1932/33 Yale North India Expedition in what is now Jhelum district of Pakistan. Locality no. 99 was assigned to that locality confined to the upper Siwaliks, Tatrot formation. This formation consists of only a single, normal magnetic polarity and it is unclear whether the underlying formational contact with older sediment is continuous and therefore, it is difficult to estimate the exact age of the Tatrot formation (Barry et al., 1982). This would be corresponding to an interval between 2.58 and 3.03 Ma by using the revised geo-magnetic calibrations. It appears more conservative to refer the Tatrot Formation to the entire Gauss Chron. YPM4127 should thus be estimated as having an age anywhere between 2.59 and 3.59 Ma (Ogg & Smith, 2004).

4. Results

A total number of 277 live specimens of *Pangshura* from Northwest province (KPK) and southeast province (Sindh) have been collected from different water bodies and sites as shown in Table 1; Fig. 2 specimens were identified, analyzed for comparisons of different parameters of morpho-metric and sexual-dimorphism.

Specimens: The collected *Pangshura* specimens were thoroughly examined during this study (Table 1-2; Fig. 2-4). The captured and collected specimens were identified and counted which include *Pangshura tecta* (122), Pangshura smithii smithii (155). We have observed in both the examined species that male were smaller across all measurements than female (Table 3; Fig. 3-4). Relationship between plastron and carapace measures indicates clear sexual-dimorphism in the shell (carapace and plastron) length/height corelationship. Smallest sized specimens of both the species which showed no sexual dimorphism were considered as Juveniles. Sanches and Bellini, 2002 described a consistent pattern of parameters for sexual-dimorphism in adult individuals in a simple and well explained manner. We have observed various tendencies with the adults specimens who demonstrating an accentuated dis-proportionality for increment of weight which has a relationship with curved length. The length and weight curved relationship in juveniles were not clear, which presented no significant differences between sexes and relative growth patterns of juveniles in both the species.

The current study on live captured specimens clearly showed that male and female individuals of both of *Pangshuran* species can be differentiated and clearly identified by sexual di-morphism. Males are always small in size as compared to female in both the studied species. The frequencies of different morpho-metric parameters among and *Pangshura* texon (Table 3; Fig. 3-4) clearly reveal sexual dimorphism in both studied species of Pangshura. We have selected random samples for biometry in both of these species and the result is as following:

- 1) In *P. smithii smithii*, females were larger with average CL 19.6 cm, CW 14.2 cm, PL 15.2 cm, PW 8.6 cm and SH 9.2 cm. Males were smaller with average CL 7.8 cm, CW 6.5 cm, PL 7.4, PW 5.9 cm and SH 4.4 cm.
- 2) While in *P. tecta* females were with average CL 17.2 cm, CW 12.8 cm, PL 15.4 cm, PW 7.8 cm and SH 8.2 cm. Males were smaller wit average CL 9.4 cm, CW 7.5 cm, PL 8.8, PW 5.4 cm and SH 4.9 cm.

P. smithii smithii were recorded more common than *P. tecta* in both the provinces. The *P. tecta* population was recorded satisfactory in KPK than in Sindh except Haleji Lake where the population status was good during current study.

Table 2: Morphometric Measurements (cm) of *Pangshura*.

Species	CL	CL			CW		PL		PW			SH			
	M	F	J	M	F	J	M	F	J	M	F	J	M	F	J
P. smithii	7.8	19.6	4.3	6.5	14.2	3.2	7.4	15.2	3.3	5.9	8.6	2.8	4.4	9.2	3.3
P.tecta	9.4	17.2	5.5	7.5	12.8	6.2	8.8	15.4	6.9	5.4	7.8	3.4	4.9	8.2	3.1

Carapace length (CL); Carapace width (CW); Plastron length (PL); Plastron width (PW); Shell height (SH); M: Male; F: Female; J: Juvenile (sub-adult). Figures in parentheses indicate nos. of M, F and J.

5. Species diagnosis, description, biology and distribution of pangshura of Pakistan

Key to the Pangshura species

Pangshura texon 4th vertebra having a slight contact with the third vertebral and overlap five neural bones and 4th vertebral shield is pointed anteriorly (Plate 2-4).

A. A total marginal shields are 24 in number; posterior margin of each carapace is feebly serrated or not serrated.

- i) If In young individuals the 3rd vertebral shield is elongated, quadr-angular or pentagonal and with almost straight posterior boundary. While the keel of the 3rd vertebral shield completed in a rounded projection *P. smithii*
- ii) If the 3rd vertebral shield is not much elongated, always pointed and pentagonal from back side. The keel of the 3rd vertebral shield completes in a spine which is backwardly projected. 2nd vertebral shield is elongated than the 3rd one. P. tecta
- iii) If the 2nd vertebral shield is shorter than the 3rd one. *P. tentoria*
- iv) If 13 pairs (26) of marginal shields are present and the posterior margin of carapace is sharply serrated. P. sylhetensis
- v) And if the carapace is tectiform and have posterior constriction of 3rd vertebra, anterior constriction on the 1st vertebra, pleural I/II sulcus with antero-medial process, 4th vertebra with antero-medial projection, contact of marginal X with 5th vertebra, wavy pleural/marginal sulcus pattern. *P. tatrotia*

6. Systematics

Kingdom-Animalia

Phylum-Chordata

Class-Reptilia

Order-Testudines

Suborder-Cryptodira

Superfamily-Testudinoidea

Family-Geoemydidae

Genus-Pangshura

i) Pangshura tecta (Gray, 1831) (Indian roofed turtle)

Synonyms

Emys tectum Gray, 1830

Emys tecta Gray, 1831

Testudo dura Hamilton, 1831 (nomen nudum)

Testudo katuya Hamilton, 1831 (nomen nudum)

Testudo khagraskata Hamilton, 1831 (nomen nudum)

Emys trigibbosa Lesson, 1831

Clemmys (Clemmys) tecta Fitzinger, 1835

Batagur (Pangshura) tecta Gray, 1856

Emys namadicus Theobald, 1860 (nomen nudum)

Clemmys tectum Strauch, 1862

Pangshura tecta Günther, 1864

Pangshura tectum Theobald, 1868

Pangshura dura Gray, 1869

Pangshura ventricosa Gray, 1870

Emys namadica Boulenger, 1889

Kachuga tectum Boulenger, 1889

Kachuga tecta Lindholm, 1929

Kachuga tectum tectum Smith, 1931

Kachuga tecta tecta Mertens, Müller & Rust, 1934

Distribution

This species is restricted to the tributaries of Indus River in Pakistan, Ganges River in India, Some water bodies of Bangladesh and Nepal (Fig. 5).

Diagnosis

This species has a rich darker brown Carapace, Reddish vertical keel and in some cases deep yellow/orange narrowly edged, plastron is yellow/orange, distinctly striped neck. A crescent like marking is present near eye red/orange in colour. Blackish head having broad bands of dull red/orange extending from back of the eye to occipital region. Limbs are darker gray with edged and yellow spotted (Plate 2A-B).

Description: This species has moderately a small head which is more pointed and shorter than the orbitals. Having elevated carapace, oval with a distinct spiked vertebral keel, especially on 3rd vertebra; 1st vertebra is as long as wide/ longer than width; 2nd and 3rd vertebrae are variable; 4th vertebra is more elongated than width, 5th vertebra is wider than length; Having pointed snout, Having irregular scales on the back of the forehead; Un-notched and serrated upper jaw; serrated ridge along the border of alveolar surface and concave (Plate 2 A-B).

Plastral formula: abd>fem>an><hum>an>gul.

Color: Brown/light brown carapace, red/orange stripe along with the first three vertebrae; plastron yellow/pink, each plastral scute have 2-4 black markings; orange/red crescent-shaped post-ocular markings on head, neck darker with thin yellowish bands.

Sexual Di-morphism: Male individuals are smaller than female, male possess a comparatively longer tail with thick base. Females possess yellow bands on top of the tail while male possess white bands. In addition, carapaces are darker in male and the irises are red while pink irises are found in females.

Habitat

Mainly lentic and in some lotic situations, preferring vegetation-chocked shallow streams (Baruah, 2010; Khan et al., 2015 and 2016). Habits

Like small rivers/lakes, not a fast swimmer.

Feeding

It feed almost all vegetation (Smith, 1933) reported it as herbivorous (Khan et al., 2015, 2016).

Threats

The main threats are Pet trade, Overfishing, Pesticides, Climate change and meat.

Breeding season

Throughout the year.

Status

The status is; Least concern (IUCN, 2019).

Protection / Conservation status

CITES Appendix I; Lower risk in the "IUCN Red list Least concern species".

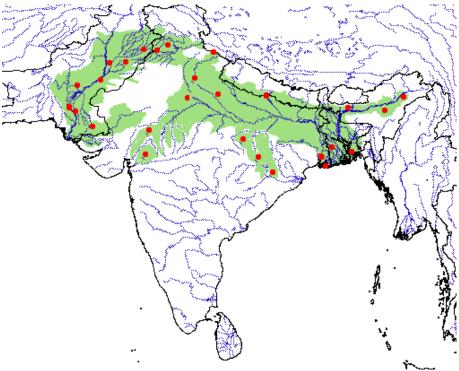
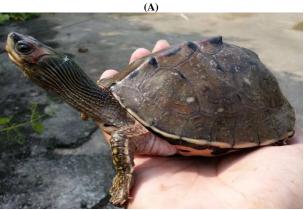


Fig. 3: Distribution Map of Pangshura tecta.



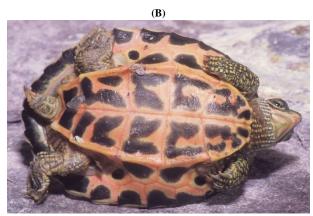


Plate 2: Pangshura tecta Dorsal View (A) Ventral View (B).

ii) Pangshura smithii (Gray, 1863) (Brown Roofed Turtle)

Synonyms
Batagur smithii Gray, 1863
Pangshura smithii— Günther, 1864
Clemmys smithii— Strauch, 1865
Pangshura smith [sic] Theobald, 1868 (ex errore)

Emia smithii— Gray, 1870

Kachuga smithii— Boulenger, 1889

Kachuga smithi [sic] M.A. Smith, 1931 (ex errore)

Kachuga amithii [sic] Rudloff, 1974 (ex errore)

Kachuga smithi smithi Moll, 1987

Kachuga smithii smithii— Moll, 1987

Pangshura smithii smithii— Das, 2001

Pangshura [sic] smithii—Das, 2001

Pangshura smithi - Gurley, 2003

Pangshura smithi smithi Joseph-Ouni, 2004

Distribution

This species of *Pangshura texon* is restricted with the tributaries of and Indus river system in Pakistan, Ganges Rivers in India, Some water bodies of Myanmar, Bangladesh and Nepal (Fig. 6).

Diagnosis

Slightly keeled and depressed carapace with olive brown in color. Dark brown/ black central ridge, with spots of russet in juveniles. Light olive/ pale grayish yellow head with a brownish spot back of eyes. Serrated jaws with pointed snout. Cream stripe on neck, pale gray limbs with dull yellowish margins of webs. 2/3 of the body consist of carapace, strongly arched (Plate 3 A&B).

Description: oval and depressed carapace, with/without a vertebral keel; vertebrae are elongated than width, except 2nd and 5th vertebrae; snout projecting beyond maxillae; Mandibles with a weak notch, serrated; broad alveolar surface. The head is comparatively short; pointed snout, smaller than the orbits and projecting much beyond the maxillae.

Two sub-species are recognized so far, based on colour pattern of head penis, limbs and shell:

P. smithii pallidipes (Gray, 1863: This Sub species is restricted to northern India and Nepal, It is not recorded in any part of Pakistan (Moll, 1987).

P. smithii smithii: This subspecies has more diverse distribution than the previous one. It is found in all water bodies of Sub-continent. It is the larger of the two sub-species and has black pigmentation on the both the sides of the head and on the anterior side of the limbs (Plate 3 A&B).

Habitat

It found in lakes/ponds/Small Rivers. They go in hibernation early December to early March (Minton, 1966) but some individuals bask during the warmest hours of the day. They are considered as shy turtles and never attempt to bite.

Habitat

Lotic/lentic environments (Moll, 1987).

Habits

This turtle is omnivorous but prefer meat of fish and frog (Minton, 1966; Das, 1985). They also eat fruits of several kinds of vegetation. Breeding Season

The main breeding season is early October (Minton, 1966).

Threats

They are significantly used as pet/meat but rarely eaten in Pakistan. The other threats are climate change and some anthropogenic activities

Status

Near threatened (IUCN, 2019)

Protection/ Conservation status

Enlisted in CITES Appendix I; IUCN enlisted it as in Lower risk.

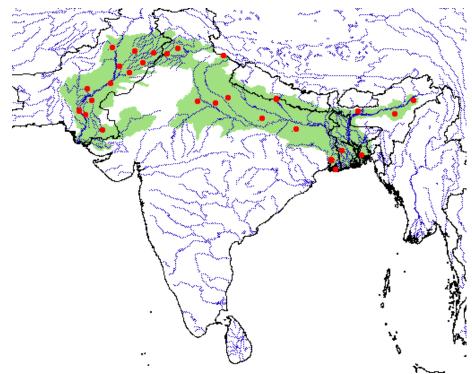
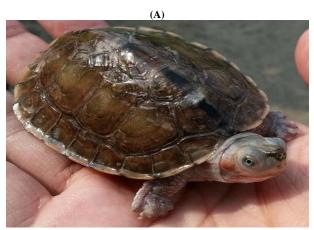


Fig. 4: Distribution Map of Pangshura Smithii.



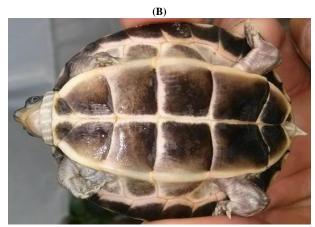


Plate 3: Pangshura smithii smithii Dorsal View (A) Ventral View (B).

iii) Tatrotia roofed turtle, Pangshura tatrotia, Joyce and Lyson, 2010

Etymology: The holotype was recovered from Tatrot Formation and hence the name was given as P. tatrotia.

Holotype: This Holotype was assigned a number of YPM 4127, It is a complete shell that documents nearly all portions of this fossil especially of carapace and plastron, This Holoype is Preserved in London.

Type locality: This Holotype was discovered during British rule in 1932-33the project was Yale North India Expedition and the locality number was 99, Tatrot Formation, Siwalik hills, Early Pliocene, about two miles northeast from Padhri village in Jhelum, Pakistan.

Diagnosis: *Pangshura tatrotia* is a fossil species of Pangshura texon which is diagnosed by the following combination of characters: Carapace is tectiform, 3rd vertebra has a posterior constriction while 1st vertebra has anterior constriction, Long antero-medial process on pleural I/II sulcus, 4th vertebra has an projection in antero-medial side, 5th vertebra has a connection with 10th marginal.

Description of Holotype No. YPM 4127

Preservation: The holotype of this fossil specimen is well preserved in a fine-grained carbonate-cemented conglomerate and has only a minor crushed area. The plastron is almost complete and well preserved as well, with the exception of some minor missing portions of the right epi-plastron and much of the xiphi-plastron. Sulci and Sutures are well preserved.

Carapace: The dorsal view of the carapace is oval shaped and lacks a distinct notch. The pygal area is unclear and the exact shape is undetermined due to damage and missing of some of the peripheral series. The anterior view of carapace showed high-domed shaped and clearly exhibits a sharp median keel. The shape of its shell may well be called roof shaped (tectate). The keel is formed by nuchal, neurals and pygal series and runs down the entire dorsal side of the carapace. At its peak point, the mid-line ridge is elevated about 0.5 cm above the level of the nearby costal-bones (Plate 4).

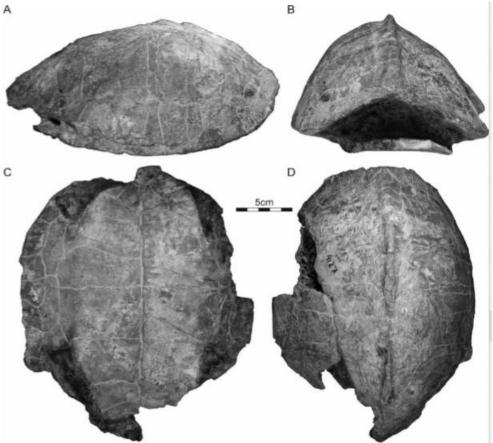


Plate 4: Some Snaps of YPM No. 4127, The Holotype of *Pangshura tatrotia* from the Early Pliocene of Pakistan. (A) Lateral View of Shell; (B) Anterior View of Shell; (C) Ventral View of Shell; (D) Dorsal View of Shell (Courtesy by: Joyce and Lyson, 2010).

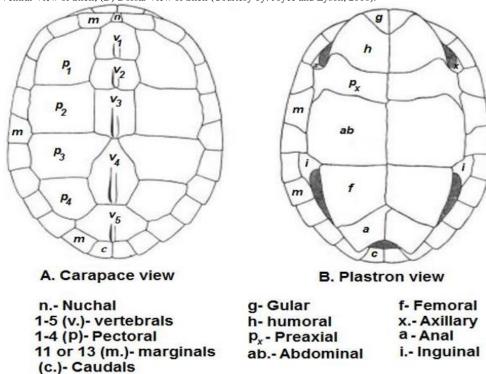


Fig. 5: Diagrams of (A, Carapace and (B, Plastron View of Pangshura Texon with Different parts of Shell (Courtesy by: Baruah et al., 2016).

7. Discussion

The present observations have conformity with Choudhury et al. (1997), Khan et al. (2015; 2016) and Baruah et al. (2016). Two species were recorded from studied areas in Pakistan; these were *P. tecta* (Gray, 1831) and P. smithii (Gray, 1863), the other two species *P. sylhetensis* (Jerdon, 1870) and *P. tentoria* (Gray, 1834) are not recorded in any area of Pakistan. In the current study, the only sub-species of P. smithii, the typical P. smithii smithii was recorded while *P. smithii pallidipes* was not recorded from Pakistan, which showed conformity with Minton (1987) and Das (1995). The current study and field surveys have identified following hot spot and potential habitats of *Pangshura* species in KPK i.e. Jindi River (Charsadda), Kabul River (Nowshehra) and Indus River (D.I.Khan) while in Sindh Sukkur

area is best hotspot for *Pangshra* Species. Machery Lake (Badin) has good population status of *P. smithii*. *P. tecta* are less common than *P. smithii* in studied area. The northwestern sites (KPK) have more *P. tecta* than Southeastern sites (Sindh) which supported Khan et al. (2015)

Pangshura tatrotia is placed as sister to *P. tecta* within the Palatochelydia clade using the fossil record and morphological data only (Plate 4). Even molecular analysis is not possible as though *P. tatrotia* lacks all molecular data, which comprises more than 99% of the data set for the identification of any species. In contrast, morphological data alone are not able to resolve the phylogenetic position of any species and same case is here in Pangshura clade. The molecular data is playing a vital role in phylogeny to resolve better the placement of any taxon but unfortunately molecular data is not possible for fossil records. In general gestalt, the extant turtle's species *P. tentoria* and *P. tecta* greatly resemble with extinct species *P. tatrotia*. It is considered as a plesio-morphic relative of *P. tecta* in the placement of the vertebral 6/5 sulcus over the 8th neural and the 1st vertebra is anteriorly constricted.

However, the autapo-morphic development of a medial keel developed by 2^{nd} vertebra indicates that this taxon is not in ancestral relationship with *P. tecta*, and rather has an autonomous side of phyletic lineage. *P. tecta* occur today in all wetlands of Sub-Continents whereas the *P. tentoria* is found only in the east of Sub-continent (Iverson 1992). The extinct species *P. tatrotia* implies the minimum divergence time of the *P. tecta* lineage is about 2.59 Ma. Unlike various other groups of testudinoid, palatochelydians are ideal for molecular calibration studies because every extant taxon exhibits highly unique morphological and Morphometric features that allow quiet diagnosis of phyletic lineages upto species level. The character analysis of this fossil showed a closed relationship to the *P. tecta* of this taxon within the family of Geoemydidae. Such types of studies on fossil testudines have been done by many authors like Karl (2002) and Karl et al. (2007, 2012 & 2019).

We suggest that the collection of more additional materials may be a more efficient way to gain further insights and innovations in the paleontology, systematics, morphological and relative evolution of this group.

8. Conclusion

The present study resulted that total of 11 pairs of marginal shields are present in both *P. tecta and P. smithii*. Sexual dimorphisms have been observed in both local species of Pangshura taxon, where males are smaller in size than females in both of species and having relatively long tails with thick bases. The present study shows the diagrammatically represented the plastral formula of the Pangshura taxon. The Extinct fossil holotype of *P. tatrotia* is considered as unique as it is complete and the first to be associated with detailed locality data record. *P. tatrotia* is described and identified as the sister of the extant turtle *P. tecta*. It is considered as a plesio-morphic relative *of P. tecta* in the placement of the vertebral 6/5 sulcus over the 8th neural and the 1st vertebra is anteriorly constricted.

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