DRAZINDERETES TETHYENSIS, A NEW LARGE TRIONYCHID (REPTILIA: TESTUDINES) FROM THE MARINE EOCENE DRAZINDA FORMATION OF THE SULAIMAN RANGE, PUNJAB (PAKISTAN)

BY

JASON J. HEAD, S. MAHMOOD RAZA, AND PHILIP D. GINGERICH

CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

Philip D. Gingerich, Director

This series of contributions from the Museum of Paleontology is a medium for publication of papers based chiefly on collections in the Museum. When the number of pages issued is sufficient to make a volume, a title page plus a table of contents will be sent to libraries on the Museum's mailing list. This will be sent to individuals on request. A list of the separate issues may also be obtained by request. Correspondence should be directed to the Publications Secretary, Museum of Paleontology, The University of Michigan, 1109 Geddes Road, Ann Arbor, Michigan 48109-1079.

VOLS. 2-29: Parts of volumes may be obtained if available. Price lists are available upon inquiry.

DRAZINDERETES TETHYENSIS, A NEW LARGE TRIONYCHID (REPTILIA: TESTUDINES) FROM THE MARINE EOCENE DRAZINDA FORMATION OF THE SULAIMAN RANGE, PUNJAB (PAKISTAN)

BY

JASON J. HEAD[1], S. MAHMOOD RAZA[2], AND PHILIP D. GINGERICH[3]

Abstract — Trionychid turtle remains from the Eocene marine Drazinda Formation of the Sulaiman Range, Pakistan, include much of the bony carapace of a large trionychid described here as *Drazinderetes tethyensis* gen. et sp. nov. *Drazinderetes* is a large trionychine with a carapace measuring ca. 800 mm long and 700 mm wide. It shares several characteristics with extant Indo-Asian *Aspideretes* including presence of a preneural element, an elongated nuchal element, and reduced lateral extensions of the nuchal costiform processes. Other trionychid remains from the Drazinda Formation include much of an extraordinarily large entoplastron, and other carapace and plastron fragments that may or may not be *Drazinderetes*. The large entoplastron represents an animal larger than the type of *D. tethyensis*, with a bony carapace estimated to have been ca. 1200 mm long and ca. 1100 mm wide: the total carapace diameter, including the leathery margin, was probably on the order of two meters, making it the largest recorded trionychid, and one of the largest of known turtles. The presence of trionychids in marine deposits of the Drazinda Formation suggests near-shore habitation and, possibly, adaptation to a fully marine environment.

INTRODUCTION

Trionychid or 'soft-shelled' turtles are a speciose, highly specialized group with a relatively rich fossil record spanning the latest Mesozoic (Late Cretaceous) and Cenozoic eras. They are carnivorous and fully aquatic, and generally indicative of fresh water habitats. Trionychids are characterized cranially by reduction of dermal roofing of the adductor chamber, and postcranially by reduction of the number of clawed digits to three and reduction of the ossified component of the carapace (Gaffney, 1979a; Meylan, 1987).

Trionychids are abundant in Paleogene deposits of Asia (e.g., Chkhikvadze, 1990; Ye, 1994), but their systematic relationships and general evolutionary history are poorly understood. Resolv-

[1]Department of Geological Sciences and Shuler Museum of Paleontology, Southern Methodist University, Dallas, Texas 75275, U.S.A.
[2]Paleontology and Stratigraphy Branch, Geological Survey of Pakistan, Plot 84, H-8/1, Islamabad. Present address: Oil and Gas Development Corporation, Islamabad, Pakistan.
[3]Museum of Paleontology and Department of Geological Sciences, The University of Michigan, Ann Arbor, Michigan 48109-1079, U.S.A.

ing the early evolutionary history of trionychids in Indo-Pakistan is important for understanding modern faunas because the region possesses the highest species diversity among extant taxa (e.g., Pritchard, 1979), and it has maintained at least some higher-order diversity since the beginning of the Neogene (West et al., 1991b; Head, 1997). Indo-Pakistan has also been considered to be the center of origin for Cyclanorbinae, the main lineage of extant African trionychids (de Broin, 1987; Meylan, et al., 1990).

Turtle fossils have been reported previously from Eocene deposits in Indo-Pakistan. These include middle Eocene trionychids from the Ypresian or Lutetian Kuldana Formation of Pakistan (de Broin, 1987: 173), and the Ypresian-Lutetian Subathu Formation (Khare, 1976: 42; Sahni et al., 1981a: 92-93; Sahni et al., 1981b: 691; Sahni et al., 1984: 363; Loyal, 1990: 14). Sahni and Mishra (1975: 3) reported *Trionyx* sp. in a faunal list for the middle Eocene of Kutch and illustrated a fragment from Harudi (plate 3: fig. 5). Trionychids reported here are the first turtles to be described from the Drazinda Formation, and include the most complete trionychid specimen recovered from the Paleogene of Indo-Pakistan. The more diagnostic remains are placed within the systematic framework of the most comprehensive recent analyses of trionychids (Meylan, 1985, 1987), and we further consider implications of recovery of unusually large and unusually well preserved trionychids in marine deposits.

ABBREVIATIONS

GSP-UM   — Geological Survey of Pakistan-University of Michigan collection, Islamabad (Pakistan)
UM   — University of Michigan Museum of Paleontology, Ann Arbor (U.S.A.)
UTA-R   — University of Texas at Arlington Department of Biology, Arlington (U.S.A.): reptile specimen.

GEOLOGICAL AND STRATIGRAPHIC SETTING

Geological Survey of Pakistan-University of Michigan field parties first surveyed the Domanda and Drazinda formations surrounding Rodho Anticline in 1992, and this area was explored again in 1996. Rodho Anticline is at the northern end of the Zinda Pir anticlinorium in western Punjab (Fig. 1) and can be approached from Taunsa by way of Satta Post on the road to Dhodak or by way of Gulki in Sanghar Nala. Geology here was mapped by Bhatti et al. (1986) and Khan et al. (1986).

The Drazinda Formation is about 330 m thick, and a stratigraphic section measured at Rodho Sharki by Gingerich and Bhatti is described in Gingerich et al. (1997: 69-71). Gingerich and Bhatti divided the Drazinda Formation into lower, middle, and upper parts. The middle part of the formation includes a lower 62 m thick unit of brown to reddish-brown gypsiferous shales with interbedded foraminiferal limestones containing abundant *Nummulites beaumonti*, a 1-2 m thick *Discocyclina sowerbyi* marker bed, and a 31 m thick green shale unit containing numerous specimens of the large gastropod *Conus colossus*. The green shale unit weathers into low hills shown in the foreground in Figure 2.

All of the larger vertebrate remains described to date were found in the middle part of the formation, either below the *Discocyclina* marker bed: e.g., *Babiacetus indicus* (Gingerich et al., 1995) and cf. *Asiatosuchus* sp. (Angielczyk and Gingerich, 1998); or above it: e.g., *Protosiren*

RODHO ANTICLINE

0 _____ 4 km

Drazinda Shale
① *Protosiren sattaensis* GSP-UM 3001 (type)
② *Babiacetus indicus* GSP-UM 3005
③ *Basiloterus hussaini* GSP-UM 3193 (type)
④ *Basilosaurus drazindai* GSP-UM 3190 (type)
⑤ H-GSP loc. 167 of West et al.
⑥ *Asiatosuchus* sp. GSP-UM 3210
☼ *Drazindaretes tethyensis* GSP-UM 3195

Domanda Shale
⑧ Remingtonocetids GSP-UM 3009, 3015
⑨ *Rodhocetus kasrani* GSP-UM 3012 (type)

Quaternary
☐ Alluvium
Miocene
▨ Vihowa and younger
▨ Chitarwata Formation
Eocene
▨ Drazinda Shale
▨ Pir Koh Limestone
☐ Domanda Shale
▨ Habib Rahi Limestone
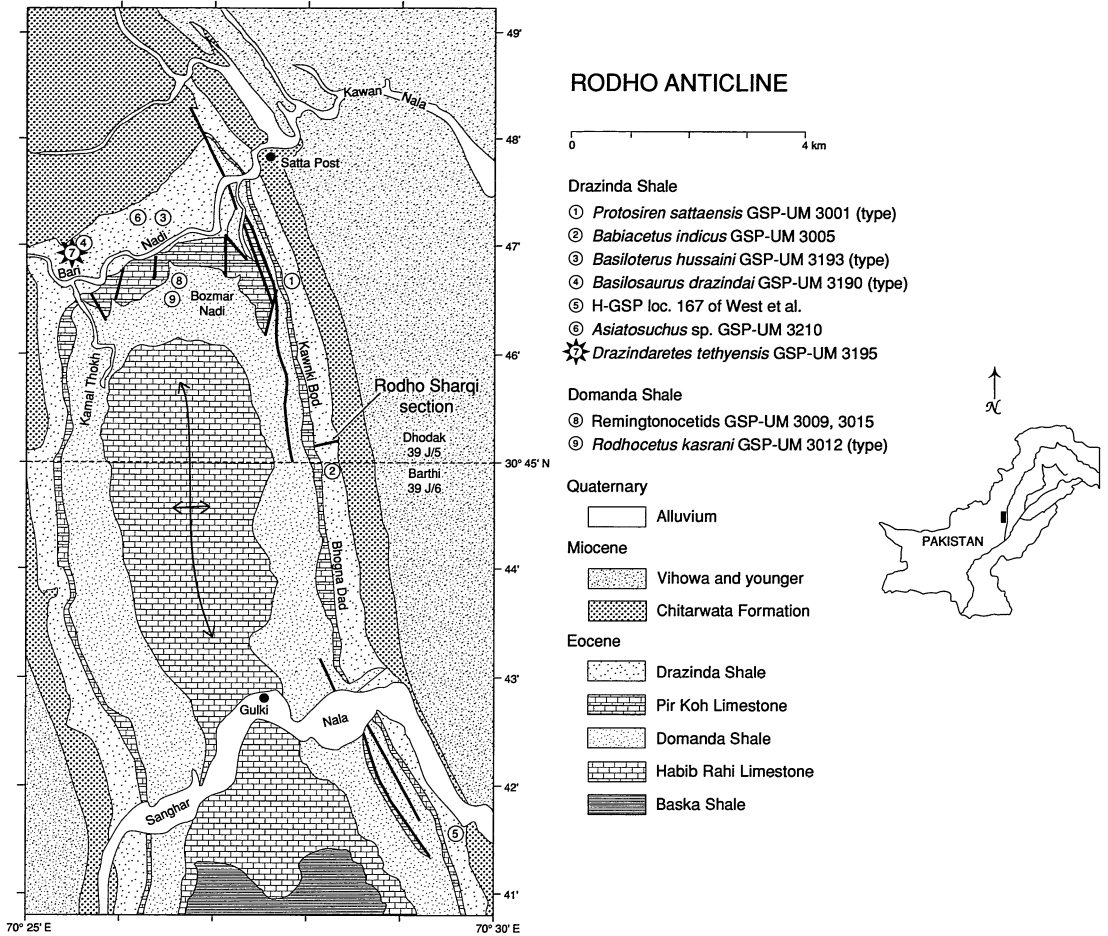▨ Baska Shale

PAKISTAN

FIG. 1 — Location map showing geology of the Rodho anticline in the Zinda Pir anticlinorium bordering the Sulaiman Range west of Taunsa in southwestern Punjab, Pakistan. Localities 1 and 2 are where the type specimen of *Protosiren sattaensis* and a skull and lower jaws of *Babiacetus indicus* were found (see Gingerich et al., 1995, for details). Localities 3 and 4 are the type localities of *Basiloterus hussaini* and *Basilosaurus drazindai* described in Gingerich et al. (1997). Locality 5 is H-GSP 167 from the 1978 survey of West et al. (1991a). Locality 6 yielded the crocodilian partial skeleton described by Angielczyk and Gingerich (1998) as cf. *Asiatosuchus* (GSP-UM 3210). Locality 7 (asterisk) is the type locality of *Drazinderetes tethyensis* described here. Locality 8 was the source of two partial skeletons of *Remingtonocetus* cf. *R. harudiensis* described by Gingerich et al. (1993, 1995). Locality 9 is the type locality of *Rodhocetus kasrani* described by Gingerich et al. (1994). Geology is from Bhatti et al. (1986) and Khan et al. (1986). Map is modified from Gingerich et al. (1995, 1997) and Angielczyk and Gingerich (1998).

sattensis (Gingerich et al., 1995), *Basilosaurus drazindae* and *Basiloterus hussaini* (Gingerich et al., 1997). Trionychids described here came from both the middle and upper parts of the Drazinda Formation.

FIG. 2 — Photograph of *Drazinderetes tethyensis* type locality (arrow, GSP-UM 3195) in Bari Nadi west of Satta Post. View is to the northeast. White collecting bags are ca. 30 cm in length. Locality is at 30°46.94' north latitude, 70°25.66' east longitude (Survey of Pakistan topographic quadrangle 39 J/5; Dhodak geological quadrangle of Bhatti et al., 1986). The specimen was found weathering from the middle of the green shale forming the upper unit of the middle Drazinda Formation in the same interval yielding *Basilosaurus* and *Basiloterus* (see stratigraphic section of Gingerich et al., 1997: fig. 9). Cliff-forming sandstone in the background here is Oligo-Miocene Chitarwata Formation overlying shales of the upper part of the Drazinda Formation.

SYSTEMATIC PALEONTOLOGY

Class REPTILIA Laurenti, 1768
Order TESTUDINES Batch, 1788
Family TRIONYCHIDAE Bell, 1828
Subfamily TRIONYCHINAE Meylan, 1987

Drazinderetes tethyensis, new genus and species
Figs. 3-5

Holotype. — GSP-UM 3195, much of a bony carapace (Figs. 3-5) found by PDG in 1996 (field no. 96-075).

Type locality. — Bari Nadi west of Satta Post in western Punjab Province, Pakistan. Locality is at 30°46.94' north latitude, 70°25.66' east longitude (Survey of Pakistan topographic quadrangle 39 J/5; Dhodak geological quadrangle of Bhatti et al., 1986).
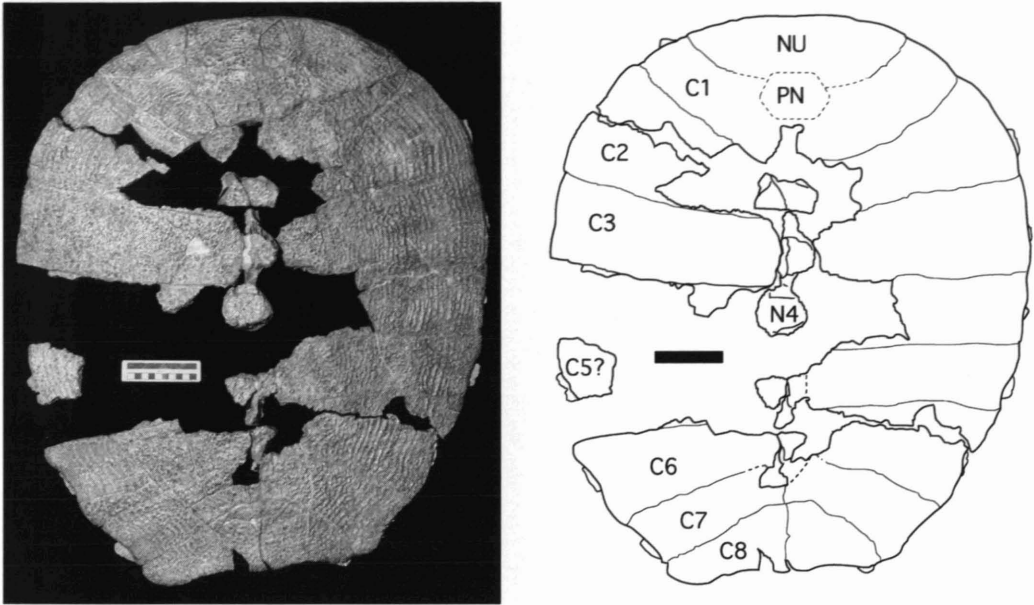
FIG. 3 — Carapace of *Drazinderetes tethyensis*, gen. et sp. nov., in dorsal view (GSP-UM 3195, holotype, photograph of cast). Anterior is at top. Scale is in cm. Abbreviations in interpretive drawing at right follow Meylan et al. (1990): *C*, costal element; *N*, neural element; *NU*, nuchal; *PN*, preneural.

Age and distribution. — The type locality is in the middle part of the upper green shale unit of the middle Drazinda Formation. This is bracketed between planktonic foraminiferal zones P14 below (Samanta, 1973) and P16-17 above (Afzal et al., 1997). Archaeocete whales and primitive sea cows from the same green shale unit indicate that this is probably in the upper part of P14 or lower part of P15 and middle Bartonian (late middle Eocene) in age (Gingerich et al., 1997). This is calibrated at about 39-38 Ma on the time scale of Berggren et al. (1995). Geographically, *Drazinderetes tethyensis* is known only from the type locality.

Diagnosis. — *Drazinderetes tethyensis* is a large trionychine turtle with a single pair of (posterior?) costiform processes (shaded in Fig. 5) that are completely fused to the ventral surface of the dermal nuchal and constrained within the lateral margins of the bony carapace. Distal ends of the costiform processes are overlapped ventrally by the first costal ribs. The bony carapace is ovoid with a slightly concave posterior margin. A preneural is present.

Etymology. — *Drazinda*, geological formation in which the type was found, and *eretes*, Gr. (masc.), rower, paralleling the root of *Aspideretes*. Specific name is from Tethys, wife of Oceanus in Greek mythology and the name of the ancient sea in which specimens described here evidently lived.

Description. — GSP-UM 3195 is a bony carapace including a complete nuchal region, nearly complete right costal series with costals 1-8 (there are eight costal pairs), portions of left costals 1-3 and 6-8, and incomplete thoracic vertebral column. The bony carapace measures approximately 800 mm long, 700 mm wide, and up to about 14 mm thick. Elements are solidly fused and the majority of neural-costal and interneural sutural contacts are obscured. The left side of the carapace was deformed during burial, but the right side preserves the original slightly-convex transverse curvature.

In dorsal view (Fig. 3), the bony carapace appears ovoid. The nuchal margin is broadly convex. The nuchal element is broad and approximately four times as wide transversely as it is long anteroposteriorly. Posterior to the nuchal the bony carapace is laterally expanded through the
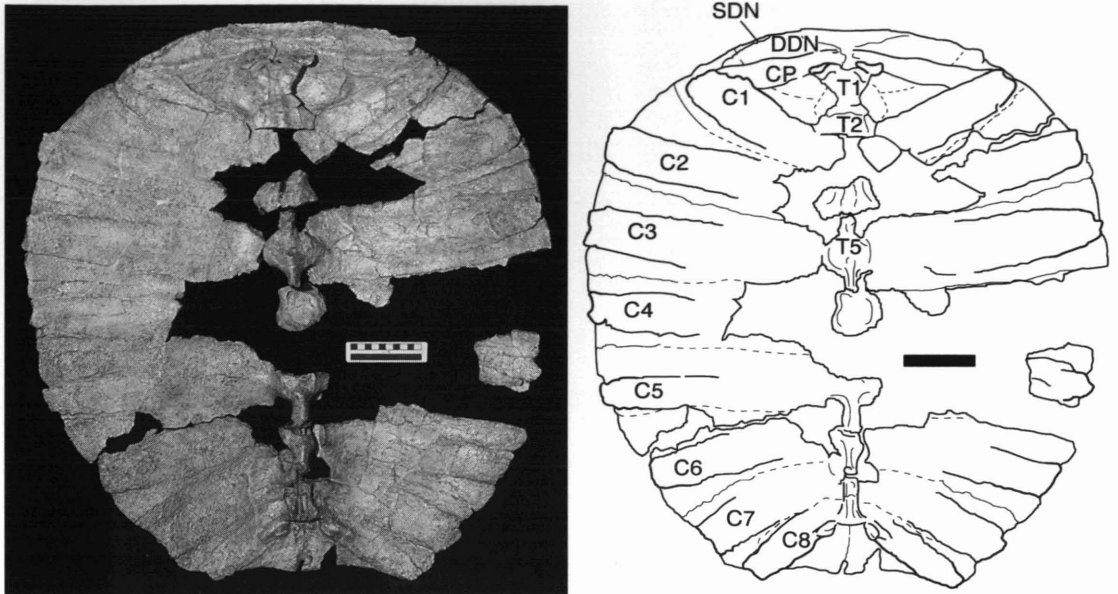
FIG. 4 — Carapace of *Drazinderetes tethyensis*, gen. et sp. nov., in ventral view (GSP-UM 3195, holotype, photograph of cast). Anterior is at top. Scale is in cm. Abbreviations in interpretive drawing at right follow Meylan et al. (1990): *C*, costal element; *CP*, costiform process; *DDN*, deep dermal nuchal; *SDN*, superficial dermal nuchal; *T*, thoracic vertebra.

second costal element, then the lateral margins of the bony carapace are more parallel through the fifth costal. From the fifth costal on the lateral margins taper and converge. The eighth costals are medially emarginated, resulting in a slightly concave posterior margin of the bony carapace.

A diamond-shaped, raised region is present on the dorsal surface of the bony carapace just posterior to the nuchal. This region is defined by sporadic, weak sutures with the first and second costal pairs, and corresponds in relative size and shape to the preneural of other trionychids (Carpenter, 1981; Meylan, 1987; Gardner and Russell, 1994). In addition, the position of the first thoracic vertebra near the posterior margin of the nuchal in GSP-UM 3195 is similar to the condition linked to the presence of a preneural (Meylan, 1987).

Dermal ornamentation consists of a strong inosculating pattern overlain by a parallel, concentric series of ridges from the lateral margins giving way to a more irregular polygonal pattern toward the midline. There is no substantial smooth lateral margin of the carapace.

In ventral view (Figs. 4-5), the ventral surface of the nuchal has a single pair of costiform processes fused to it. The processes are posteriorly-angled with sinuous anterior margins, similar to the posterior costiform processes of *Chitra indica* and some cyclanorbines (Meylan, 1985; Meylan et al., 1990). The shape of the processes may represent either fusion of the anterior costiform processes to the posterior processes, or loss of the anterior processes. The costiform processes are recurved laterally and do not extend beyond the lateral margins of the nuchal. The distal margins of the processes are overlapped ventrally by the first thoracic ribs. There are no suprascapular fontanelles separating regions of the posterior margin of the nuchal from the first costals.

The lateral-most sutural contacts between the first costal pair and the nuchal are preserved and indicate that the deep dermal nuchal and costiform processes project caudolaterally approximately 45 mm beyond the superficial dermal nuchal before they are overlapped by the first costal rib. A slight separation between the superficial and deep dermal nuchal is present along the anterolateral margin of the nuchal.
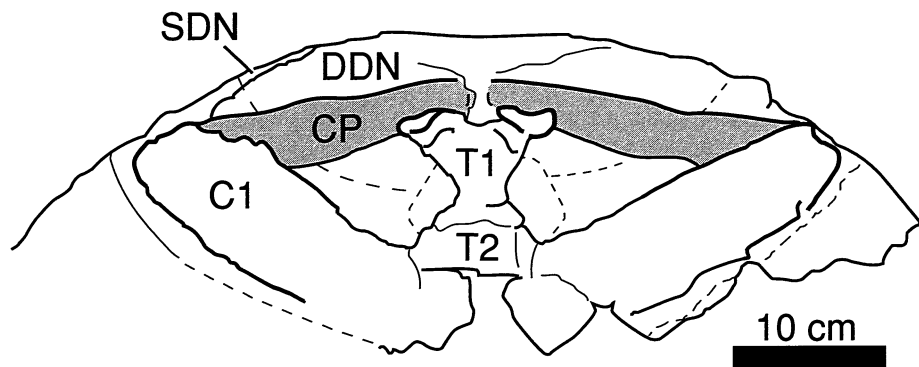
FIG. 5 — Detail of ventral surface of carapace of *Drazinderetes tethyensis*, gen. et sp. nov. (GSP-UM 3195, holotype, photograph of cast). Anterior is at top. Abbreviations: *C*, costal element; *CP*, costiform process; *DDN*, deep dermal nuchal; *SDN*, superficial dermal nuchal; *T*, thoracic vertebra. Note the single pair of (posterior?) costiform processes (shaded) that are completely fused to the ventral surface of the dermal nuchal, constrained within the lateral margins of the bony carapace, and overlapped ventrally by distal ends of the first costal ribs. Note too the paired articular processes for the posteriormost cervical vertebra on the anterior surface of the first thoracic element (*T1*).

Along the posterior midline of the bony carapace, prominent sutures preserve intercostal articulation between the middle to posterior regions of the seventh costal series. The midline of the carapace toward the anterior region of the seventh costals is poorly preserved, but several small sutures define the last neural positioned between the anterior-most margins of the seventh costals. The costal ribs heads are extremely thin and do not extend far beyond the lateral margins of the bony carapace as in some trionychids (Meylan, 1985; 1987), and are squared to convex in outline. The lateral margins of the bony carapace are ventrolaterally angled in transverse view (transverse profile "B" of Gardner and Russell, 1994: fig. 2F).

The preserved thoracic vertebral column of GSP-UM 3195 includes portions of the first through ninth vertebral centra. The first thoracic does not possess an anterior central articulation for the eight cervical vertebra. Instead, the anterior floor of the neural canal is a flat, horizontal plate of bone with a slight median keel. The prezygapophyses are widely separated, with saddle-shaped articular surfaces (Fig. 5), as in other trionychids. The articular surfaces of the prezygapophyses are bordered posteriorly by a deep sulcus. The rest of the thoracic series possess elongate centra that are tightly fused to the carapace. There are no prominent tuberosities for articulation with the tenth thoracic vertebra present on the ventral surface of the eighth costals, indicating that the tenth thoracic did not contact the carapace.

TRIONYCHIDAE, genus and species indet.

GSP-UM 3019

GSP-UM 3019 (Fig. 6) is a large entoplastron, including a complete left ramus, well preserved medial region, and much of the right ramus. It was collected by SMR and M. Anwar in 1992 (field number 92-024) in the upper part of the Drazinda Formation in Sori Nala in the Zinda Pir structure south of Rodho Anticline. The entoplastron is 573 mm long as measured from the distal tip of the left ramus to the apex of the medial region. A 77 mm distal length of the right ramus was not recovered. The element is boomerang-shaped, a diagnostic characteristic of trionychids (Meylan, 1987). The medial region and anterior portions of the rami are flattened in cross section. Anteri-
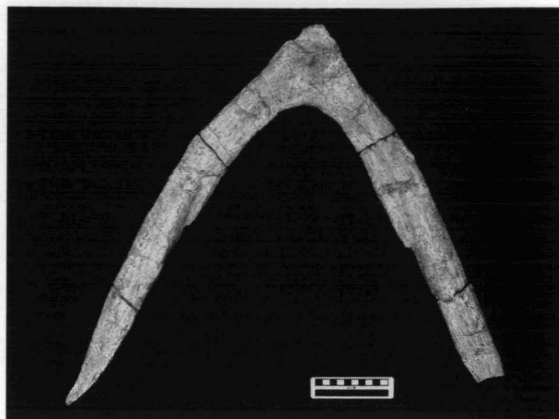
FIG. 6 — GSP-UM 3019, trionychine entoplastron (cast) in ventral view. Scale is in cm. Note large size (length 573 mm) and flattened apex.

orly, the apex is pointed and brief, unlike some trionychids in which the anterior margin of the entoplastron is flattened and broad (e.g., Cyclanorbinae, *Apalone ferox*; Meylan, 1987).

The rami diverge from the sagittal plane at an angle of approximately 40 degrees. They are slightly recurved at approximately a third of their length, and become progressively swollen mediolaterally. The distal 105 mm of the rami are triangular in cross section with wide, rugose medial margins for the articulation of the anterior processes of the hyoplastra. A shallow, longitudinal groove is present on the ventral surfaces of the rami from the point of recurvature to the region where they become triangular in cross-section. The distal tip of the left ramus is pointed and laterally curved.

Carapace size. — To determine the size of the bony carapace we would expect to have been associated with GSP-UM 3019 we measured carapace lengths and widths, and associated entoplastron lengths in a sample of thirty *Apalone spinifera* (Table 1). Regression of carapace length on entoplastron length and substitution of the 573 mm entoplastron length for GSP-UM 3019 yields an estimated carapace length of ca. 1200 mm (Fig. 7). Regression of carapace width on entoplastron length and substitution of the 573 mm entoplastron length for GSP-UM 3019 yields an estimated carapace width of ca. 1100. These measurements can only serve as an approximation, probably conservative, for carapace size, as the carapace of *Apalone* includes of only seven costal pairs and is reduced relative to the plastron. The bony carapace of GSP-UM 3019 may have been considerably larger than these estimates.

GSP-UM 3184

GSP-UM 3184 (Fig. 8A) is a carapace fragment with two fused costal elements, including the dorsal surface and section of the lateral margin. The side, left or right, cannot be determined. It was collected by M. Anwar in 1996 in Bhogna Dad (field number 96-064) from brown shale of the lower part of the middle Drazinda Formation below the *Discocyclina sowerbyi* marker bed. Ventrally, GSP-UM 3184 is highly weathered, and only small sections of the ventral surface are present. The maximum thickness of the fragment is 18 mm, making it somewhat thicker than the carapace the type of *Drazinderetes tethyensis*, suggesting that it may represent the carapace of a larger trionychid and may possibly be conspecific with GSP-UM 3019.

The dorsal surface preserves the inosculate sculpturing characteristic of trionychids. The lateral margin slopes ventrolaterally from the dorsal surface at a shallow angle and terminates as a

TABLE 1 — Measurements of 30 *Apalone spinifera* (sex not determined) collected from Moss Lake, Texas (University of Texas, Arlington, Department of Biology reptile collections). Measurements were made by palpating formalin-preserved specimens. All measurements are in mm.

Speciman number	Entoplastron length	Carapace length	Carapace width
UTA-R 10547	61	155	155
UTA-R 10548	32	60	74
UTA-R 10549	77	170	186
UTA-R 10551	44	120	130
UTA-R 10553	95	235	215
UTA-R 10554	68	156	180
UTA-R 10555	56	125	144
UTA-R 10558	43	115	118
UTA-R 10560	40	100	105
UTA-R 10563	35	70	95
UTA-R 10564	47	123	120
UTA-R 10568	40	110	118
UTA-R 10569	67	125	143
UTA-R 10570	66	168	179
UTA-R 10571	72	178	190
UTA-R 10573	75	185	200
UTA-R 10575	85	223	255
UTA-R 10576	98	223	240
UTA-R 10578	88	188	210
UTA-R 10581	32	90	98
UTA-R 10582	34	95	110
UTA-R 10583	40	105	120
UTA-R 10586	45	118	130
UTA-R 10587	70	160	190
UTA-R 10588	42	98	120
UTA-R 10589	41	89	97
UTA-R 10591	28	69	78
UTA-R 10592	37	100	125
UTA-R 10594	33	85	100
UTA-R 10597	38	90	98

thin ridge. A weakly preserved suture between the costals is preserved toward the medial region of the fragment, and the lateral margin is dorsally flared and elevated above the regions for the costal rib heads on either side of the suture. The smooth lateral margin is quite different from that of *Drazinderetes tethyensis*.

GSP-UM 3185

GSP-UM 3185 (Fig. 8B) is an incomplete right hypoplastron, including the posterior and lateral margins, with paired processes for a ligamentous connection with the carapace. It was collected by PDG in 1996 (field number 96-065) from the middle Drazinda Formation of Bari Nadi. The processes for ligaments arise from a thickening of the posterolateral margin of the element and diverge beyond the lateral margins of the hypoplastral sculpturing. The element becomes progressively thinner anteriorly, from 9 mm thick at the posterolateral margin to 3 mm thick at the
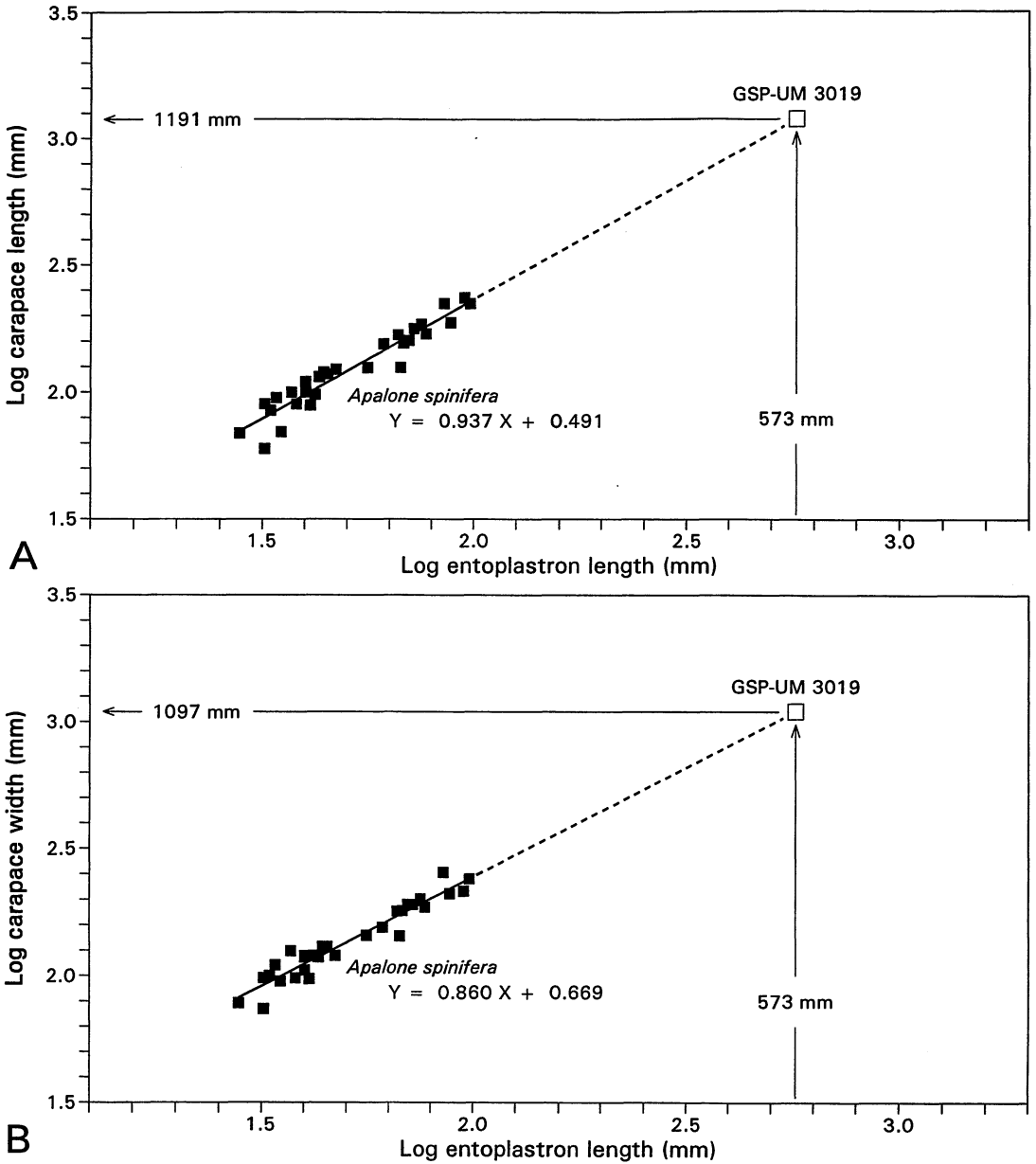
FIG. 7 — Relationship of bony carapace length (A) and width (B) to entoplastron length for 30 specimens of
Apalone spinifera (measurements used here are listed in Table 1). Comparison of entoplastron of GSP-
UM 3019 with those of the extant sample yields estimates of ca. 1200 mm for the length and ca. 1100 mm
for the width of the bony carapace. The leathery margin of the full carapace was larger, of course, and
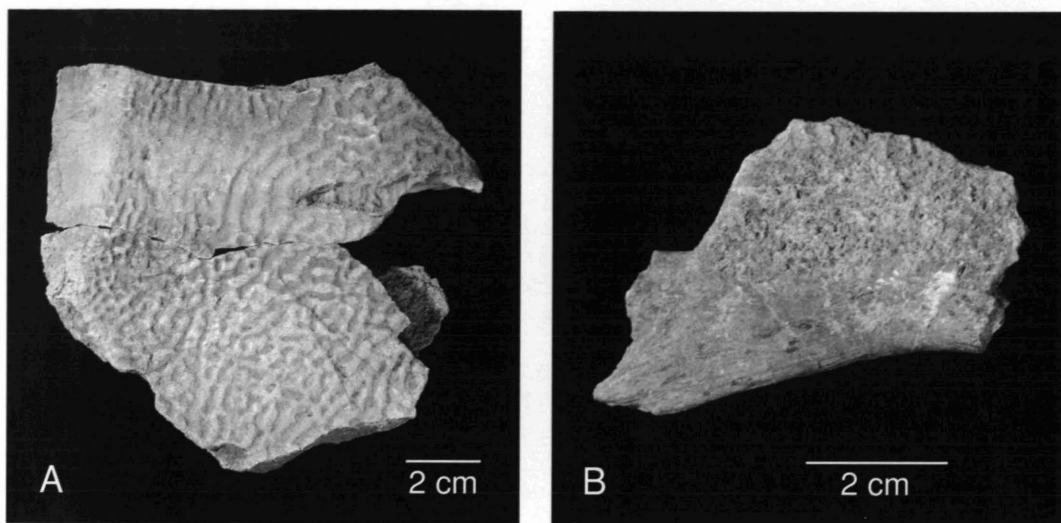possibly on the order of two meters in diameter.

FIG. 8 — A, GSP-UM 3184, trionychine carapace fragment in dorsal view (illustration is approximately one-half natural size and smooth lateral margin is at left). B, GSP-UM 3185, trionychine right hypoplastral fragment in ventral view (illustration is approximately natural size). Note projections at lower left for ligamentous attachment.

preserved anterior margin. The relatively small size of this specimen indicates that it came from a much smaller individual, possibly immature, than any of the specimens described above.

DISCUSSION

Phylogenetic Relationships of *Drazinderetes*

Drazinderetes tethyensis is easily identifiable as a trionychid based on the loss of peripheral elements and scute sulci, the flattened carapace, heavily sculpted dorsal surface of the carapace, and loss of a central articulation between the cervical and first thoracic vertebrae (Meylan, 1985; 1987). Subfamilial relationships within Trionychidae are poorly resolved, and determining the systematic positions of fossil specimens is often a process of exclusion from established lineages. Therefore, our placement of *Drazinderetes* must be considered preliminary, pending thorough systematic analysis of the majority of fossil taxa. The primary divisions within Trionychidae are the subfamilies Cyclanorbinae and Trionychinae (Loveridge and Williams, 1957; Meylan, 1987). *Drazinderetes* is considered a trionychine because it possesses the reduced costiform processes of the group, and lacks the concave posterolateral margins and kyphotic transverse carapace profile characteristic of cyclanorbines (Meylan et al., 1990; Gardner and Russell, 1994).

Drazinderetes cannot be allied with any known coeval fossil lineages. These lineages include *Plastomenus* ("Plastomenidae" of Hay, 1908), Ulutrionychini, and Paraplastomeni (Kordikova, 1994a,b). *Drazinderetes* shares contact between the posteromedial margins of the seventh costals with plastomenids, but lacks the hypertrophied eighth costal elements, thickened carapace, and "abrupt or peculiarly terminated costal bones" of the group (Hay, 1908; Hutchison and Archibald,

1986, pg. 12). Similarly, *Drazinderetes* cannot be referred to either Ulutrionychini or Paraplastomeni because it lacks neotenic characteristics of ulutrionychids and it lacks the extensive lateral extension of the carapace described for paraplastomenids.

The phylogenetic analysis of extant trionychids by Meylan (1987) provides the most extensive framework of interrelationships and character distributions with which to determine the systematic status of *Drazinderetes*. Based on the character distributions of Meylan's analysis, *Drazinderetes* shares several characteristics with modern Indo-Asian trionychines. A wide nuchal element is present in the genus *Aspideretes*, as well as *Pelodiscus sinensis*, *Dogania subplanus*, *Amyda cartilaginous*, and *Pelochelys bibroni* (Meylan, 1987; a wide nuchal also occurs in several members of Trionychini). Among these taxa, *Drazinderetes* and *Aspideretes* both lack suprascapular fontanelles and share complete enclosure of the costiform processes within the nuchal and presence of a preneural element with *Aspideretes*.

The presence of a separate preneural between the nuchal and first neural element is the most disputed characteristic used to determine trionychid interrelationships. The preneural was originally a diagnostic characteristic of the wastebasket-taxon *Aspideretes* of Hay (1908; much of Hay's fossil *Aspideretes* has since been subsumed into other taxa or considered 'nomen dubium' by Gardner et al., 1995). Subsequent studies considered the preneural to be primitive for trionychids (e.g., Webb, 1962; Carpenter, 1981; Meylan, 1985, 1987). Meylan (1987) hypothesized that the preneural is actually the first neural with fusion of the first and second neurals derived for trionychids, and retention of the first neural characteristic of his redefined *Aspideretes*. Cherepanov (1995) determined that the preneural has a separate embryological origin from the rest of the neural series, contradicting Meylan's hypothesis. Gardner et al. (1995) considered the polarity of the presence of a preneural equivocal at best among trionychines. Here we consider the presence of a preneural, in conjunction with other aforementioned characters, evidence of a closer relationship between *Drazinderetes* and *Aspideretes* than either has to other trionychid taxa. Absence of characteristics diagnostic of other lineages and shared geographic provenance also support relationship of *Drazinderetes* and *Aspideretes*.

The oldest aspideretid known previously comes from the lower-middle Miocene of Pakistan (Head, 1995). *Drazinderetes* extends the temporal range of the lineage into the Eocene. This range extension is the first record of an extant Asian lineage extending back across the Paleogene-Neogene boundary, but is not unexpected: aspideretids have been considered ancestral to either Pelodiscini (sensu Meylan, 1987) or both Pelodiscini and Trionychini (Meylan, 1987: fig. 30), indicating a long evolutionary history. Members of Trionychini are known from the Campanian of North America (Gardner et al., 1995), and if an ancestral relationship exists between aspideretids and Trionychini, then the aspideretid lineage might be expected to extend into the Cretaceous.

Diversity of Drazinda Trionychids

It is possible that all of the trionychid remains described here are referable to *Drazinderetes tethyensis*, and that the disparities in size and form between specimens reflect different ontogenetic stages or sexual dimorphism. However, the only specimen preserving morphology comparable to that in the type is GSP-UM 3184, and its conspicuously smooth lateral margin is quite different from any part of the margin of GSP-UM 3195, suggesting that they represent different taxa. The type GSP-UM 3195 could possibly represent a sub-adult stage of *Drazinderetes*, with GSP-UM 3019 representing a larger and fully mature specimen; however, the complete fusion of the carapace and short costal rib projections of GSP-UM 3195 are characteristic of fully mature trionychids. Until additional specimens are recovered, only GSP-UM 3195 can be recognized as *Drazinderetes*, and the other remains must be considered indeterminate. Similarly, Drazinda specimens cannot really be compared to the remains reported from other Eocene deposits in Indo-Pakistan as those are either too fragmentary or incompletely undescribed.

GSP-UM 3019 lacks any form of plastral callosity, which indicates a reduced number of callosities across the plastron — a derived characteristic of Trionychinae (Meylan, 1987). The

TABLE 2 — Comparison of the range of estimated whole-carapace diameters of *Drazinderetes tethyensis* GSP-UM 3195 (holotype) and GSP-UM 3019 (above dashed line) with measured carapace diameters of other large chelonian taxa. Measurements of other taxa are from: *Stupendemys*, Wood (1976); *Archelon*, Wieland (1909); *Protostega*, Zangerl (1953); *Dermochelys* maximum size values, Pritchard (1971); *Geochelone*, Auffenberg (1974). See text for explanation of range calculations.

Taxon	Whole carapace length (mm)	Whole carapace width (mm)	Temporal distribution	Geographic distribution	Depositional environment
Drazinderetes tethyensis (GSP-UM 3195)	1000-1455	814-921	Eocene	Pakistan	Marine
Trionychidae indet. (GSP-UM 3019)	1500-2182	1279-1447	Eocene	Pakistan	Marine
Dermochelys coriacea	1850	950	Pleist.?-Recent	Pan-Oceanic	Marine
Stupendemys geographica	2500	1950	Pleistocene	Venezuela	Fresh/marine
Geochelone altas	~2000	—	Plio-Pleistocene	N. America, Asia	Terrestrial
Archelon ischyros	1930	2180	Late Cretaceous	N. America	Marine
Protostega gigas	1370	1450	Late Cretaceous	N. America	Marine

number of plastral callosities is diagnostic for trionychine subdivisions, but the sequence of callosity loss is not known. Absence of any additional plastral elements precludes determination of the exact number of callosities, and thus further taxonomic resolution of GSP-UM 3019. GSP-UM 3184 is possibly conspecific with GSP-UM 3019, but both GSP-UM 3184 and GSP-UM 3185 are fragmentary and lack diagnostic subfamilial characteristics.

It should be noted that many of the reported difficulties in determining the systematic relationships of trionychid turtles are based on studies that have ignored much of the fossil record. Trionychids do possess considerable interspecific variation in their osteology (e.g., Dalrymple, 1977), however assertions of rampant homoplasy have little meaning until the evolutionary history of Trionychidae is more firmly established.

Body Size

The bony carapace of trionychids is not the whole carapace. In all trionychids there is an additional cartilaginous extension surrounding the bony carapace and extending the lateral and posterior margins. The contribution of the bony carapace to the whole carapace is highly variable across species, ranging from 80% of total length and 86% of total width (*Apalone*) to 55% of total length and 76% of total width (*Dogania subplanus*). As there are no diagnostic characteristics present in *Drazinderetes tethyensis* (GSP-UM 3195) and Trionychidae indet. (GSP-UM 3019) permitting one to select a single extant model for carapace size, the whole carapace diameters estimated here are given as a range between the minimum and maximum contributions seen in extant trionychines. The 800 mm length of GSP-UM 3195 yields a minimum whole-carapace length of about 1000 mm and a maximum length of about 1455 mm. The 700 mm width of GSP-UM 3195 yields a minimum whole carapace width of about 814 mm and a maximum width of about 921 mm. The 1200 mm length estimated for GSP-UM 3019 yields a minimum whole

carapace length of about 1500 mm and a maximum length of about 2182 mm. The 1100 mm width estimated for GSP-UM 3019 yields a minimum whole-carapace width of about 1279 mm and a maximum width of about 1447 mm.

Estimated carapace dimensions indicate that GSP-UM 3019 represents the largest recorded trionychid. Previously, the largest trionychid specimen was a 970 mm long bony carapace from the Eocene freshwater Bridger Formation of Wyoming (Gaffney, 1979b). Among extant trionychids, large specimens of *Pelochelys*, *Cyclanorbis*, and *Chitra* possess bony carapaces longer than 400 mm (Meylan, 1987), however there is no indication that any of these taxa approach a meter in whole carapace length.

Comparison of the estimated full carapace of GSP-UM 3019 to carapace measurements of other large taxa indicates that GSP-UM 3019 is among the largest known turtles (Table 2). Only the pelomedusid pleurodire *Stupendemys geographica* (Wood, 1976) possesses a longer carapace than the maximum estimate for GSP-UM 3019, and the only other taxa to approach the maximum estimate are the protostegid *Archelon ischyros* and the giant tortoise *Geochelone atlas* (Wieland, 1909; Auffenberg, 1974). The minimum estimate of carapace length for GSP-UM 3109 is equivalent to average lengths of the largest extant turtle, the giant leatherback *Dermochelys coriacea* (Pritchard, 1971). Other large fossil turtle taxa are either too fragmentary to permit comparison of carapace size, or have not been directly measured (e.g., *Atlantochelys* Parris, 1996; *Mesodermochelys* Hirayama and Chitoku, 1997).

Marine Habitat

There are three scenarios for occurrence of trionychids in shallow marine sediments of the Drazinda Formation. First, the remains were transported postmortem from freshwater or brackish environments; however, there are no supporting indicators of such transport in the Drazinda Formation. Second, the remains indicate infrequent habitation of marine environments by predominantly freshwater taxa; some extant trionychids are capable of inhabiting strongly saline environments, and one, *Pelochelys*, has been recorded at sea (Rhodin et al., 1993). Third, the remains represent adaptation of a trionychid lineage to the shallow marine environments of eastern Tethys.

The lack of supporting evidence of postmortem transport and the diversity of remains reported here suggest that active marine habitation may be the most likely explanation for the occurrence of trionychids in the Drazinda Formation. Large body size is a characteristic of marine turtles (Table 2), and the unusual size of GSP-UM 3195 (carapace; type of *Drazinderetes tethyensis*), GSP-UM 3019 (entoplastron), and 3184 (carapace fragment) suggests permanent habitation in Tethys. If some or all of the remains represent ontogenetic stages of a single lineage, then permanent habitation is most probable as there are no known records of sub-adults of freshwater taxa in marine environments. Fossil trionychids have been recovered from other near-shore marine environments (de Broin, 1987); however, Drazinda Formation specimens present the most compelling evidence that some trionychids may have been fully marine.

ACKNOWLEDGMENTS

of Michigan, and by the Geological Survey of Pakistan. This report was completed with support from the U.S. National Science Foundation (EAR-9714923).

LITERATURE CITED

AFZAL, J., A. M. KHAN, and N. A. SHAFIQUE. 1997. Biostratigraphy of Kirthar Formation (middle to late Eocene), Sulaiman Basin, Pakistan. Pakistan Journal of Hydrocarbon Research, Islamabad, 9: 15-33.

ANGIELCZYK, K. D. and P. D. GINGERICH. 1998. New specimen of cf. *Asiatosuchus* (Crocodyloidea) from the middle Eocene Drazinda Formation of the Sulaiman Range, Punjab (Pakistan). Contributions from the Museum of Paleontology, University of Michigan, 30: 163-189.

AUFFENBERG, W. 1974. A checklist of fossil land tortoises (Testudinidae). Bulletin of the Florida State Museum, Biological Sciences, 18: 121-251.

BERGGREN, W. A., KENT, D. V., SWISHER, C. C., and AUBRY, M.-P. 1995. A revised Cenozoic geochronology and chronostratigraphy. In W. A. Berggren, D. V. Kent, M.-P. Aubry, and J. A. Hardenbol(eds.), Geochronology, Time Scales and Global Stratigraphic Correlations: A Unified Temporal Framework for an Historical Geology, Society of Economic Geologists and Mineralogists Special Volume 54, Tulsa, pp. 129-212.

BHATTI, M. A., M. AKHTAR, and M.-H. ABBASI. 1986. Geological map of Dhodak. Geological Survey of Pakistan, Geological Map Series, 4: 157 (one sheet).

BROIN, F. de. 1987. Lower vertebrates from the Early-Middle Eocene Kuldana Formation of Kohat (Pakistan): Chelonia. Contributions from the Museum of Paleontology, University of Michigan, 27: 151-186.

CARPENTER, K. 1981. Preneural in the evolution of *Trionyx*. Copeia, 1981: 456-457.

CHEREPANOV, G. O. 1995. Ontogenetic development of the shell in *Trionyx sinensis* (Trionychidae, Testudinata) and some questions on the nomenclature of bony plates. Russian Journal of Herpetology, 2: 129-133.

CHKHIKVADZE, V. 1990. The Paleogene turtles of the USSR (Paleogenovyye cherepakhi SSSR). Tbilisi Metsniereba (in Russian). 95 pp.

DALRYMPLE, G. H. 1977. Intraspecific variation in the cranial feeding mechanism of turtles of the genus *Trionyx* (Reptilia, Testudines, Trionychidae). Journal of Herpetology, 11: 255-285.

GAFFNEY, E. S. 1979a. Comparative cranial morphology of Recent and fossil turtles. Bulletin of the American Museum of Natural History, 164: 67-376.

————. 1979b. Description of a large trionychid turtle shell from the Eocene Bridger Formation of Wyoming. Contributions to Geology, University of Wyoming, 17: 53-57.

GARDNER, J. D., and A. P. RUSSELL. 1994. Carapacial variation among soft-shelled turtles (Testudines: Trionychidae), and its relevance to taxonomic and systematic studies of fossil taxa. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 193: 209-244.

————, A. P. RUSSELL, and D. B. BRINKMAN. 1995. Systematics and taxonomy of soft-shelled turtles (Family Trionychidae) from the Judith River Group (mid-Campanian) of North America. Canadian Journal of Earth Sciences, 32: 631-643.

GINGERICH, P. D., S. M. RAZA, M. ARIF, M. ANWAR, and X. ZHOU. 1993. Partial skeletons of *Indocetus ramani* (Mammalia, Cetacea) from the lower middle Eocene Domanda Shale in the Sulaiman Range of Pakistan. Contributions from the Museum of Paleontology, University of Michigan, 28: 393-416.

————. 1994. New whale from the Eocene of Pakistan and the origin of cetacean swimming. Nature, 368: 844-847.

————, M. ARIF, M. A. BHATTI, H. A. RAZA, and S. M. RAZA. 1995. *Protosiren* and *Babiacetus* (Mammalia, Sirenia and Cetacea) from the middle Eocene Drazinda Formation, Sulaiman Range, Punjab (Pakistan). Contributions from the Museum of Paleontology, University of Michigan, 29: 331-357.

————, M. ARIF, M. A. BHATTI, M. ANWAR, and W. J. SANDERS. 1997. *Basilosaurus drazindai* and *Basiloterus hussaini*, new Archaeoceti (Mammalia, Cetacea) from the middle Eocene Drazinda Formation, with a revised interpretation of ages of whale-bearing strata in the Kirthar Group of the Sulaiman Range, Punjab (Pakistan). Contributions from the Museum of Paleontology, University of Michigan, 30: 55-81.

HAY, O. P. 1908. The fossil turtles of North America. Publications of the Carnegie Institution of Washington, 75: 1-568.

HEAD, J. J. 1995. Two new trionychids (Reptilia, Testudines) from the Miocene of Pakistan: evolution of Aspideretini. Journal of Vertebrate Paleontology 15 (suppl. 3): 33A (abstract).

————. 1997. Reptile paleontology of the Dhok Pathan Formation, Siwalik Group, Pakistan: preliminary results. Records of the Geological Survey of Pakistan, 109: 58-62.

HIRAYAMA, R. and T. CHITOKU. 1996. Family Dermochelyidae (Superfamily Chelonioidea) from the Upper Cretaceous of North Japan. Transactions and Proceedings of the Palaeontological Society of Japan, 184: 597-622.

HUTCHISON, J. H. and J. D. ARCHIBALD. 1986. Diversity of turtles across the Cretaceous/Tertiary boundary in northeastern Montana. Palaeogeography, Palaeoclimatology, Palaeoecology, 55: 1-22.

KHAN, A. A., M. AKHTAR, I. HUSSAIN, and T. MASOOD. 1986. Geological map of Barthi. Geological Survey of Pakistan, Geological Map Series, 4: 176 (one sheet).

KHARE, S. K. 1976. Eocene fishes and turtles from the Subathu formation, Beragua Coal Mine, Jammu and Kashmir. Journal of Paleontological Society of India, 18: 36-43.

KORDIKOVA, E. G. 1994a. About systematics of fossil trionychids in Kazakhstan. Selevinia, 2: 1-10.

———. 1994b. Review of fossil trionychid localities in the Soviet Union. Courier Forschungsinstitut Senckenberg, 173: 341-358.

LOVERIDGE, A., and WILLIAMS, E. E. 1957. Revision of the African tortoises and turtles of the suborder Cryptodira. Bulletin of the Museum of Comparative Zoology, 115: 163-557.

LOYAL, R. S. 1990. Lithostratigraphy of the basal Subathu Formation (upper Palaeocene-middle Eocene) exposed in the stratotype, Kuthar River, Subathu, Himachal Pradesh, India, with introductory notes on physiography and tectonics. Tertiary Research, Leiden, 12: 1-16.

MEYLAN, P. A. 1985. Evolutionary relationships of recent trionychid turtles: evidence from shell morphology. Studia Geologica Salamancensia, Volumen Éspecial, 1: 169-188.

———. 1987. The phylogenetic relationships of soft-shelled turtles (Family Trionychidae). Bulletin of the American Museum of Natural History, 186: 1-101.

———, B. S. WEIG, and R. C. WOOD. 1990. Fossil soft-shelled turtles (Family Trionychidae) of the Lake Turkana Basin, Africa. Copeia, 1990: 508-528.

PARRIS, D. C. 1996. Large cheloniids in the Cretaceous of the Atlantic coastal plain. Journal of Vertebrate Paleontology, 16 (suppl. 3): 57A (abstract).

PRITCHARD, P. C. H. 1971. The leatherback or leathery turtle *Dermochelys coriacea*. International Union for Conservation of Nature and Natural Resources (IUCN), Monographs, 1: 1-39.

———. 1979. Encyclopedia of Turtles. T. F. H. Publications, Neptune, N.J. 895 pp.

RHODIN, G. J., A. M. RUSSELL, and P. M. HALL. 1993. Distribution, osteology, and natural history of the Asian giant softshell turtle, *Pelochelys bibroni*, in Papua New Guinea. Chelonian Conservation and Biology, 1: 19-30.

SAHNI, A., R. S. BATRA, and S. B. BHATIA. 1984. Vertebrate assemblage from the upper Subathu (Middle Eocene) of the Bilaspur area, Himachal Pradesh, India. Proceedings of the 10th Indian Colloquium on Micropalaeontology and Stratigraphy, 357-368.

———, S. B. BHATIA, J.-L. HARTENBERGER, J.-J. JAEGER, K. KUMAR, J. SUDRE, and M. VIANEY-LIAUD. 1981a. Vertebrates from the type section of the Subathu formation and comments on the paleobiogeography of the Indian subcontinent during the Early Palaeogene. Bulletin of the Indian Geological Association, 14: 89-100.

———. 1981b. Vertebrates from the Subathu formation and comments on the biogeography of Indian subcontinent during the early Paleogene. Bulletin de la Société Géologique de France, Série 7, 23: 689-695.

——— and V. P. MISHRA. 1975. Lower Tertiary vertebrates from western India. Monograph of the Paleontological Society of India, 3: 1-48.

SAMANTA, B. K. 1973. Planktonic foraminifera from the Paleocene-Eocene succession in the Rakhi Nala, Sulaiman Range, Pakistan. Bulletin of the British Museum (Natural History), Geology, 22: 421-482.

WEBB, R. G. 1962. North American Recent soft-shelled turtles (Family Trionychidae). University of Kansas Publications on Natural History, 13: 429-611.

WEST, R. M., J. R. LUKACS, S. T. HUSSAIN, and M. ARIF. 1991a. Geology and palaeontology of the Eocene Drazinda Shale Member of the Kirthar Formation, central western Pakistan. Part I: Introduction. Tertiary Research, Leiden, 12: 97-103.

WEST, R. M., J. H. HUTCHISON, and J. MUNTHE. 1991b. Miocene vertebrates from the Siwalik Group, western Nepal. Journal of Vertebrate Paleontology, 11: 108-129.

WIELAND, G. R. 1909. Revision of the Protostegidae. American Journal of Science, 27: 101-130.

WOOD, R. C. 1976. *Stupendemys geographicus*, the world's largest turtle. Breviora, 436: 1-31.

YE, X. 1994. Fossil and Recent Turtles of China. Science Press, Beijing, 114 pp.

ZANGERL, R. 1953. The vertebrate fauna of the Selma Formation of Alabama. Part III. The turtles of the family Protostegidae. Fieldiana Geology, Memoirs, 3: 61-144.