THE FIRST JURASSIC TURTLE FROM INDIA

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ABSTRACT. A primitive cryptodiran turtle, *Indochelys spatulata* gen. et sp. nov., is described from the Early Jurassic Kota Formation, a member of the Upper Gondwana Group in the Pranhita-Godavari Valley, Deccan, India. The shell morphology of *Indochelys* differs substantially from that of the Triassic *Proganochelys* of Germany but is significantly similar to the oldest known Early Jurassic cryptodire, *Kayentachelys*, from the Kayenta Formation of Arizona. *Indochelys* also shares many shell characters with the Late Jurassic North American turtles, in particular *Dinochelys*. The new family Indochelyidae is proposed, which probably has the same phyletic status as that of Kayentachelyidae, with both evolving simultaneously in different regions.

THE origin of turtles is still disputed, but recent analyses have suggested either an origin from the Permian pareiasaurs (Lee 1995, 1997) or from the diapsid reptiles (Rieppel and DeBraga 1996; DeBraga and Rieppel 1997; Hedges and Poling 1999), presumably also during the Permian. The earliest known testudine is *Proganochelys quenstedti* from the Late Triassic of Germany, and is regarded as the sister group of all other turtles (Gaffney and Meeker 1983). A second species of *Proganochelys*, *P. ruchae*, is the oldest turtle from Asia, found in the Norian Huai Hin Lat Formation of Thailand in association with ostracodes, dipnoans, actinopterygians, capitosaurs, plagiosaurs, phytosaurs and numerous estheriids and bivalves (De Broin *et al*. 1982; De Broin 1984). An unnamed proganochelyid skull is also recorded from the Early Jurassic Elliot Formation of South Africa, and is the earliest known African turtle (Gaffney 1986). *Proterochersis robusta*, the oldest known pleurodire, is recorded from the same horizon in Germany as *Proganochelys quenstedti* (Fraas 1913), thus demonstrating the presence of the Pleurodira in the Upper Triassic. The earliest cryptodire and the oldest known turtle from North America is *Kayentachelys aprix*, a primitive cryptodire from the Early Jurassic Kayenta Formation of Arizona (Gaffney *et al*. 1987). There are numerous Late Jurassic turtle records from North America (Gaffney 1979), Europe (Romer 1957) and China (Yeh 1983).

From the Cretaceous onwards, the record of fossil turtles becomes more prolific throughout the world. From the Indian subcontinent, pelomedusid turtles are known from the Infra- and Intertrappean Beds (Carter 1852; Hislop and Hunter 1855; Lydekker 1890; Sukeshwala 1947; Jain 1977) of central India. These beds are considered to be Upper Cretaceous (Pascoe 1964; Robinson 1967). Pelomedusids are also known from the Upper Eocene and Oligocene of the Fayum, Egypt, and from the Miocene (Burdigalian) of Saudi Arabia. These Asian and African pelomedusids appear to represent a branch off the common African-South American pelomedusid stem, with *Carteremys pisdurensis* Jain, 1977, as their earliest representative (De Broin 1987). Finally, the Early–Middle Eocene carettochelyid cryptodire, *Chorlakkichelys shahi*, is known from carapacial and plastral scutes from the Kuldana Formation of Pakistan (De Broin 1987).

The purpose of this paper is to describe the shell morphology of the oldest non-proganochelyid chelonian discovered in the Early Jurassic Kota Formation of the Upper Gondwana Group in the Pranhita-Godavari Valley, Deccan, India.

GEOLOGICAL BACKGROUND

The Kota Formation, a member of the Upper Gondwana Group of rocks, crops out on the east and west banks of the Pranhita and Godavari rivers, and is characterized by the presence of a highly fossiliferous limestone bed as well as the regular, consistent assemblages of fluviatile and lacustrine sandstone and clays (King 1881; Kutty 1969; Rudra 1972). A generalized stratigraphy of this outcrop is shown in Text-figure 1, and the lithological succession as exposed in the 'Kota' type area is shown in Text-figure 2.

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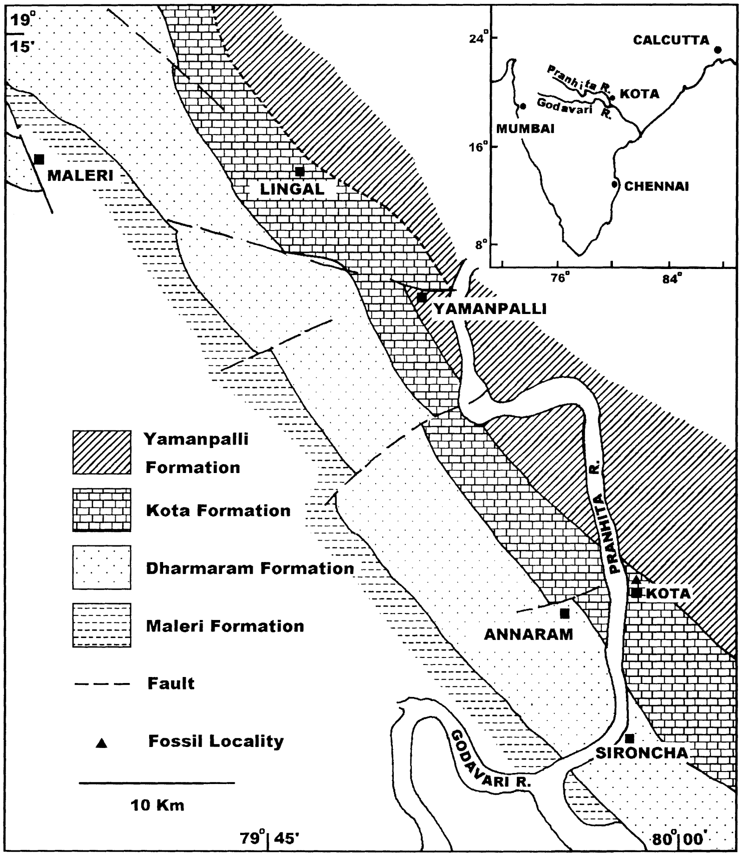
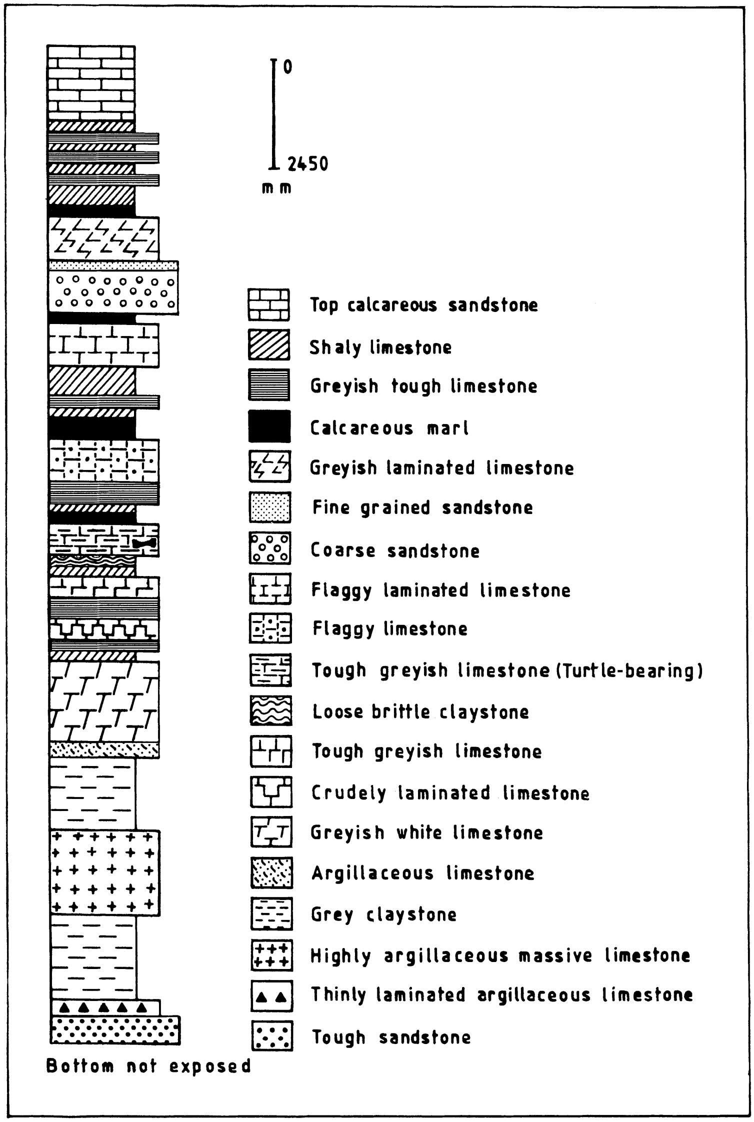


TEXT-FIG. 1. General geology of the area showing the fossil locality in the Kota Formation (inset: location of Kota village).

The Kota Formation is well known for its rich fossil content. Fossil fishes include the semionotid genera *Lepidotes*, *Paradapedium*, *Tetragonolepis*, the halecomorph genus *Pholidophorus* (Jain 1973; Yadagiri and Prasad 1977), and the coelacanth *Indocoelacanthus* (Jain 1974). On the basis of these fossil fishes, the age of the formation is considered to be Early Jurassic (Jain 1983). Seven estheriid-bearing units in the Kota argillaceous limestone at the type locality indicate a Jurassic age for the formation (Tasch *et al*. 1973). Govindan (1975) found the freshwater ostracode *Darwinella* at Kota, and suggested that the age of the formation may extend into the Middle Jurassic. The presence of the primitive sauropod dinosaur *Barapasaurus tagorei* (Jain *et al*. 1975), and the kuehnotheriid mammals *Kotatherium haldanei* (Datta, 1981), *Trishulotherium kotaensis* and *Indotherium pranhitai* (Yadagiri, 1984) also suggest an Early Jurassic age for the formation. As well as the above-mentioned vertebrates and invertebrates, the formation has also yielded numerous charophytic gyrogonites, wood and fragmentary insects. The fauna that it contains suggests a dominantly freshwater depositional environment.

MATERIAL AND METHODS

The specimen studied was found *in situ*, embedded in the hard limestone of the Kota Formation at 11·5 m above the bed of the Pranhita River. Both the carapace and plastron of the specimen were found to be well preserved apart from the tips of the posterior region, the mid-posterior marginal fringe on the left side and the marginal part on the right side. The central part of the plastron is also missing. No skull or postcranial materials



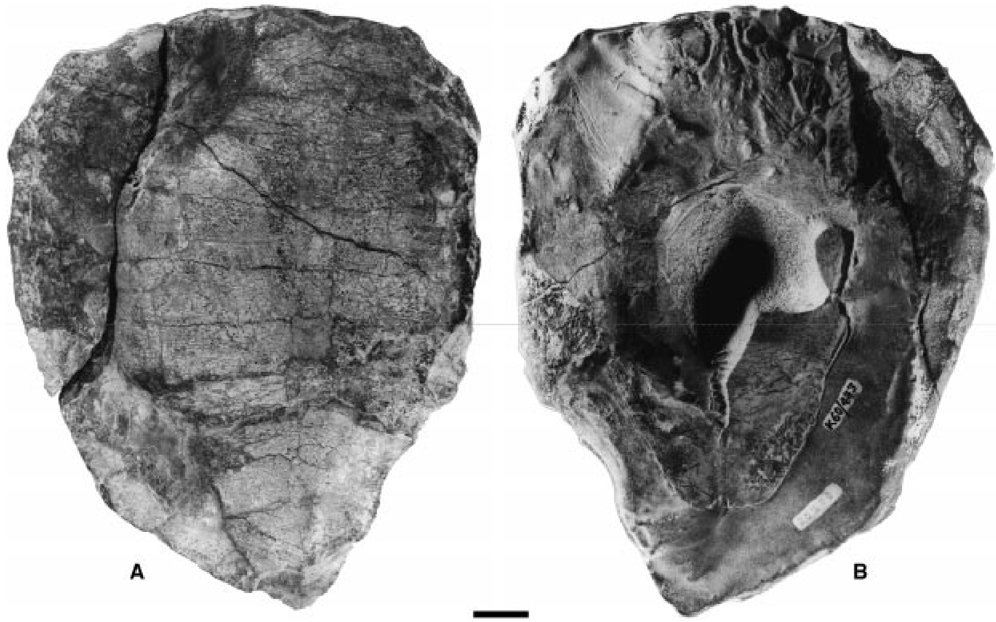
TEXT-FIG. 2. Diagrammatic section representing lithostratigraphic units exposed in Kota type area.

were found. Deep X-ray also failed to detect any further bony elements within either the shell cavity or the surrounding matrix. The matrix was separated by mechanical means as well as by acid treatment.

SYSTEMATIC PALAEONTOLOGY

Order TESTUDINES BATSCH, 1788
Gigaorder CASICHELYDIA Gaffney, 1975
Megaorder CRYPTODIRA Dumeril and Bibron 1835 (as Cryptodères)
Family INDOCHELYIDAE fam. nov.

Diagnosis. As for *Indochelys spatulata*, the only genus and species.



TEXT-FIG. 3. *Indochelys spatulata* gen. et sp. nov., holotype GSI 20380. A, dorsal view; B, ventral view. Scale bar represents 20 mm.

Genus INDOCHELYS gen. nov.

Type species. *Indochelys spatulata* gen. et sp. nov.

Derivation of name. *Indo*- for Indian subcontinent; *chelys*, Greek for turtle.

Diagnosis. As for the type and only species.

Indochelys spatulata sp. nov.

Text-figures 3–5

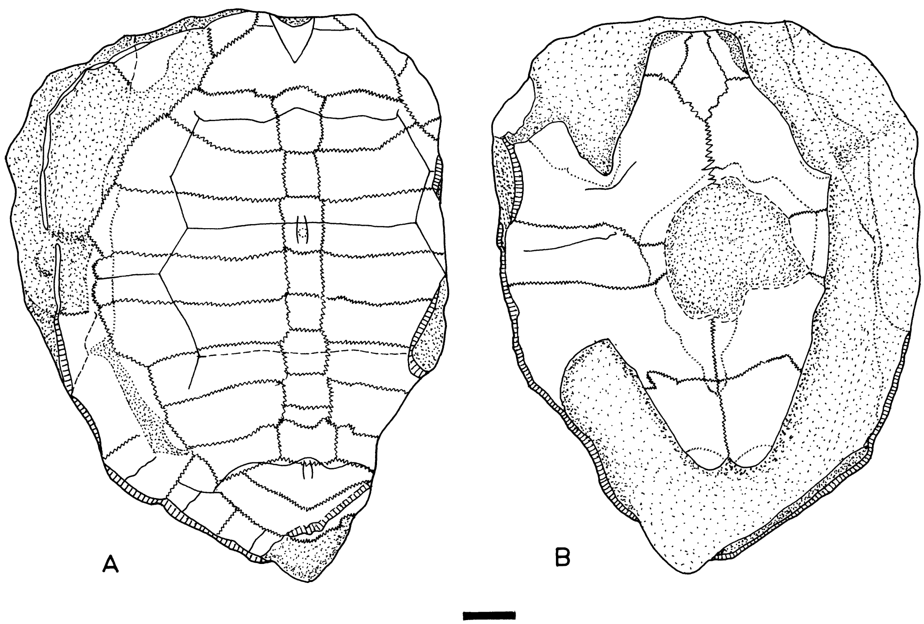
Holotype. A nearly complete shell (GSI 20380, in the collections of the Geological Survey of India, Calcutta).

Type locality. 10 km above the confluence of the Pranhita and the Godavari rivers near the village of Kota (18° 54′ N; 79° 58′ E), Gadchiroli District, Maharastra, India.

Horizon and age. Bedded Limestone Member of the Kota Formation of the Upper Gondwanan Group, Early Jurassic.

Derivation of name. With reference to the spatulate shape of the entoplastron.

Diagnosis. Shell low, oval with tapered posterior, surface smooth, lacking ornamentation; nuchal bone large, almost encompassed by the first vertebral scute; nine neurals, broad and drum-shaped; eight paired costals arranged almost in parallel, first costal articulating only with first and second peripherals; eleven paired peripherals; two large and wide suprapygals, the anterior triangular, the posterior crescent-shaped; scutes thin, five broad vertebrals, the third one widest, covering half of the shell width, the fifth completely enclosed by the last paired marginals and paired supracaudals; cervical scute present, V-shaped with



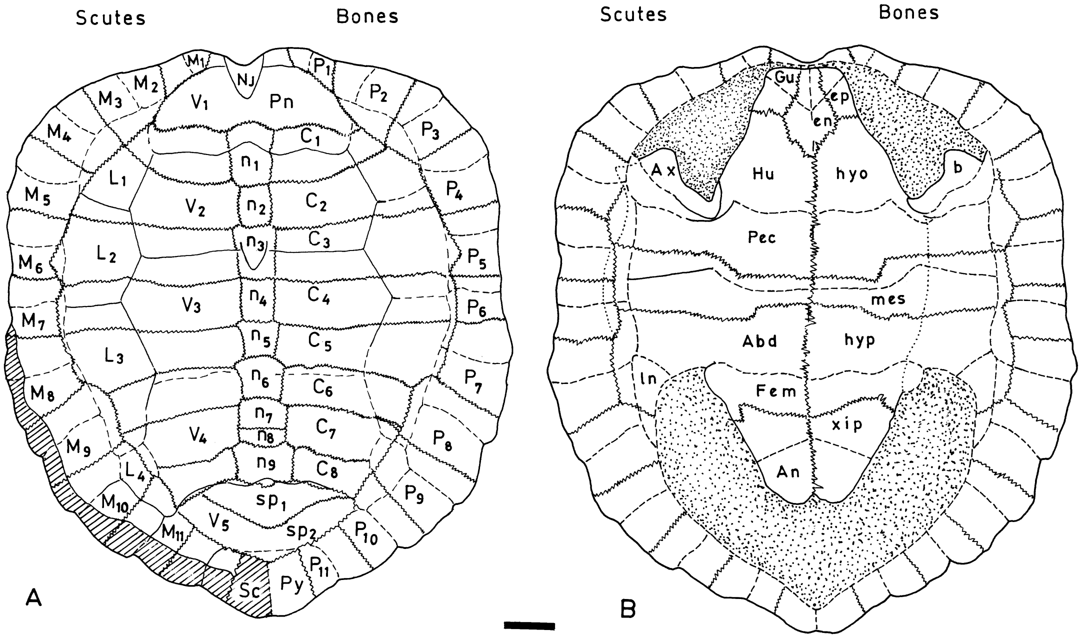
TEXT-FIG. 4. *Indochelys spatulata* gen. et. sp. nov., holotype, GSI 20380, interpretive drawing. A, dorsal view; B, ventral view. Solid lines (except outline) represent the scute borders; serrated lines represent sutures; broken lines represent inconspicuous scute borders; hatched areas represent broken parts of the specimen and dotted areas represent space filled with matrix; for abbreviations, see Table 1. Scale bar represents 20 mm.

incurved anterior margin; no supramarginal scutes (shared with *Kayentachelys*); eleven paired, squarish, marginal scutes; four paired, pleural scutes longer than broad (shared with *Proganochelys*); plastron relatively small and narrow with truncated anterior margin not protruding beyond the cervical scute; a very small gap between carapace and plastron all along the anterior margin; plastron having eleven elements including a pair of mesoplastra; entoplastron broad, spatulate, extending to the anterior margin of the shell and separating the epiplastra (shared with *Kayentachelys*); paired gular scutes extend to entoplastron almost a third of its length; one pair of mesoplastra, narrowing towards the mid-line; plastro-carapace bridge one-third of shell length.

Description. This monotypic genus is represented only by the holotype (Text-fig. 3). The shell is low, heart-shaped, 227·5 mm long and 213·0 mm wide. The maximum shell height is 48·1 mm attained at the sixth neural. Both carapace and plastron are smooth and without any ornamentation except for two small prominences on the third and eighth neurals. The dimensions of individual elements are given in Table 2.

Carapace (Text-figs 4A, 5A). The anterior margin of the carapace is incurved in the nuchal region; otherwise, the margin is nearly smooth, entire and sharp. The posterior region is mostly serrated, but is slightly notched in the pygal region. The shell is slightly depressed longitudinally all along the neural region. The anterior half of the carapace slopes down considerably from the first neural, thus forming a small hump over it. This probably indicates the point of attachment of the last cervical with the first fixed thoracic vertebra. However, the area enclosed by this anterior part of the carapace and the plastron below provides little space for retraction of the head and neck. The posterior half of the carapace is slightly scalloped at the posterior end. The nuchal region consists of a large nuchal bone which is almost covered by the first vertebral scute. The neural series consists of nine broad, drum-shaped to hexagonal neurals (n1–n9); the second neural is almost spherical in outline and the eighth is comparatively small.

Eight paired costals (c1–c8) are almost parallel to each other and are separated by the neurals medially. Each costal extends to the peripherals and none of them forms costoperipheral fontanelles. Each costal is narrower towards the



TEXT-FIG. 5. Restored shell morphology of *Indochelys spatulata* gen. et sp. nov. A, dorsal view; B, ventral view; conventions as for Text-figure 4. Scale bar represents 20 mm.

neurals and broader at the peripherals except for the first costal in which the situation is just the reverse. The first costal articulates only with the second and third peripherals rather than with the first through third peripherals.

Eleven paired peripherals (p1–p11) are all squarish or rectangular in shape and each is supported either by a single costal or by two adjacent ones; p2 is supported by both c1 and the nuchal whereas p1 is fused only to the nuchal. There are two suprapygals. The anterior suprapygal (sp1) is triangular and attaches to the last costal (c8) and the last neural (n9). The posterior suprapygal (sp2) is crescentic and is posteriorly girdled by the pygal, the partly paired p10 and the paired p11. The pygal was probably broad.

The epidermal scutes are thin and preserved in only a few patches. The interior relief of the scute margin is clearly impressed as grooves on the exterior relief of the dermal bones. There are five broad, prominent vertebral scutes (V1–V5). The third (V3) is widest and covers about 53 per cent. of the width of the shell. The second, third and fourth vertebral scutes are hexagonal in outline. They have almost straight margins whereas the first one has a mushroom-shaped outline with its posterior margin undulated. The fifth vertebral is bowl-shaped and its posterior margin is enclosed by the last paired marginals and the paired supracaudals.

TABLE 1. Abbreviations.

Dorsal elements		*Ventral elements*	
Scutes	*Bones*	*Scutes*	*Bones*
Pn, cervical	nu, nuchal bone	Gu, gular	ep, epiplastron
V, vertebral	n, neural	Hu, humeral	en, entoplastron
L, pleural	c, costal	Pec, pectoral	hyo, hyoplastron
M, marginal	p, peripheral	Abd, abdominal	hyp, hypoplastron
Sc, supracaudal	sp, suprapygal	Fem, femoral	mes, mesoplastron
	py, pygal	An, anal	xip, xiphiplastron
		Ax, axillary	b, buttress
		In, inguinal	

TABLE 2. Measurements

Maximum shell length	227·5 mm	Maximum shell height	432·0 mm
Maximum shell width	213·0 mm	Maximum median length of plastron	169·5 mm

Bones	*Number*	*Paired/Unpaired*	*Size in mm, length × width*
Nuchal (nu)	1	unpaired	24·2 × 82·1
Neural (n)	9	"	variable
Suprapygal (sp1)	1	"	18·6 × 55·2
Suprapygal (sp2)	1	"	16·5 × 71·7
Pygal (py)	16	"	23·0 × 35·0
Costal (c)	22	8 paired	variable
Peripheral (p)	2	11 paired	variable
Epiplastron (ep)	1	1 paired	19·0 × 14·0
Entoplastron (en)	2	unpaired	35·0 × 22·5
Hyoplastron (hyo)	2	1 paired	50·1 × 50·0
Mesoplastron (mes)	2	"	9·5 × 11·2
Hypoplastron (hyp)	2	"	46·7 × 46·1
Xiphiplastron (xip)	2	"	31·3 × 31·0
Bridge (b)	2	"	62·5 × 34·2

Scutes	*Number*	*Paired/Unpaired*	*Size in mm, length × width*
Cervical (Pn)	1	unpaired	13·9 × 14·0
Vertebral (V)	5	"	variable
Supracaudal (Sc)	2	1 paired	variable
Pleural (L)	8	4 paired	variable
Supramarginal: not clear			
Marginal (M)	22	11 paired	variable

Neural	*Maximum median, length in mm*	*Maximum median, width in mm*
First neural (n1)	25·2	15·5
Second neural (n2)	17·1	12·8
Third neural (n3)	22·6	13·0
Fourth neural (n4)	16·2	12·6
Fifth neural (n5)	15·0	13·8
Sixth neural (n6)	17·1	15·8
Seventh neural (n7)	13·0	18·2
Eighth neural (n8)	8·9	18·2
Ninth neural (n9)	14·1	21·0

Vertebrals	*Maximum median, length in mm*	*Maximum median, length in mm*
First vertebral (V1)	18·1	82·6
Second vertebral (V2)	45·0	102·5
Third vertebral (V3)	52·6	114·5
Fourth vertebral (V4)	41·7	98·5
Fifth vertebral (V5)	31·2	74·0

The well preserved cervical scute (Pn) is triangular with an incurved anterior margin, and extends medially into the first vertebral scute. Four asymmetrical pleural scutes (L1–L4) are present on either side of the vertebral scutes. Each pleural scute originates from the pointed marginal ends of the two adjacent vertebral scutes and is irregularly elongated.

Eleven paired, squarish marginal scutes (M1–M11) lie along the periphery of the carapace. The second, third, fourth and part of the fifth border the first pleural scute; the fifth and sixth border the second pleural; the seventh, eighth and ninth border the third pleural; and part of the ninth and tenth border the fourth pleural scute. The first marginal scute (M1) and the last (M11) are attached to the first and fifth vertebrals respectively.

Plastron (Text-figs 4B, 5B). The plastron is comparatively small and narrow; its maximum length is 169·5 mm. There is a wide gap between the plastron and the posterior margin of the shell. This probably provided free space for the movement of the hind limbs and the tail. The most prominent element in the plastron is the entoplastron (en). The entoplastral suture is highly serrated and its lateral margin on each side of the midline of the shell runs straight to meet the extreme anterior margin of the shell and separates the paired epiplastra (ep) on each side of it. The middle of the entoplastron is widest, and gradually tapers posteriorly to meet the mid-line, imparting a spatulate shape to the entoplastron. Two epiplastra, one on each side of the entoplastron, are distinct in the specimen. The epiplastral suture runs from the plastral margin as the hyo-epiplastral suture straight for some distance towards the mid-line of the plastron and suddenly turns anteriorly to merge with the entoplastral suture. Thus the paired epiplastra remain separated by the rostral process of the entoplastron. Thin, indistinct, gular scutes cover almost a third of the entoplastron. However, the intergular scutes are not very clearly seen in this specimen.

The hyoplastron (hyo) is broader than the hypoplastron (hyp). Paired razor-shaped mesoplastra (mes) are present in the mid-region of the plastron. Parts of the hyoplastron, hypoplastron and mesoplastron are not discernible in the middle part of the platform owing to the effect of erosion. Their probable outlines are depicted in Text-figure 5B. The xiphiplastron (xip) is much wider and longer than the epiplastron, and the impression of the pelvic ankylation is not formed. The humeral scutes (Hu) are much wider than the femorals (Fem) whereas the pectoral (Pec) and abdominal (Abd) scutes are almost equal in size.

The plastro-carapace bridge is 62·5 mm long and is about 54 per cent. of the total shell length. There is an impression of the axillary scutes (Ax) and inguinal scutes (In) which are presumed to be the traces of inframarginal scutes (Text-fig. 4B). However, no other inframarginal scutes are visible in the present specimen.

The possibility of development of a buttress (b) in the specimen is conjectured because of the tendency of inward bony growth of the antero-lateral plastral lobe towards the axio-carapacial region of the shell.

DISCUSSION

It is evident from the above description that *Indochelys spatulata* preserves many of the dermal and epidermal characters of carapace and plastron. In the following discussion we attempt to determine the relationship of this genus, and to place it systematically based on comparisons of the shell morphology. In the absence of a skull, we cannot take cranial morphology into consideration.

One attempt has been made to classify the Testudines using shell morphology. Zangerl (1969) proposed a classification of the order Testudines (as Chelonia) on the basis of progressive adaptive characters of the dermal and epidermal shield cover. Four major levels of shell organization were recognized, namely Amphichelydia, Mesochelydia, Metachelydia and Neochelydia, and each given subordinal status. Comparison of *Indochelys* with these four sub-ordinal levels demonstrates that it possesses most of the characters associated with the Mesochelydia in that it has nine neurals, five moderately large vertebral scutes, eight paired costal bones, eleven paired peripherals, four paired, moderately large, pleurals, one pair of mesoplastra, and gular scutes covering about one third of the entoplastron. On the other hand, the absence of supramarginal and inframarginal scutes, and the reduction of the marginal scutes to 22 suggest an approach to the more advanced metachelydian grade. However, because the information content of turtle skulls is so much greater, Zangerl's classification has not been widely used subsequently and '. . can be viewed as an aberration in the development of natural groups of turtle taxa and has been justifiably ignored by other workers. .' (Gaffney 1984, p. 292).

Recent phylogenetic analyses of the turtles are based almost entirely on cranial morphology. In the absence of a skull, we are unable to place *Indochelys* precisely in the cladogram of higher categories of turtles and their near relatives as proposed by Gaffney and Meylan (1988). However, an attempt is made to place it among the higher categories and determine its nearest relatives by utilizing some features of the shell morphology.

It is now recognised that the head retraction mechanisms of pleurodires and cryptodires arose within these groups, and that primitive members of both groups lacked this ability. In *Indochelys*, the anterior shell opening all along the anterior margin barely provides enough space to accommodate a retracting head and neck, whether the head is withdrawn by a sideways bending of the neck, as in pleurodires, or straight back into the shell, as in cryptodires (Romer 1957). It is probable that the head of *Indochelys* still could not be withdrawn, as in primitive turtles like *Proganochelys* and the most primitive pleurodires and cryptodires.

The shell morphology of *Proganochelys* differs substantially from that of *Indochelys*. Although they share general or primitive testudinate characters, such as four pairs of pleural scutes and one pair of mesoplastra (Gaffney 1985), in other respects *Proganochelys* differs from *Indochelys* in all aspects of carapacial and plastral bones and scutes.

The shell morphology of *Indochelys spatulata* more closely resembles that of the primitive cryptodiran *Kayentachelys aprix* (Gaffney *et al.* 1987) from the Early Jurassic of Arizona. The most striking shared characters of these two genera are found in the anterior region of the plastron. In both genera, the entoplastron is the same shape and size, extending up to the tip of the anterior plastral margin and thus separating the paired epiplastra for nearly their entire length. In both genera, the entoplastron is a broad, inverted, leaf-like structure, and modified into a spatulate shape. *Kayentachelys* has a pair of gular and intergular scutes. The gular scutes are completely separated by the intergular scutes, which meet for most of their length along the mid-line and extend from the epiplastron onto the entoplastron. In *Indochelys*, the gulars are distinct. The intergulars are less distinct but probably conform to the same shape and size as those of *Kayentachelys*. In both *Indochelys* and *Kayentachelys* supramarginal scutes are absent.

In other respects *Indochelys* may be more derived than *Kayentachelys*. It has eight paired costals (nine in *Kayentachelys*), the first costal sutures with the second and third peripherals (first three in *Kayentachelys*). There are two wide suprapygals (one small suprapygal in *Kayentachelys*) and apparently no inframarginal scutes (four pairs in *Kayentachelys*).

From the comparative study of morphological characters, it is very clear that the Early Jurassic *Indochelys* shares several shell characters with the North American Late Jurassic genus *Dinochelys* (Gaffney 1979). Although the similarity of *Indochelys* to *Dinochelys* is greater than to any other Mesozoic European and North American genera (*Glyptops*, *Trinitichelys*, *Pleurosternon*, *Plesiochelys*), it differs from *Dinochelys* in that its third vertebral scute is widest, covering about 53 per cent. of the shell-width. In *Dinochelys* the third vertebral scute is the widest, covering about 62 per cent. of the shell-width. The plastron in *Indochelys* also has a smoothly rounded anterior edge whereas in *Dinochelys* it is produced into lobes owing to indentation of the gular and intergular sulci. *Dinochelys* is usually a thick-shelled turtle (Gaffney 1979) whereas *Indochelys* is thin-shelled.

Thus the shell morphology of different Mesozoic genera belonging to different families ranging from the Late Triassic to Late Jurassic demonstrates that *Indochelys* has certain characters that are not comparable with any other Mesozoic forms. Consequently, the new family Indochelyidae is suggested for this genus. However, there are certain characters in the new family that are shared with other families. This is because the shell has a structural complexity with limited potential differentiation. Thus, evolutionary modifications in the turtles have tended to lead to the same features in virtually all the phyletic lines. This has resulted in a great deal of parallelism among them.

The inverted T-like entoplastron is slightly modified into a ‘spatulate’ shape in *Indochelys spatulata*. This feature and others, namely the ischia articulating to the xiphiplastron, the presence of a cervical scute, the absence of mid-plastral fontanelles, the immovable anterior plastral lobe, the strongly ossified shell, and a possible buttress in the specimen, are all cryptodiran in nature. The retention of mesoplastra precludes *Indochelys* from membership of the Eucryptodira (Eucryptodire character 2: Gaffney and Meylan 1988, p. 177) and places it within the basal grade of cryptodires with the kayentachelyids, pleurosternids and baenids.

The vertebral scutes are much broader than long (the pleural scutes being longer), the nine neurals sutured to vertebrae, the epiplastra separated ventrally by the rostral process of the entoplastron, and only one pair of mesoplastra meeting along the mid-line, are all rather archaic in character. These prove reasonably beyond doubt that we are dealing here with a relatively archaic cryptodiran turtle. It is, therefore, postulated that *Indochelys* and *Kayentachelys* belonged to two distinct lineages and evolved in parallel, perhaps emerging simultaneously within the same ancestral cryptodiran stock of the single monophyletic heterogenous Casichelydia in two geographically isolated land masses.

The spherical low-domed carapace, plano-convex flat shell, moderately short length of the bridge, small plastron size, and broad and upcurved posterolateral peripherals indicate that *Indochelys spatulata* is undoubtedly an amphibious or aquatic turtle, like *Kayentachelys* (Gaffney *et al*. 1987).

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REFERENCES

CARTER, H. J. 1852. Geology of island of Bombay. *Journal of the Bombay Branch of the Royal Asiatic Society*, **21**, 161–215.

DATTA, P. M. 1981. The first Jurassic mammal from India. *Zoological Journal of the Linnean Society*, **73**, 307–312.

DEBRAGA, M. and RIEPPEL, O. 1997. Reptile phylogeny and the interrelationships of turtles. *Zoological Journal of the Linnean Society*, **120**, 281–354.

DE BROIN, F. 1984. *Proganochelys ruchae* n. sp., chélonien du Trias supérieur de Thaïlande. *Studis Geological Salamanticentia*, Vol. Especial **1** (*Studia Palaeocheloniológica*), 87–97.

—— 1987. Lower vertebrates from the Early Middle Eocene Kuldana Formation of Kohat (Pakistan): Chelonia. *Contributions from the Museum of Paleontology*, *University of Michigan*, **27**, 169–185.

—— INGAVAT, R., JANVIER, P. and SATTAYARAK, N. 1982. Triassic turtle remains from north-eastern Thailand. *Journal of Vertebrate Paleontology*, **2**, 41–46

FRAAS, E. 1913. *Proterochersis*, eine Pleurodire Schildkrote aus dem Keuper. *Jahreschefte des Vereins fur Vaterladische Naturkunde in Württemberg*, **79**, 13–30.

GAFFNEY, E. S. 1979. The Jurassic turtles of North America. *Bulletin of the American Museum of Natural History*, **162**, 91–136.

—— 1984. Historical analysis of theories of chelonian relationship. *Systematic Zoology*, **23**(3), 283–301.

—— 1985. The shell morphology of the Triassic turtle *Proganochelys*. *Neues Jahrbuch für Geologie und Paläontologie*, *Abhandlungen*, **170**, 1–26.

—— 1986. Triassic and Early Jurassic turtles, 983–987. *In* PADIAN, K. (ed.). *The beginning of the age of dinosaurs*. Cambridge University Press, Cambridge, pp. 183–188.

—— and MEEKER, L. J. 1983. Skull morphology of the oldest turtles: a preliminary description of *Proganochelys quenstedti*. *Journal of Vertebrate Paleontology*, **3**, 25–28.

—— HUTCHINSON, J. H., JENKINS, JR., F. A. and MEEKER, L. J. 1987. Modern turtle origins: the oldest known cryptodire. *Science*, **237**, 289–291.

—— and MEYLAN, P. A. 1988. A phylogeny of turtles, 157–219. *In* BENTON, M. J. (ed.). *The phylogeny and classification of the tetrapods, Vol. 1. Amphibians, reptiles, birds.* Clarendon Press, Oxford, 377 pp.

GOVINDAN, A. 1975. Jurassic freshwater Ostracoda from the Kota Limestone of India. *Palaeontology*, **18**, 201–206.

HEDGES, S. B. and POLING, L. 1999 A molecular phylogeny of reptiles. *Science*, **283**, 898–901.

HISLOP, S. and HUNTER, R. 1855. On the geology of the neighbourhood of Nagpur, central India. *Quarterly Journal of the Geological Society, London*, **10**, 470–474.

JAIN, S. L. 1973. New specimens of Lower Jurassic holostean fishes from India. *Palaeontology*, **16**, 149–177.

—— 1974. *Indocoelacanthus robustus* n. gen. n. sp. (Coelacanthidae, Lower Jurassic). The first fossil coelacanth from India. *Journal of Paleontology*, **48**, 49–62.

—— 1977. A new fossil Pelomedusid turtle from the Upper Cretaceous Pisdura sediments, central India. *Journal of the Palaeontological Society of India*, **20**, 360–365.

—— 1983. A review of the genus *Lepidotes* (Actinoptergii; Semionotiformes) with special reference to the species from Kota Formation (Lower Jurassic), India. *Journal of the Palaeontological Society of India*, **28**, 7–42.

—— KUTTY, T. S., ROYCHOWDHURY, T. and CHATTERJEE, S. 1975. The sauropod dinosaurs from the Lower Jurassic Kota Formation of India. *Proceedings of the Royal Society, London, Series B*, **188**, 221–228.

KING, W. 1881. The geology of the Pranhita Godavari Valley. *Memoir of the Geological Survey of India*, **18**, 151–311.

KUTTY, T. S. 1969. Some contributions to the stratigraphy of the Upper Gondwana Formation of the Pranhita-Godavari Valley, Central India. *Journal of the Geological Society of India*, **10**, 33–48.

LEE, M. S. Y. 1995. Historical burden in systematics and the interrelationships of 'parareptiles'. *Biological Reviews*, **70**, 459–547.

—— 1997. Pareiasaur phylogeny and the origin of turtles. *Zoological Journal of the Linnean Society*, **120**, 197–280.

LYDEKKER, R. 1890. Note on certain vertebrate remains from the Nagpur District. Part of a chelonian plastron from Pisdura. *Record of the Geological Survey of India*, **23**, 22–23.

PASCOE, E. H. 1964. *A manual of the geology of India and Burma*, 3. 3rd edition. Geological Survey of India, Calcutta.

RIEPPEL, O. and DE BRAGA, M. 1996. Turtles as diapsid reptiles. *Nature*, **384**, 453–455.

ROBINSON, P. L. 1967. The Indian Gondwana formations, a review. *International Union of Geological Sciences, First Symposium on Gondwana Stratigraphy*, 201–268.

ROMER, A. S. 1957. *Osteology of the reptiles*. University of Chicago Press, Chicago, 772 pp.

RUDRA, D. K. 1972. A discussion on the Kota Formation of the Pranhita-Godavari Valley, Deccan, India. *Quarterly Journal of the Geological, Mining, and Metallurgical Society of India*, **44**, 213–216.

SUKESHWALA, R. N. 1947. A fossil tortoise (*Testudo leithii*) from the Intertrappean of the Worli Hill, Bombay. *Abstract, Proceedings of the Indian Science Congress, 33rd Session*, **3**, 97.

TASCH, P., SASTRY, M. V. A., SHAH, S. C., RAO, R. R. J., RACO, C. N. and GHOSH, S. C. 1973. Estheriids of the Indian Gondwana: significance for continental drift. *3rd Symposium on Gondwana Stratigraphy*, Australia, 445–452.

YADAGIRI, P. 1984. New symmetrodonts from Kota Formation (Early Jurassic) India. *Journal of the Geological Society of India*, **25**, 514–521.

—— and PRASAD, K. N. 1977. On the discovery of new *Pholidophorus* fishes from the Kota Formation Adilabad District, Andhra Pradesh. *Journal of the Geological Society of India*, **20**, 436–444.

YEH, H. K. 1983. Chinese Triassic turtles. *Newsletter of the Vertebrate Paleontological Association*, **91** (2).

ZANGERL, R. 1969. The turtle shell. 311–339. *In* GANS, C., BELLAIRS, A. D'A. and PARSONS, T. (eds). *Biology of the reptiles, Volume 1*. Academic Press, London and New York, 373 pp.

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