A Preliminary Report on Southeast Asia's Oldest Cenozoic Turtle Fauna from the Late Middle Eocene Pondaung Formation, Myanmar.

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Abstract. - Late middle Eocene fossils from the Pondaung Formation of central Myanmar document Southeast Asia's oldest Cenozoic turtle fauna. Although the material is fragmentary, seven distinct turtle taxa are recognized. These include a podocnemid pleurodire, anosteirine and carettochelyine carettochelyids, two or more trionychine trionychids, and a testudinid. Of these, only the carettochelyine carettochelyid is complete enough to recognize as a new taxon, *Burmemys magnifica*, gen. et sp. nov. The Pondaung turtle fauna is one of the best known of its age from Southeast Asia but comparisons with the limited literature of the Eocene faunas from China, Mongolia, and the Indian subcontinent indicate it is probably biogeographically unique. Among the recognized genera, only *Anosteira* is known from other Eocene Asian localities, and the presence of pleurodires is unusual.

Key words. - Reptilia, Testudines, Carettochelyidae, *Burmemys*, Myanmar, Pondaung Formation, Paleontology, Eocene.

Introduction

The origins of Southeast Asia's herpetofauna are poorly understood, as there are few fossils that document the origin of the major groups inhabiting the region. The oldest known herpetofauna from this region is from the Pondaung Formation, a late middle Eocene (approx. 37 Ma) set of rocks exposed in the Chindwin-Irrawaddy Basin of Myanmar (formerly Burma). The Pondaung fauna is best known for its mammalian fauna (e.g., Colbert, 1938; Tsubamoto et al., 2000), and little attention has been devoted to the remainder of the fauna. In prior reports, Buffetaut (1978) noted the presence of both unidentified crocodilians and dyrosaurids; Sahni (1984) and Rage (1987) noted unidentified Lacertilia. These reports were based primarily on a rather limited collection made by Barnum Brown in 1922 and housed in the American Museum of Natural History, New York. Savage and Russell (1983) and Broin (1987) list "Pelomedusid/Emydidae", "Carettochelyoidea", and trionychids from the Pondaung. Outside the Pondaung region, the only other report of turtles from Southeast Asia is Ducrocq et al.'s (1992) mention of two types of ?Emydidae from the late Eocene site of Krabi, Thailand. Here we present a preliminary description of the turtles based on a more thorough study of these collections, and additional collections in the University of California Museum of Paleontology, Berkeley, California.

Localities and age. - Fossils occur in a number of localities occurring in the upper 100+ meters of the otherwise marine Pondaung Formation. The majority of the specimens discussed here come from localities to the west and northwest of Mogaung village, Myaing Township, central Myanmar (Fig. 1), that have been collected intermittently over the past 80 years. As a consequence, most specimens have limited, descriptive locality data that provides locations based on distances from known villages. Recent fieldwork has provided detailed, GPS based mapping of the most productive outcrops and permit us to place most of the historic localities in a more accurate and stratigraphically detailed framework. Those localities we can place with confidence are shown in Figure 1. Localities whose positions are approximate are shown with dashed lines. Concordances for localities that have been published under more than one name or number are provided in the caption of Figure 1 and are based on Colbert (1938), maps on file at the American Museum of Natural History, field notes of J. Wyatt Durham and Donald E. Savage on file at the University of California Museum of Paleontology, data contained in Tsubamoto et al. (2000, 2002) and Gunnell et al. (2002), and field observations by PAH and RLC.

Fossils occur in place and as erosional lag coming out of reddish to purplish mudstones (Fig. 2 A-C). Fossil wood is also commonly found (Fig. 2D), attesting to the presence of the ancient forest. Soe et al. (2002) interpreted sediments including these localities as swale-fills and/or paleosols deposited in an ancient floodplain; stratigraphic sections for these localities are contained in Gunnell et al. (2002). Based on comparisons of temporal distribution and faunal resemblance data of the
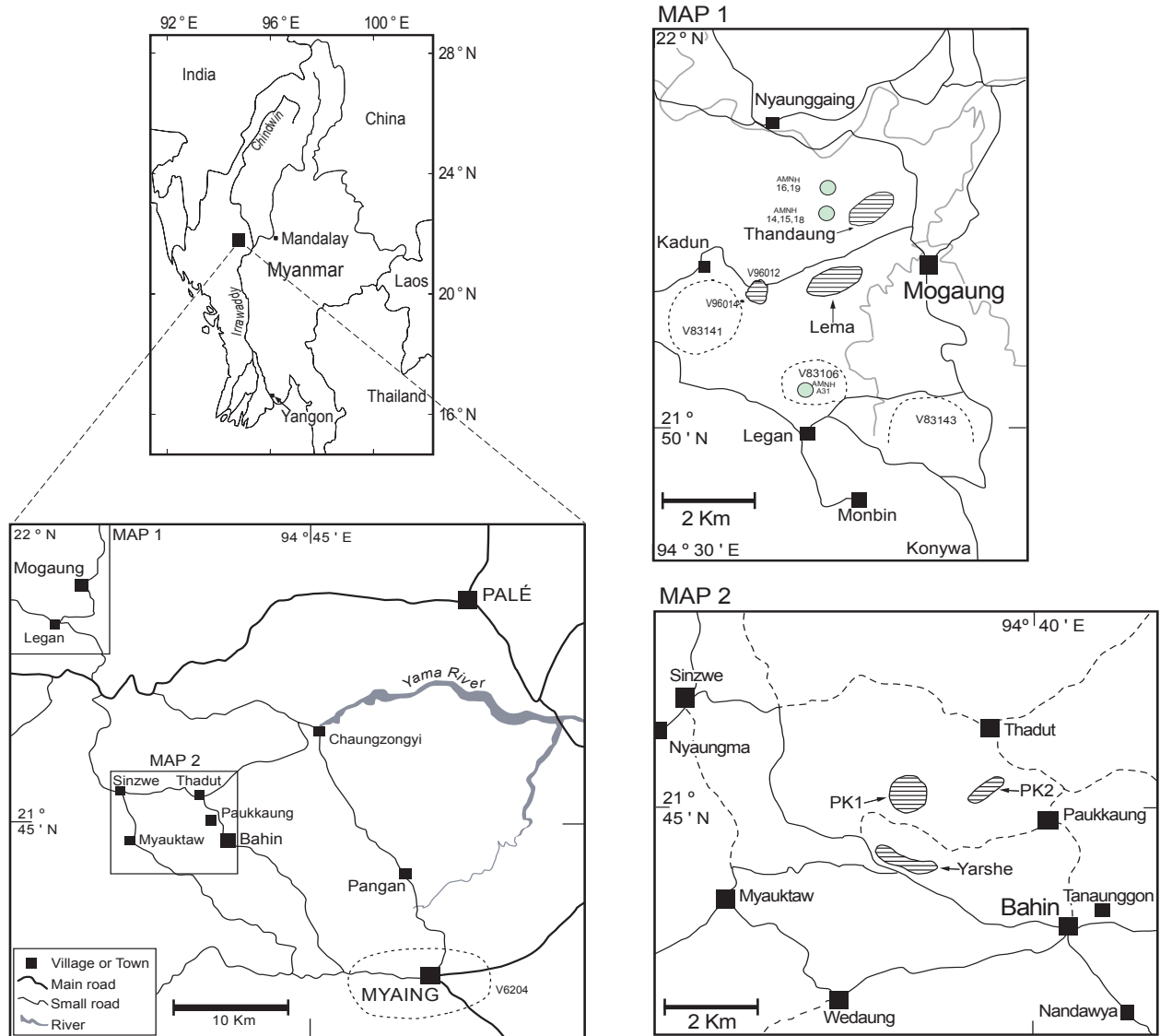
Figure 1. Locality Map of Pondaung Formation localities. V78090=Thandaung kyitchaung and possibly AMNH localities A14-16, 18-19; V83106, 3.5 mi SW of Mogaung = AMNH A31; V83111 "1.25 mi NW Paukkaung" probably equals Pk2; V83116 probably equals Yarshe kyitchaung. V96001-V96002 = AMNH A22 and Lema kyitchaung; V98019 "Thidon or near Bahin", possibly equal to Pk1 or Pk2.

Pondaung mammalian fauna with other Asian and North American mammal faunas, as well as additional constraining evidence from marine invertebrates, Holroyd and Ciochon (1994) concluded that the Pondaung fauna is best considered latest middle Eocene in age and broadly contemporaneous with Asian faunas assigned to the Sharamurunian Land Mammal Age, a finding confirmed by recent fission-track dates that provide a date of 37.2 +/- 1.2 Ma (Tsubamoto et al., 2002).

Abbreviations. - AMNH, American Museum of Natural History, New York, New York, U.S.A.; UCMP, University of California Museum of Paleontology, Berkeley, California, U.S.A.

Systematic Paleontology

Testudines Batsch, 1788
Pleurodira Cope, 1865
Pelomedusoides Cope, 1868
Podocnemididae Cope, 1868
?Podocnemididae unident.

Referred Material. - UCMP locality V83108: UCMP 153798, right peripheral 3. UCMP locality V83113: UCMP 147052, partial left hypo-xiphiplastron. UCMP locality V96002: UCMP 142245, left incomplete epiplastron.
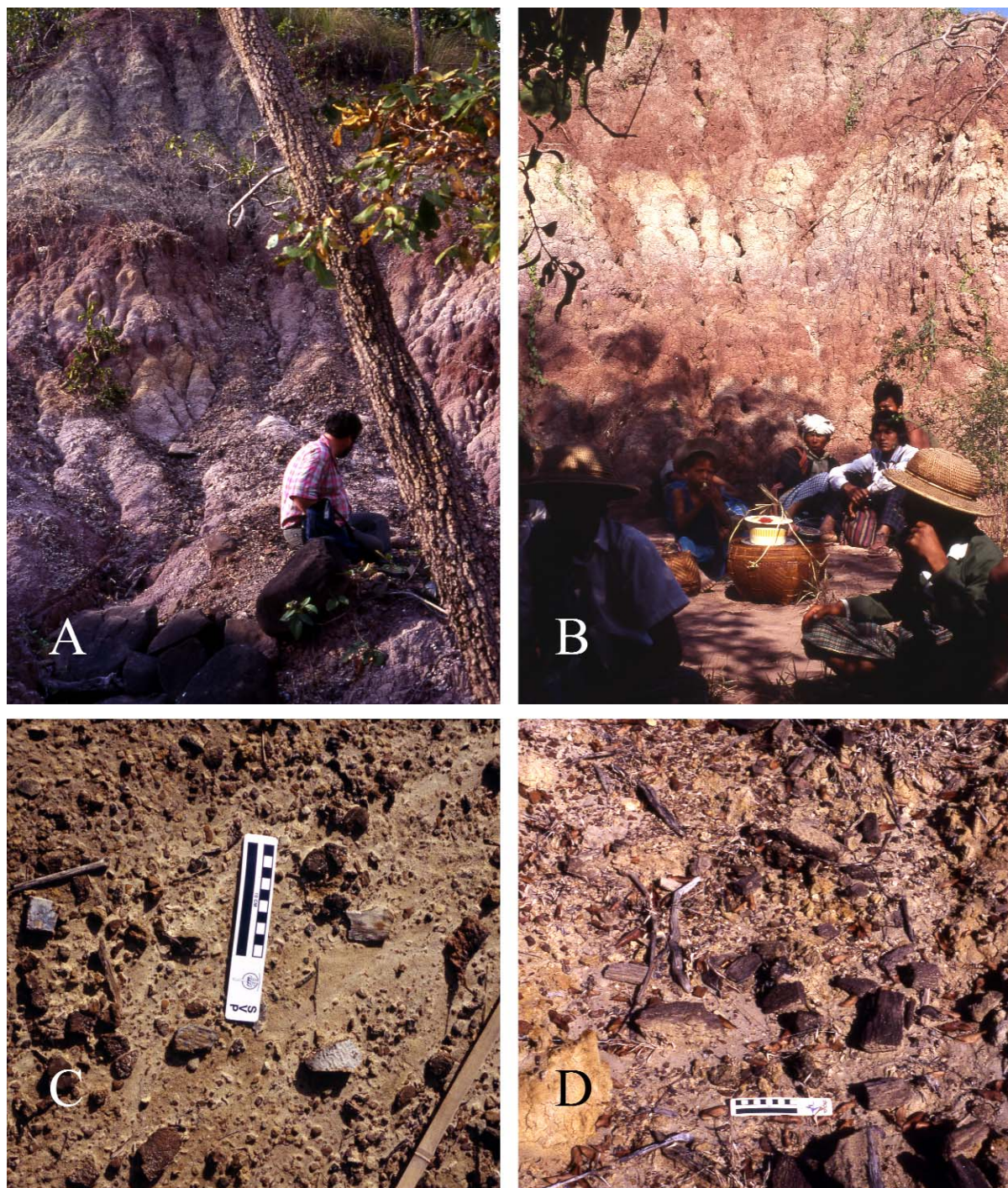
Figure 2. Fossil localities of the Pondaung Formation. **A**. UCMP locality V96001, Lema kyitchaung; **B**. UCMP locality V96002, Lema kyitchaung; **C**-**D**. UCMP locality V96007, near Mogaung, showing the common occurrence as float of both turtle bone (**C**) and petrified wood (**D**) on the surface.

Description. - The epiplastron (UCMP 142245, Fig. 3A) lacks the posterolateral part but is otherwise well preserved. The scale covered surfaces are very finely textured with delicate but well-defined sulci. Faint growth corrugations are present on the gular scale (extragular of Hutchison and Bramble, 1981). There is a prominent anteriorly-projecting gular spur, and the epi-plastron margin is distinctly concave between the midline and the gular spur. There is an intergular scale (gular of Hutchison and Bramble, 1981) spanning the midline that projects anteriorly into the anterior embayment. The scales overlap extensively onto the dorsal surface with little exposure of the visceral surface. The intergular expands slightly posteriorly on the ventral surface and
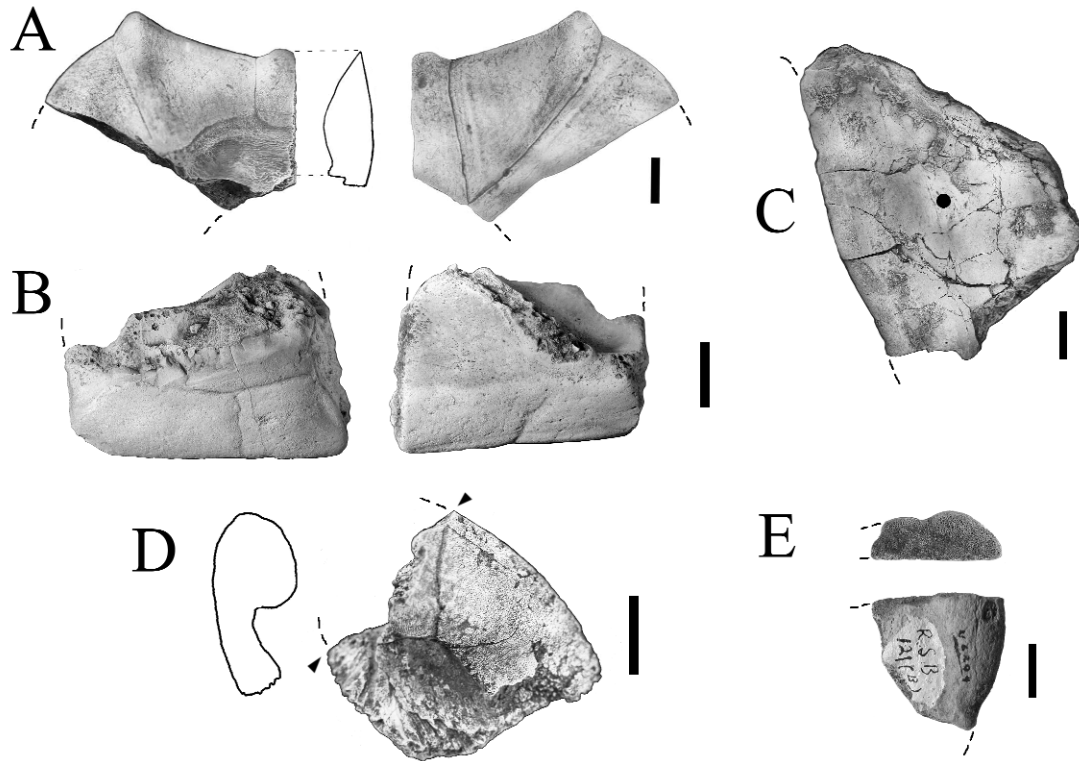
Figure 3. **A**-**C**. Podocnemidae? indet. **A**. UCMP 142245, incomplete left epiplastron, dorsal, medial suture and ventral views. **B**. 153798, right peripheral 3, external and visceral views. **C**.UCMP 147052, hypo-xiphiplastron fragment, dorsal view, spot indicates center of bump. **D**-**E**. Testudinidae. **D**. UCMP 142226, partial right epiplastron, cross-section (as indicated) and dorsal views. **E**. UCMP 149166, partial right xiphiplastron, dorsal view. Scale bars equal 1 cm.

extends onto the entoplastron. Dorsally the intergular extends slightly more than one-half the length of the inter-epiplastral suture and is parallel-sided. On the ventral surface, the gular is triangular with the lateral margins converging to a point at the entoplastron margin.

The hypo-xiphiplastron fragment, UCMP 147052 (Fig. 3C), is broken on all the edges except the free margin. It exhibits a narrow overlap of the femoral and anal scales onto the dorsal surface (less than one-fifth the transverse length as preserved). The swelling at the anterolateral corner indicates an ascendant hypoplastral buttress. The sutures are fused. A short expanse of the femoral-anal scale sulcus is preserved at the extreme posterior end. Medial to the scale margins on the dorsal side is a large elliptical swelling that has a smooth surface and may have been divided by the hypo-xiphiplastron suture.

The peripheral 3 (UCMP 153798, Fig. 3B) lacks the dorsal margin. The body of the peripheral is robust and without a change in plane between the pleural and marginal surfaces. The surface is smooth and unsculptured. The sulci are shallow but well defined. The free margin is acutely angled. On the visceral side, the marginal scales rise up from only about one-third of the peripheral depth. There is no indication of an axillary scale. The finely dentate suture for the hyoplastron buttress rises anteriorly and may have overlapped peripheral 2-3 suture. There is a gap in the hyoplastral suture near the posterior margin, for passage of the musk duct. The length between the anterior and posterior sutures along the free margin of the peripheral is 37.9 mm.

Discussion. - The dorsal scale overlap, truncated anterior margin, undivided intergular, and relatively thick epiplastra resemble selected extant or fossil Pelomedusoides (Bothremydidae, Podocnemididae, and Pelomedusidae). The prominent epiplastral spurs resemble those of the pelomedusid *Kenyemys* Wood, 1983, from the Pliocene of Kenya. However, the Pondaung form differs in the greater excavation of the gular embayment, intergular extending onto the entoplastron, and restriction of the gular scales to the epiplastra (i.e., not reaching the midline). The scale arrangement is similar to that of the podocnemidid *Neochelys* Bergounioux, 1954 (Broin, 1977; Jimènez et al., 1994) from the Eocene of Europe. *Neochelys* may also possess a relatively prominent gular spur (Broin, 1977, fig. 59), but differs in the less extensive dorsal overlap of the scales and lesser development of an epiplastral embayment.
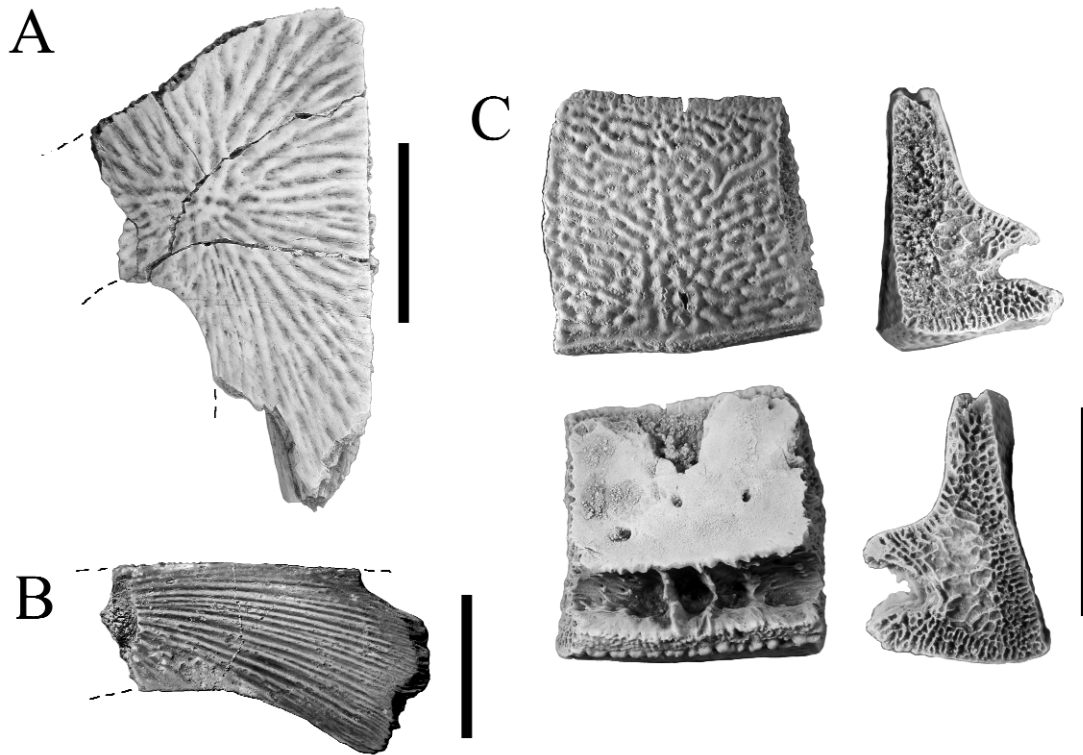
Figure 4. *Anosteira* sp., **A**. UCMP 131736, right hypoplastron, ventral view. **B**. UCMP 131737, lateral fragment of left hypoplastron, ventral view. **C**. UCMP 147030, left peripheral 6, external, posterior, visceral, and anterior views. Scale bars equals 1 cm.

The presence of a prominent musk duct on the peripheral 3, absence of an axillary scale, and strong indication of a hyoplastral buttress rising onto the first costal is consistent with *Neochelys*-like pleurodires. The hypoplastron fragment may be referable to the same taxon, but the area of the pelvic sutures is broken off.

The general similarity to at least some *Neochelys* favors a placement of the Pondaung Formation specimens in the Podocnemididae.

Cryptodira Cope, 1868
Testudinidae Gray, 1825
Testudinidae undet.

Referred Material. - UCMP locality V6204: UCMP 149166, right xiphiplastron fragment. UCMP locality V96009: UCMP 142226, partial right epiplatron.

Description. - The epiplastron (UCMP 142226, Fig. 3D) lacks the gular region. The remaining part of the free margin is greatly thickened along the anterior edge of the dorsal scale covered portion. The posterior rim of this thickened gular area overhangs the visceral surface. The ventral surface is longitudinally convex. The sutures are moderately thick and dentate.

The anterolateral part of a right xiphiplastron (UCMP 149166, Fig. 3E) is referred to the Testudinidae on the basis of the strong overlap of the femoral scale dorsally, its inflated appearance, and fairly porous surface texture.

Discussion. - The morphology of the epiplastron is typical of testudinids and a few batagurids. The rather porous bone, inflation of the gular area, and general nature of the sutures and surface texture agrees best with that of a testudinid. The overhang of the posterior gular rim is derived in testudinids and absent or poorly developed in such tortoises as *Hadrianus* Cope, 1872, *Stylemys* Leidy, 1851, *Sharemys* Gilmore, 1931, *Kansuchelys* Yeh, 1963, and *Ergilemys* Ckhikvadze, 1972. The epiplastron thus resembles more derived tortoises such as *Testudo* Linnaeus, 1858.

Testudinoidea Fitzinger, 1826, indet.

Referred material. - UCMP locality V96019: UCMP 147051, posterior part of left hypoplastron. UCMP locality V78090: UCMP 170495, partial neural. UCMP locality V98109: UCMP 170522, shell fragments.

Description. - The hypoplastron is represented by a fragment (UCMP 147052) that preserves the portion
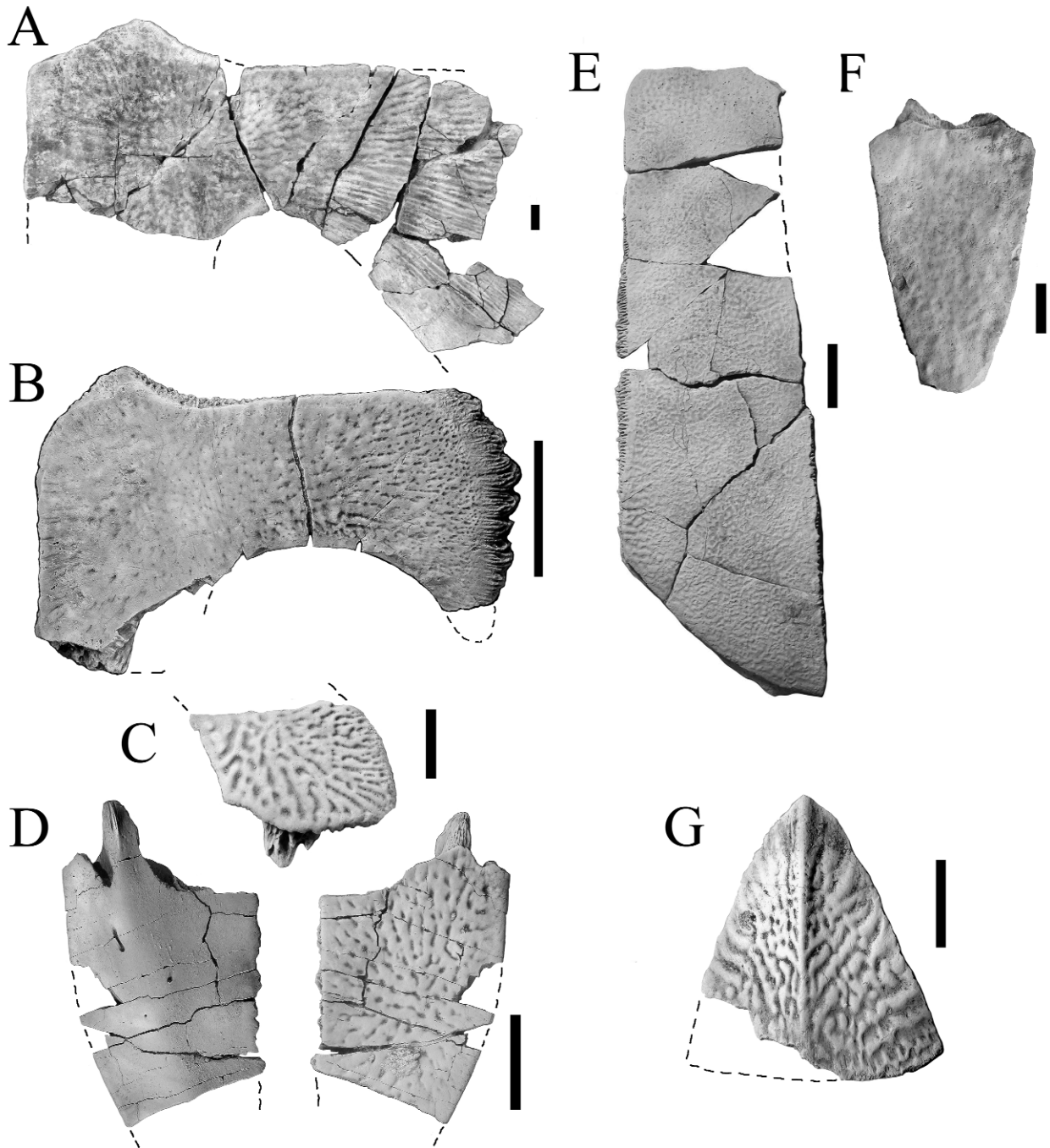
Figure 5. *Burmemys magnifica* gen. et sp. n. **A**. UCMP 61212, adult left hypoplastron (type), ventral view. **B**. UCMP 131745. juvenile left hypoplastron, ventral view. **C**. UCMP 154993, posterior part of juvenile left epiplastron, ventral view. **D**. UCMP 131747, anterior part of juvenile left xiphiplastron, dorsal and ventral view. **E**. UCMP 157444, juvenile left costal 2, external view. **F**. UCMP 147022, neural, external view. **G**. UCMP 157442, suprapygal, external view. Scale bars equals 1 cm.
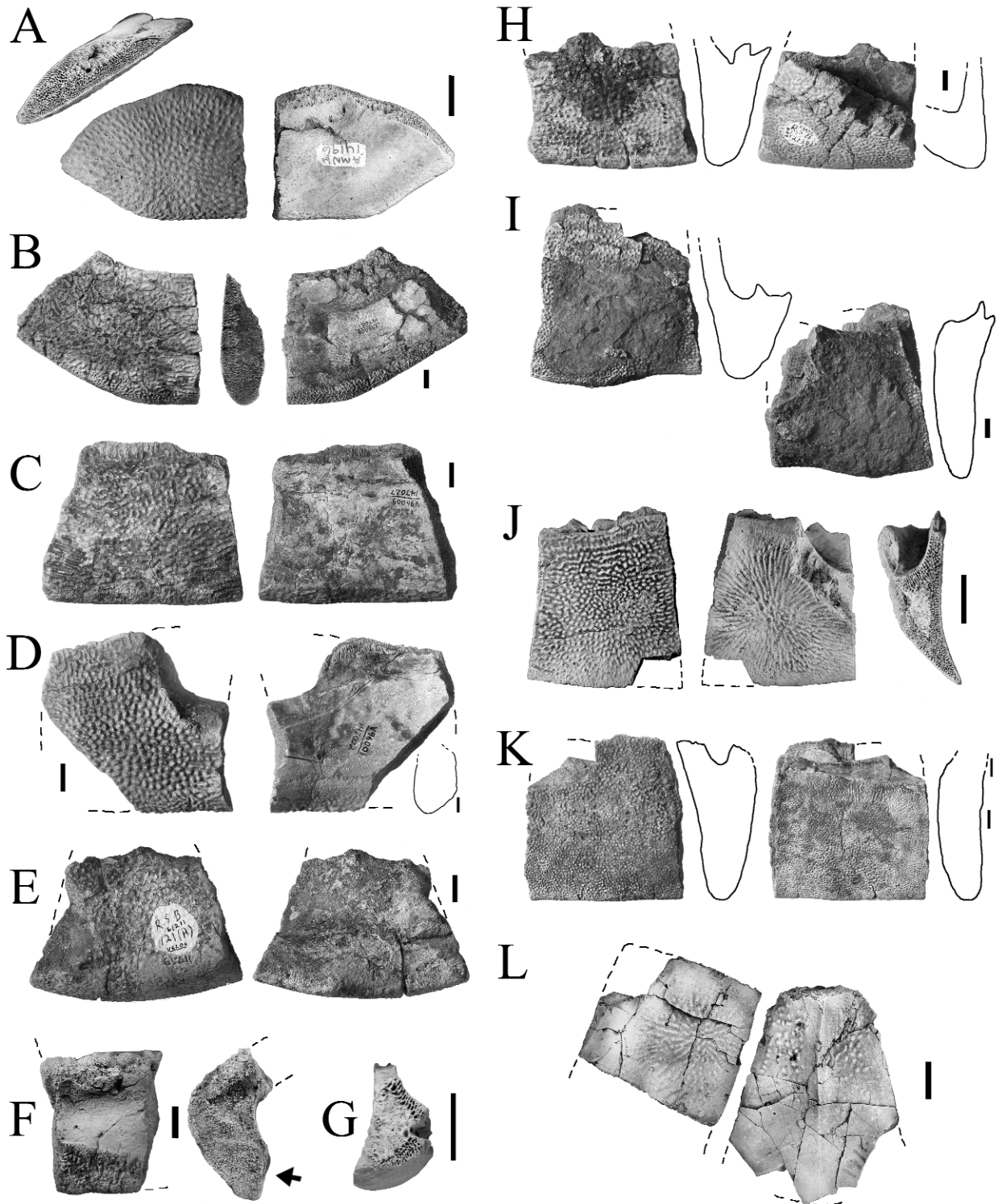
Figure 6. *Burmemys magnifica* gen. et sp. n. **A**. AMNH 14196, left peripheral 1, anterior suture, external and visceral views. **B**. UCMP 147021, left peripheral 1, external, posterior suture and visceral views. **C**. UCMP 147027, left peripheral 2, external and visceral views. **D**. UCMP 147002, left peripheral 3, external, visceral and posterior suture views. **E**. UCMP 61211, left peripheral 4, external and visceral views. **F**. UCMP 147001, left peripheral 4 fragment, visceral and posterior suture views (arrow points to flat hyoplastral suture). **G**. UCMP 131756, juvenile left peripheral 5, suture view. **H**. UCMP 61218, left peripheral 6, external, posterior suture, visceral and anterior suture views. **I**. UCMP 142223, right peripheral 7, external, anterior suture, visceral, posterior suture views. **J**. UCMP 157445, juvenile left peripheral 7, external, visceral, and anterior suture views. **K**. UCMP 142244, right peripheral 8, external, anterior suture, visceral and posterior views. **L**. AMNH 1911, left peripheral 10 and pygal, external view. Scale bars equal 1 cm.

posterior to the buttress. The free margin is slightly convex. The femoral scale distinctly but narrowly overlaps the dorsal side. The margin dorsal margin of the scale is marked by a shallow sulcus and the bone continues to thicken medially before thing nearer the midline. A partial neural (UCMP 170495) has a distinct carina with a rounded top.

Discussion. - The referred fragmentary specimens do not appear to belong to other known taxa in the fauna and agree in general morphology with testudinoids, probably testudinids or batagurids. The neural resembles those of carinate batagurids.

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Carettochelyidae Boulenger, 1887
Anosteirinae Lydekker, 1889
Anosteira Leidy, 1871
Anosteira sp.

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Referred material. - UCMP locality UCMP V78090: UCMP 131752, peripheral 9 or 10; UCMP 131754, hypoplastron fragment; UCMP 131755, posterior fragment of nuchal; UCMP 147115, neural. UCMP locality V83106: UCMP 131736, medial right hypoplastron fragment; UCMP 131737, lateral hypoplastron fragment; UCMP 131741, peripheral 7; UCMP 131742, peripheral 8; UCMP 131744, costal fragments; UCMP 131746, anterior fragment of a right peripheral 6. UCMP locality V96001: UCMP 147005, hypoplastron fragment; UCMP 147011, left peripheral 7. UCMP locality V96002: UCMP 147030, left peripheral 6. UCMP locality V96008: UCMP 147024, right peripheral 2. UCMP locality V96009: UCMP 142225, peripheral 9 or 10. Description: The hyoplastron resembles those seen in typical *Anosteira* and *Pseudanosteira* Clark, 1932, and lacks the truncated anteromedial articulation of the new genus described below. This specimen differs from *Allaeochelys* Noulet, 1867, in having a narrower posterior lobe and narrower bridge area.

The peripherals are referred to *Anosteira* on the basis of their small size and well-formed sutures. Most also show the presence of weekly-defined sulci on the external surface. All the peripherals have sharp marginal carina, and the surface is finely pustulate. The gomphotic pits for reception of the plastron on peripheral 6 (UCMP 147030, Fig. 4C) lie within a longitudinal trough that traverses the peripheral. The latter is 12.6 mm along the free margin carina and 12.5 mm from the carina to the costal suture. A partial peripheral 6 (UCMP 131746) has the trough on the plastral suture filled with 8-9 vertically elongated pits and a sharp lateral carina. The two gomphotic pits on peripheral 7 also occur within a trough, but on peripheral 7 the trough is only approximately two-thirds the length of the bone. The

peripheral 7 (UCMP 147011) is 12.0 mm along the carina. The specimen tentatively identified as peripheral 9 or 10 (UCMP 131752) is deeper than long (16 mm along the margin, 18 mm in depth).

The posterior nuchal fragment has the typical carettochelyid nuchal pedicle. A faint transverse sulcus is present, and another faint longitudinal sulcus near the midline is visible.

A small neural (UCMP 147115) is also referred to *Anosteira* on the basis of the small size and patterned surface, narrow length to width ratio, and low and broad central carina.

Discussion. - *Anosteira* is known from both Asia (5 species) and North America (1 species) in the Eocene. The closely related genus *Pseudanosteira* is limited to North America and distinguishable from *Anosteira* only by details of the top of the carapace. No elements in the Pondaung collection resemble *Pseudanosteira*. The presence of sulci on the peripherals, nuchal, and costal fragments indicates it should be assigned to *Anosteira*. The Pondaung specimen is most parsimoniously referred to *Anosteira* in the absence of any evidence that *Pseudanosteira* occurs anywhere in Asia. Previous records of *Anosteira* are confined to China and Mongolia.

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Carettochelyinae Boulenger, 1887

Burmemys magnifica gen. et sp. nov.

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Holotype. - UCMP 61212, adult left hypoplastron (Fig. 5A) from UCMP Locality V6204 (near Myaing), found by J. Wyatt Durham, late Professor of Paleontology at the University of California, Berkeley.

Paratypes. - AMNH locality "1 mile northeast of Gyat, Magwe Province": AMNH 1911, pygal, peripheral 10 fragment, and costal fragment. AMNH locality "1 mile north of Koniwa": AMNH 1919, left first peripheral; AMNH 1928, distal half of right first peripheral; AMNH 14196, partial left peripheral 1; AMNH 14197, plastron fragment. UCMP locality V6204: UCMP 61211, left peripheral 4; UCMP 61218, left peripheral 6. UCMP locality V78090: UCMP 131750, juvenile lateral hypoplastron fragment, UCMP 131751, juvenile peripheral fragment; UCMP 131753 juvenile xiphiplastron fragment; UCMP 154994, proximal costal fragment. UCMP locality V83106: UCMP 131738, juvenile right hypoplastron; UCMP 131739, juvenile hypoplastron fragment; UCMP 131745, juvenile left hypoplastron. UCMP locality V83111: UCMP 128406, right peripheral 2. UCMP locality V83116: UCMP 131748, hypoplastron fragment. UCMP locality V83143: UCMP 131747,

anterior part of left xiphiplastron. UCMP locality V96001: UCMP 147001, left peripheral 4 fragment; UCMP 147002, partial left peripheral 3; UCMP 147003, anterior peripheral fragment; UCMP 147009, neural; UCMP 147010, peripheral fragment; UCMP 147012, juvenile medial hypoplastron fragment. UCMP locality V96002: UCMP 142244, right peripheral 8; UCMP 154984, anterior peripheral fragment. UCMP locality V96008: UCMP 147021, left first peripheral; UCMP 147023, posterior peripheral fragment; UCMP 147027, left peripheral 2; UCMP 147028, partial right peripheral 1; UCMP 147029 distal fragment of a costal. UCMP locality V96009: UCMP 142223, right peripheral 7. UCMP locality V99498: UCMP 157443, neural; UCMP 157446, shell fragments.

Referred material. - UCMP locality V96001: UCMP 147004, plastron fragment. UCMP locality V83106: UCMP 131740, hyoplastron fragment. UCMP locality V78090: UCMP 131756, juvenile left peripheral 5; UCMP 154993, posterior fragment of left epiplastron. UCMP locality V99498: UCMP 157442, suprapygal; UCMP 157444, left costal 2; UCMP 157445, left peripheral 7.

Diagnosis. - *Burmemys* is distinguished from other carettochelyines by the combination of asymmetrical articulation of the hyo-hypoplastra, narrow hypoplastral bridge, and large size (estimated carapace length greater than 1000 mm).

Description. - The holotype hypoplastron (UCMP 61212, Fig. 5A) is massive. The anterior suture of the left hypoplastron consists of two sutures. The suture with the left hyoplastron is sinusoidal, curving anteromedially, and joins a distinct, straight and anteromedially-facing suture, presumably for articulation with the right hyoplastron. The ventral sculpture consists of a pattern of irregular, closely-spaced tubercles that radiate from a focal point lateral to the middle of the medial moiety. Laterally, the tubercles coalesce into ridges radiating laterally. The sutures are finely dentate and thick (13 mm). The lateral margin and posterior half of the medial part is broken away in the type, but these are preserved in the juvenile specimen (UCMP 131745, Fig. 5B). The width of the medial part of the hypoplastron measured from the apex of the inguinal notch to the plastral midline is only one-half or less of the maximum hypoplastral width. The inguinal notch is open and not confined as in *Carettochelys* Ramsey, 1887. The anterior-posterior width of the bridge area is one-half or less the width of the xiphiplastral lobe of the hypoplastron. The referred juvenile specimens exhibit the same sutur-

al shapes as the adult (type) but the inguinal notches are shallower, sculpture less organized, and lateral extent of the lateral arm of the bridges are shorter.

The posterior part of a juvenile epiplastron (UCMP 154993, Fig. 5C) is referred to *Burmemys* on the basis of the convex curvature of the lateral margin that indicates a short and rounded anterior lobe, and an obtuse angle between the entoplastral and hyoplastral sutures indicating a short and broad entoplastron.

Two xiphiplastra (UCMP 131747, Fig. 5D; UCMP 131753) are referred to *Burmemy*s on the basis of relatively larger size, converging (non-parallel) medial and lateral margins of the anterior moiety, and thinning rather than thickening toward the midline suture. Both specimens are small (proximal width of UCMP 131747 is 20 mm) and thus considered as juveniles.

The juvenile left costal (UCMP 157444, Fig. 5E) is nearly uniformly thin, parallel sided, and sculptured with a subdued and random pattern of low pustules and short ridges. The distal margin forms about a 45 degree angle to the sides. There are no sulci. The parallel sides and high angle of the distal margin indicate a second costal.

The distal end of an adult costal (UCMP 147029) is subtlety sculptured with longitudinal irregular ridges. The distal suture is weakly dentate but patent except above the rib. The rib ends protrudes prominently. Although damaged, the distal width is about 70 mm.

A large neural (UCMP 147009, Figs. 5F) is relatively narrow, lacks a midline carina, and has subtle sculpture of very shallow dimples. It has a midline length of 51 mm, maximum width of 32 mm, and maximum thickness of the lateral side of 15.4 mm.

The suprapygal (UCMP 157442, Fig. 5G) is triangular with a distinct medial carina. The surface sculpture consists of irregular vermiform ridges that radiate from the central area of the posterior margin. It is longer than wide (32.2 mm long, 31.5 mm wide).

At least nine peripheral positions are represented. The sculpture is variable consisting of distinct tubercles at one extreme to anastomosing pits and ridges at the other. The free margins of adult specimens are rounded but may be acute in juveniles. There are no indications of scale sulci.

The first peripheral exhibits distinct sutures with the first costal, nuchal and second peripheral. The free margin perimeter is asymmetrically curved. The largest specimens (AMNH 1919, Fig. 6A; UCMP 147021, Fig. 6B) have perimeter lengths of 114 and 119 mm, maximum depths of 90 and 81 mm, maximum thicknesses at the posterior suture of 33 and 27 mm, and maximum thicknesses at anterior suture of 28 and 25 mm respectively.

The two second peripherals differ in size. UCMP 147026 (Fig. 6C) is massive with a free margin length of 82 mm, maximum depth of 67 mm, and maximum thickness of the anterior suture of 20 mm. Comparable measurements of UCMP 128406 are 45, 40, and 11 mm respectively. The second peripheral is roughly rectangular in external view.

The only specimen referred to the third peripheral (UCMP 147002, Fig. 6D) is lacking the anteroventral and posterodorsal corners. The anterior part of the dorsal suture is a semi-scarf joint – probably for the rib end of the first costal. The peripheral thickens noticeably towards the posterior suture and reaches a thickness of 32 mm at the suture.

The fourth peripheral (UCMP 61211, Fig. 6E) is damaged anteriorly and dorsally and locally abraded. Its length along the lateral carina is 75 mm. The free margin curves posteromedially on the posterior moiety to form a plastral articulation. The plastral articular surface is relatively flat but deep (up to 16 mm) and without pits for the hyoplastral buttress or normal dentations, thus indicating a weakly ligamental and kinetic joint. The lateral carina is broadly rounded. The peripheral 4 fragment (UCMP 147001, Fig. 6F) also shows this rather flat and deep (19 mm) hyoplastral suture.

A small peripheral, probably a left peripheral 5 (UCMP 131756, Fig. 6G) is considered a juvenile of this species. The plastral arm is very short with a longitudinal trough enclosing a series of gomphotic pits. The lateral carina is slightly rounded and broadly upturned. The length of the lateral carina is 22 mm and has a posterior thickness of about 9 mm.

A relatively complete left peripheral 6 (UCMP 61218, Fig. 6H) has a damaged plastral margin and lacks the dorsal suture. The plastral and costal arms converge posteriorly. The plastral articulation is broken anteriorly but posteriorly has a longitudinal trough indicating interdigitation with the hypoplastron. The lateral carina is rounded and slightly upturned. The length along the lateral carina is 82 mm.

A peripheral 7 (UCMP 142223, Fig. 6I) of an adult measures 99 mm along the marginal carina, 100 mm from the carina to costal margin, posterior thickness of 29 mm and an anterior thickness of more than 45 mm. The hypoplastral suture is damaged but trough-like, extends about half-way along the medial side, and appears to have housed one or two recessed pits. The isolated peripheral 7 (UCMP 157445, Fig. 6J), a presumed juvenile, closely resembles *Carettochelys* with the hypoplastral buttress rising up the central part of the medial side. The free margin is sharp and broadly upturned. The length of the free margin is about 34 mm.

The adult peripheral 8 (UCMP 142244, Fig. 6K) is massive and slightly shorter than deep (97 mm along the lateral carina and 105 mm from the carina to costal

suture). An anteriorly-deepening trough divides the medial surface into dorsal and ventral arms anteriorly.

The pygal (AMNH 1911, Fig. 6L) is distinctly trapezoidal with a short anterior side and a low but sharp medial crest. The sculpture consists of widely spaced irregular tubercles that fade out near the medial crest and free margin. An associated posterior peripheral 10 fragment has a sculpture of irregular ridges and tubercles that radial from a central focus.

Discussion. - The absence of scales and large size place *Burmemys* in the Carettochelyinae. Of the three Eocene genera of Carettochelyinae, *Burmemys* differs from all in the presence of two distinct anterior articular sutures on one of the hypoplastra. This most likely represents an asymmetrical articulation with the hyoplastra, with one of the hyoplastra extending well across the midline to form an angled articulation with the opposite hypoplastron. Even where the hyo-and hypoplastra are not mirror images with one of the hypoplastra contacting the opposite hyoplastron (e.g., *Anosteira* in Hay, 1908, Fig. 353), the midline suture remains straight as in other Paleogene carettochelyids and the plastral midline suture usually exhibits some limited kinesis. This asymmetry is not unusual in turtles, but within carettochelyids was known only to a lesser degree in some *Carettochelys*. The hypoplastron in extant *Carettochelys insculpta* Ramsey, 1887 may cross the midline to form a short angled suture with the opposite hyoplastron (AMNH 84212, and Rooij, 1915, fig. 123a). This occurs on the left hyoplastra on both of these.

Burmemys resembles anosteirines and differs from extant *Carettochelys*, *Hemichelys* Lydekker, 1887, (pl. XII, fig. 2) from the Eocene of the Punjab, and *Chorlakkichelys* Broin, 1987 (pl. 1, fig. 2) from the Eocene of Pakistan in the relatively broad inguinal notch. *Burmemys* additionally differs from *Chorlakkichelys* and *Carettochelys* in having a distinctly narrow bridge area. The general proportions of the hypoplastron resemble those of *Allaeochelys* from the Eocene of Europe (Broin, 1977, Pl. XV1, Fig. 3). The suprapygal differs from *Allaeochelys*, *Carettochelys*, *Hemichelys* and probably *Chorlakkichelys* in being longer than wide.

Burmemys is also the largest carettochelyid described to date. Based on scaling up of the elements in comparison to other carettochelyids, we can estimate that the shell length of *Burmemys* exceeded 1000 mm. This estimate suggests that *Burmemys* is among the largest turtles known, but is smaller than estimates Head et al. (1999) provided for Eocene trionychids from Pakistan, which may have reached more than 2000 mm in length, and is smaller than the giant Bridgerian trionychid from Wyoming (Gaffney, 1979).
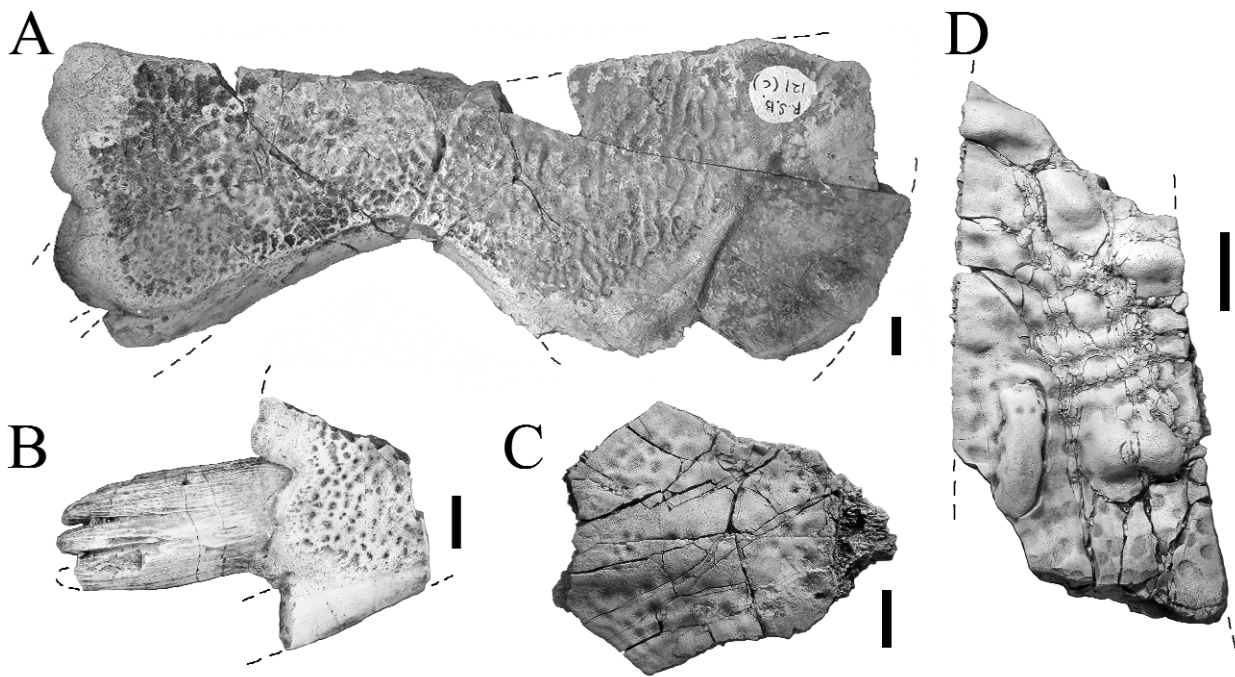
Figure 7. Trionychinae. **A**. UCMP 61213, right hypoplastron, ventral view. **B**. UCMP 1537993, fragment of right hypoplastron, ventral view. **C**. UCMP 147022, neural, external view. **D**. UCMP 170520, costal fragment, external view. Scale bars equals 1 cm.

Trionychidae Gray, 1825
Trionychinae Gray, 1825
Trionychinae genus indet.
Trionychinae, large form

Referred material. - UCMP locality V6204: UCMP 61213, right hypoplastron. UCMP locality V78090: UCMP 170497, costal fragments. UCMP locality V83116: UCMP 153799, fragment of right hypoplastron. UCMP locality V83143: UCMP 173809, plastron fragment. UCMP locality V96001: UCMP 147020, costal fragment. UCMP locality V96002: UCMP 154983, costal proximal fragment. UCMP locality V96008: UCMP 147022, neural. UCMP locality V96009: UCMP 142222, plastron fragment.

Description. - The hypoplastron (UCMP 61213, Fig. 7A) lacks the projecting spines (present in UCMP 153799, Fig. 7B) but is otherwise relatively complete. The calloused area has well defined edges and covers most of the ventral surface, except for the long offset shelf on the medial edge. The calloused area is sculptured with distinct pits and ridges, while the shelf is amorphously roughened. The buttress is composed of two protruding spikes. The posteromost of these is broken off at the base, but the larger anterior one is divided

into three fluted points at its tip.

The isolated neural (UCMP 147022, Fig. 7C), probably 6 or 7, is hexagonal and narrows distinctly posteriorly. The dorsal surface is weakly sculptured, lack sulci, and is flat anteriorly but is formed into a central carina posteriorly. The neural is 46 mm long and 50 mm wide.

Discussion. - The large size of the hypoplastron and general conformation indicates a trionychine and generally resembles *Pelochelys* Gray 1864, *Chitra* Gray 1844, and *Pelodiscus* Fitzinger 1835 in these features, but differs in having a wide, unsculptured medial shelf. Additional material would be needed to refine identification.

Trionychinae, small form

Referred material. - UCMP locality V6204: UCMP 61210 plastron fragment. UCMP locality V83106: UCMP 147116, two costal fragments.

Description. - Two distal costal fragments exhibit a well-defined sculpture of pits and ridges with indications of longitudinal welts. The pattern extends to the free margin with only a slight sculpture-free zone at the free margin, suggesting an adult turtle of relatively small

size in comparison with the preceding taxon. The sculpture resembles that of a trionychine rather than a cyclanorbine such as *Lissemys* Smith, 1931.

Trionychinae, ornate form

Referred material. - UCMP locality V98109: UCMP 170520, two costal fragments.

Description. - The costal fragments (UCMP 170520, Fig. 7D) exhibit a striking sculpture of large, elongate tubercles rising above a surface composed of a generally organized pattern of longitudinal rows of shallow pits and low rides. The longitudinal axes of the raised tubercles vary from anterior-posterior to medial-lateral and are large (11-15 mm) relative to the overall size of the larger costal fragment (maximum preserved width of 32 mm). Carapace sculpturing varies between individuals and also ontogenetically, but the peculiar sculpture shows some resemblance to that seen in some extant *Aspideretes* Hay, 1904.

Discussion

In addition to the turtles, a variety of other lower vertebrates are present in the Pondaung Formation including a carcharhinid shark, *Galeocerdo* Müller and Henle 1837 (UCMP 142238), a clariid catfish (UCMP 128411), at least four species of agamid lizards (UCMP 128410, 130290, 142227, 142232), paleophid and colubroid snakes (see Head et al, in prep.), and a minimum of two crocodilians, including a pristichampsine crocodylian (UCMP 147127) and a dyrosaurid (Buffetaut, 1978).

Unfortunately, reports on Asian lower vertebrates of comparable age (Sharamurunian Asian Land Mammal Age or late middle Eocene) are few. Thus, the limited literature, combined with the fragmentary nature of the Pondaung fossils themselves, make detailed comparisons with other faunas difficult. Nonetheless, comparisons with known Sharamurunian lower vertebrate faunas reveal only a few similarities between the Pondaung and any other locality. Pleurodires are previously undescribed from Asia, although Broin (1987) notes the presence of "Pelomedusidae and/ or Emydidae" from the middle Eocene of Pakistan and Oligocene of India. An adocid was described by Gilmore (1931) from the late middle Eocene of Mongolia, but none were identified in the Pondaung assemblage. The carettochelyid genus, *Anosteira*, has been reported from age-equivalents in Manchuria (Zangerl, 1947) and Guangdong, China (Sun Ailing et al., 1992) and from slightly younger sediments in Shandong and Guangdong provinces (Yeh, 1963). The only other carettochelyines described from Asia are

Chorlakkichelys and *Hemichelys* from the early middle Eocene of Pakistan (Lydekker, 1887; Broin, 1987), and *Burmemys* is the most easterly and southerly Eocene record of the subfamily. Trionychids, as elsewhere, are an important part of the fauna, but our material is not sufficiently diagnostic to make any meaningful biogeographic comparisons. Testudinids are widely reported in Chinese and Mongolian Eocene faunas (Gilmore, 1931; Ye, 1963), but all of these appear to be more generalized forms similar to *Hadrianus* or *Kansuchelys*. The Pondaung form appears to be more like the modern *Testudo*, and thus distinct from contemporaneous Chinese and Mongolian taxa.

Among other reptiles, the only other agamid lizard known in the Asian Sharamurunian is *Tinosaurus yuanquensis* from the Heti Formation (Li, 1991), but it is a diminutive form that bears no resemblance to the Pondaung agamids. Crocodilians are known elsewhere, but not in detail. In overall diversity, the Pondaung fauna shares more general resemblances to the better-known Irdinmanhan faunas, especially that of the Kuldana Formation of Pakistan (Broin, 1987).

Based on the fragmentary evidence available to date, several observations can be made regarding the Pondaung lower vertebrate fauna. Faunal endemicity is supported by the number of unique taxa, and the composition of the turtle fauna is unusual with trionychoids (especially carettochelyids) dominating. Faunal composition and the large size of these turtles are consistent with an interpretation of these sites as representing a warm, tropical floodplain environment, deposited fairly near shore. The aquatic habits of most of the lower vertebrates suggest that during late middle Eocene time the Pondaung region was a well-drained floodplain environment, a finding consistent with previous geological interpretations (e.g., Bender, 1983, Soe et al., 2002).

Acknowledgments

Literature Cited

Batsch, A. J. G. C. 1788. Versuch einer Anleitung zur Kenntniss und Geschichte der Thiere und Mineralien. Vol. 1. Akademische Buchhandlung, Jena. viii + 528 pp.

Bender, F. 1983. The Geology of Burma. Beiträge zur Regionalen Geologie der Erde, Band 16, 293 pp.

Boulenger, G. A. 1887. On a new family of pleurodiran turtles. Annals and Magazine of Natural History 19:170-172.

Broin, F. de. 1977. Contribution à l'étude des chéloniens. Chéloniens continentaux du Crétacé et du Tertiaire de France. Mémoires du Muséum National d'Histoire Naturelle, N. Ser. C, 38:1-423.

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(7):169-185.

Buffetaut, E. 1978. A dyrosaurid (Crocodilia, Mesosuchia) from the upper Eocene of Burma. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 5:273-281.

Ckhikvadze, V. M. 1972. O sistematichekom polozhenii tretichnykh gigantskikh sukhoputnykh cherepakh Palearktiki. [On the systematic positions of the Tertiary gigantic land turtles of Palearctic]. Bulletin of the Academy of Sciences of the Georgian R.S.S. 65(3):745-748.

Clark, J. 1932. A new anosteirid from the Uinta Eocene. Annals of the Carnegie Museum 21:161-170.

Colbert, E. 1938. Fossil mammals from Burma in the American Museum of Natural History. Bulletin of the American Museum of Natural History 74:255-436.

Cope, E D. 1865. Third contribution to the herpetology of tropical America. Proceedings of the Academy of Natural Sciences of Philadelphia 1865:185-198.

Cope, E D. 1868. On the origin of genera. Proceedings of the Academy of Natural Sciences, Philadelphia 1868:92-93.

Cope, E. D. 1872. Second account of new vertebrata from the Bridger Eocene of Wyoming Territory. Proceeding of the American Philosophical Society 12:466-468.

De Rooij, N. 1915. Reptiles of the Indo-Australian Archipelago, Lacertilia, Chelonia, Emydosauria. E. J. Brill, Leiden. 1: xiv + 384 pp.

Ducrocq, S., E. Buffetaut, H. Buffetaut-Tong, R. Helmcke-Ingavat, J.-J. Jaeger, Y. Jongkanjanasoontorn, and V. Suteethorn. 1992. A Lower Tertiary vertebrate fauna from Krabi (South Thailand). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 184(1): 101-122.

Fitzinger, L. J. 1826. Neue Classification der Reptilien nach ihren natürlichen Verwandtschaften nebst einer Verwandtschafts-Tafel und einen Verzeichnisse der Reptilien-Sammlung des k. k. Zoologischen Museum's zu Wien. J. G. Hübner, Wien, viii + 66 p.

Fitzinger, L., 1835. Entwurf einer systematischen Anordnung der Schildkröten nach den Grundsätzen der natürlichen Methode. Annalen der Wiener Museums des Naturgeschichte 1:103-128.

Gilmore, C. W. 1931. Fossil turtles of Mongolia. Bulletin of the American Museum of Natural History 59:213-257.

Gray, J. E. 1825. A synopsis of the genera of reptiles and Amphibia, with a description of some new species. Annals of Philosophy, London. Ser. 2 10:193-217.

Gray, J. E. 1844. Catalogue of tortoises, crocodiliens, and amphisbaenians in the collection of the British Museum. British Museum (Natural History), London. viii + 80 pp.

Gray, J. E. 1864. Revision of the species Trionychidae found in Asia and Africa, with description of some new species. Proceedings of the Zoological Society of London 1864: 76-98.

Gunnell, G. F., R. L. Ciochon, P. D. Gingerich, and P. A. Holroyd. 2002. Re-assessment of *Pondaungia* and *Amphipithecus* (Primates) from the late middle Eocene of Myanmar with comments on "Amphipithecidae." Contributions from the Museum of Paleontology, University of Michigan 30: 337-372.

Hay, O. P. 1904. On the existing genera of the Trionychidae. Proceedings of the Americana Philosophical Society 42:268-249.

Hay, O. P. 1908. Fossil turtles of North America. Carnegie Institute of Washington, Publication 75: 568 pp.

Head, J. J., P. A. Holroyd, J. H. Hutchison, and R. L. Ciochon. in prep. First report of snakes (Serpentes) from the late middle Eocene Pondaung Formation, Myanmar.

Head, J. J., S. M. Raza, and P. D. Gingerich. 1999. *Drazinderetes tethyensis*, a new large trionychid (Reptilia: Testudines) from the marine Eocene Drazinda Formation of the Sulaiman Range, Punjab (Pakistan). Contributions from the Museum of Paleontology, University of Michigan 30:199-214.

Holroyd, P. A. and Ciochon, R. L. 1994. Relative ages of Eocene primate-bearing deposits of Asia. Pp. 123-141. In J. G. Fleagle and R. F. Kay (eds.), Anthropoid Origins. Plenum Press, New York.

Hutchison, J. H., and D. M. Bramble. 1981. Homology of the plastral scales of the Kinosternidae and related turtles. Herpetologica 37:73-85.

Jiménez, E., M. A. Cuesta, and S. G. Tudanca. 1994. Vertebrados fósiles del Eoceno de Fuentesaúco (Zamora). Studia Geologica Salamanticensia 29:7-21.

Leidy, J. 1851. [Fossil tortoises from Nebraska Territory]. Proceedings of the Academy of Natural Sciences, Philadelphia 5: 326-327.

Leidy, J. 1871. [Remarks on extinct turtles from Wyoming Territory, *Anosteira ornata* and *Hybemys arenarius*.] Proceedings of the Academy of Natural Sciences, Philadelphia 1871: 102-103.

Li, Jingling. 1991. Fossil reptiles from Zhaili member, Heti Formation, Yuanqu, Shanxi. Vertebrata PalAsiatica 29(3):190-203.

Linnaeus, C. 1758. Systema Naturae 10th ed., vol. 1. Stockholm, 824 pp.

Lydekker, R. 1887. Eocene chelonians from the Salt-Range. Paleontologica Indica 4:59-65.

Lydekker, R. 1889. Chapter III. Class Reptilia – continued. Orders Anomodontia, Sauropterygia, and Chelonia. Pp. 1053-1118. In: H. A. Nicholson and R. Lydekker, Manual of Paleontology. Vol 2. W. Blackwood and Sons, Edinburgh. 3rd ed.

Müller, J., and J. Henle. 1837. Gattungen der Haifische und Rochen nach einer von ihm mit Hrn. Henle unternommenen gemeinschaftlichen Arbeit über die Naturgeschichte der Knorpelfische. Bericht der Akademie der Wissenschaften, Berlin 1:111-118.

Noulet, J. B. 1867. Nouveau genre de Tortues fossiles sous le nom d'*Allaeochelys*. Mémoires de l' Académie des sciences, Toulouse (6e sér.) 5:172-177.

Ramsey, E. P. 1886 [1887]. On a new genus and species of fresh water tortoise from the Fly River, New Guinea. Proceedings of the Linnean Society of New South Wales (2)1:158-162.

Rage, J.-C. 1987. Lower vertebrates from the early-middle Eocene Kuldana Formation of Kohat (Pakistan): Squamata. University of Michigan Contribution from the Museum of Paleontology 27:187-193.

Sahni, A. 1984. Upper Cretaceous-early Palaeogene palaeobiogeography of India based on terrestrial vertebrate faunas. Mémoires de la Sociéte´ géologique de France, N. S. 147: 125-137.

Savage, D. E., and D. E. Russell. 1983. Mammalian Paleofaunas of the World. Addison-Wesley, Reading Massachusetts. 432 pp.

Smith, M. A. 1931. The fauna of British India, including Ceylon and Burma. Reptilia and Amphibia. Vol. 1. Loricata, Testudines. Taylor and Francis, London. 185 pp.

Soe, Aung Naing, Myitta, Soe Thura Tun, Aye Ko Aung, Tin Thein, B. Marandat, S. Ducrocq, & J.-J. Jaeger. 2002. Sedimentary facies of the late Middle Eocene Pondaung Formation (central Myanmar) and the

paleoenvironments of its anthropoid primates. Comptes Rendus Palevol 1:153-160.

Sun, A., J. Li, X. Ye, Z. Dong, L. Lou. 1992. The Chinese fossil reptiles and their kins. Science Press, Beijing. 242 pp.

Tsubamoto, T., N. Egi, M. Takai, N. Shigehara, Aye Ko Aung, Tin Thein, Aung Naing Soe and Soe Thura Tun. 2000,: A preliminary report on the Eocene mammals of the Pondaung fauna, Myanmar. Asian Paleoprimatology 1: 29-101.

Tsubamoto, T., Takai, M., Shigehara, N., Egi, N., Soe Thura Tun, Aye Ko Aung, Maung Maung, Danhara, T., and Suzuki, H. 2002. Fission-track zircon age of the Eocene Pondaung Formation, Myanmar. Journal of Human Evolution 42: 361-369.

Wood, R. C. 1983. *Kenyemys williamsi*, a fossil pelomedusid turtle from the Pliocene of Kenya. Pp. 74-85. In: A. G. Rhodin et al. (eds). Advances in Herpetology and Evolutionary Biology.

Ye (Yeh), X. 1963. Fossil turtles of China. Palaeontologica Sinica, new Series C (18):112 pp.

Zangerl, R. 1947. A new anosteirine turtle from Manchuria. Fieldiana, Geology 10:13-21.