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The Camfield fossil chelid fauna: II. Two new species of Australian *Chelodina* (Testudines: Chelidae)

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Abstract

The fossil turtle fauna of the middle Miocene Bullock Local Fauna, Camfield Beds, Northern Territory, Australia is specimen-rich in chelids; however, the fossils are highly fragmented and many have only been identified to genus level until recently. Joseph-Ouni, Yates & McCord (2024) reexamined these specimens, resulting in the formal recognition of two new fossil species of the short-necked *Elseya*. In this current contribution we highlight the fossil representation of the long-necked chelid genus *Chelodina*; fortuitously it is highly diagnostic and allows formal diagnosis of two new species, one in the subgenus *Chelodina* as *C.* (*Chelodina*) *aquanimare* sp. nov. and the other in the subgenus *Chelydera* as *C.* (*Chelydera*) *nerophis* sp. nov.

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Introduction

The Bullock Creek fossil site of Northern Territory, Australia dates to approximately 14 to 13 million years ago in the mid-Miocene and occurs within the Camfield Beds, which are comprised mostly of limestone and siltstone with some light colored calcareous sandstone. The fossils are confined to the limestone facies (Megirian & Murray 1999). Megirian & Murray (1999) comprehensively surveyed the fossil chelid assemblage from the site and those authors formally described a new genus and species of fossil short-necked turtle, *Birlimarr gaffneyi,* and proposed the presence of at least another 4-5 chelid taxa which were only identified at the genus levels, *Chelodina* and *Elseya/ Emydura*.

Joseph-Ouni *et al.* (2024) recently reexamined the fossil specimens attributed only to genus level and with the broad progress of Australian chelid turtle morphology and taxonomy over the last few decades (Thomson *et al*., 1997; Thomson, 2000; McCord & Thomson, 2002; Yates, 2013; Cann & Sadlier, 2017; Joseph-Ouni *et al.* 2022a,b; 2023) were able to formally describe and diagnose two new species of the short-necked genus *Elseya, E. camfieldensis* and *E. mudburra*.

Though relatively poor in complete specimens, numerous fragments are fortuitously highly diagnostic for the long-necked turtle genus *Chelodina*, including costal bones and associated suture scars and several epiplastra, allowing us to formally describe and illustrate two

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new fossil species here. One is attributed to the subgenus *Chelodina* and the other to the subgenus *Chelydera*. These new taxa join the previously described *Chelodina (Chelodina) murrayi* Yates, 2013, from the late Miocene Alcoota Local Fauna, raising the number of fossil species of *Chelodina* from the Northern Territory to three.

Methods

High resolution digital photographic images of the Northern Territory Museum's registered fossil turtle specimens were obtained from multiple angles and compared to extant and fossil chelid turtle specimens in the Queensland Museum (QM), Australian Museum (AM) and Museums and Art Galleries of the Northern Territory (NTM), and high quality photography of specimens of extant chelid turtles.

As noted by Megirian & Murray (1999), the Bullock Creek fossil turtle specimens were originally extracted from limestone matrix using dilute (=10%) acetic acid. Additional specimen cleaning, preservation and organization was conducted by A. Yates.

All published literature and figures regarding the fossil specimens were consulted.

We employ the nomenclature of the shell of Zangerl (1969). Thus 'costal' is reserved for those bones of the carapace, and 'pleural' refers to the lateral outer keratinous scutes covering the costal bones. Likewise, the term 'nuchal' is reserved for the specific bone and the anterior median scute of the carapace margin is referred to as the 'cervical scute'. Lastly, 'peripherals' is used for the outermost ring of carapace bones, and 'marginals' used for the keratinous scutes covering the peripheral bones.

Marginal scutes number 12 on each side of the carapace, and we use the shorthand designation of M# (i.e. anteriormost marginal is M1, the next M2 etc.); likewise pleural scutes number 4 on each side of the carapace and we use P# for shorthand reference; and vertebral scutes number 5 medially on the carapace, and we use V#, numbering from anterior to posterior.

For the plastral scutes, the following short-hand notations are used: IG= intergular scute; IH = interhumeral sulcus; IP= interpectoral sulcus; IAb= interabdominal sulcus; IF= interfemoral sulcus; IAn= interanal sulcus. The gular scutes are denoted as G.

The nomenclature of the shell buttresses and scars, and pelvis and pelvic scars, follows that of Joseph-Ouni *et al.* (2022a; 2023).

Discussion

The fossil freshwater chelid turtles excavated from the mid-Miocene Bullock Creek Fossil Site in the late 1980s and 1990s of Northern Territory, Australia represents a highly species-rich assemblage which was comprehensively illustrated and addressed by Megirian & Murray (1999). Those authors formally described a new genus and species of fossil short-necked turtle, *Birlimarr gaffneyi,* but refrained from further formal nomenclature, instead proposing the presence of at least another 4-5 chelid taxa identified at the genus levels - *Chelodina* and *Elseya/ Emydura*.

Joseph-Ouni *et al.* (2024) reexamined these latter specimens of the Bullock Creek fossil fauna turtles registered in the Northern Territory Museum and were able to confidently propose the diagnosability of two new fossil *Elseya* species, *E. camfieldensis* and *E. mudburra.*

Amongst the remaining specimens are fragmented but fortuitously highly diagnostic remains of the long-necked turtle genus *Chelodina*. Megirian & Murray (1999) correctly assessed that there were remains of two distinct types of *Chelodina* present amongst the Bullock Creek fossil fauna, and accordingly denominated them as *Chelodina* sp. A (our new species of the subgenus *Chelydera* below) and *Chelodina* sp. B (our new species of the subgenus *Chelodina* above). Those authors deliberately chose an epiplastron of each in order to directly comparatively illustrate the concept of their two species via differences in scute sulci and bone morphology but were hesitant to assign more than a few other specimens.

With the foundational work of Megirian & Murray (1999) and with the increase of knowledge of morphology amongst the family Chelidae in Australia in the last three decades, we are again able to confidently diagnosis and formally describe two new fossil chelid species. These are assigned to the genus *Chelodina* in separate subgenera, *Chelodina* (*Chelodina*) *aquanimare* sp. nov. and *Chelodina* (*Chelydera*) *nerophis* sp. nov. These species are considered sympatric spatially and temporally in the middle Miocene with the formerly described fossil turtle species of the Bullock Creek fossil fauna.

Taxonomy

Chelodina (Chelodina) aquanimare

Fig. 1

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Holotype:- NTM P10182, a complete and undamaged right epiplastron (Figure 1), excavated from the 'Blast Site', Camfield Station, Northern Territory (Latitude 17 00'S. Longitude 131 30'E.), Bullock Creek Local Fauna, mid-Miocene.

A mid-Miocene fossil species of long-necked turtle of the family Chelidae, assigned to the genus *Chelodina* based on the morphology of the epiplastron.

A mid-Miocene fossil species of long-necked turtle of the family Chelidae, assigned to the genus *Chelodina* based on the morphology of the shape of the epiplastron with clear intergular sulci showing the anterior border encapsulated by the presence of gular scutes (in medial contact). It can be distinguished from the sub-

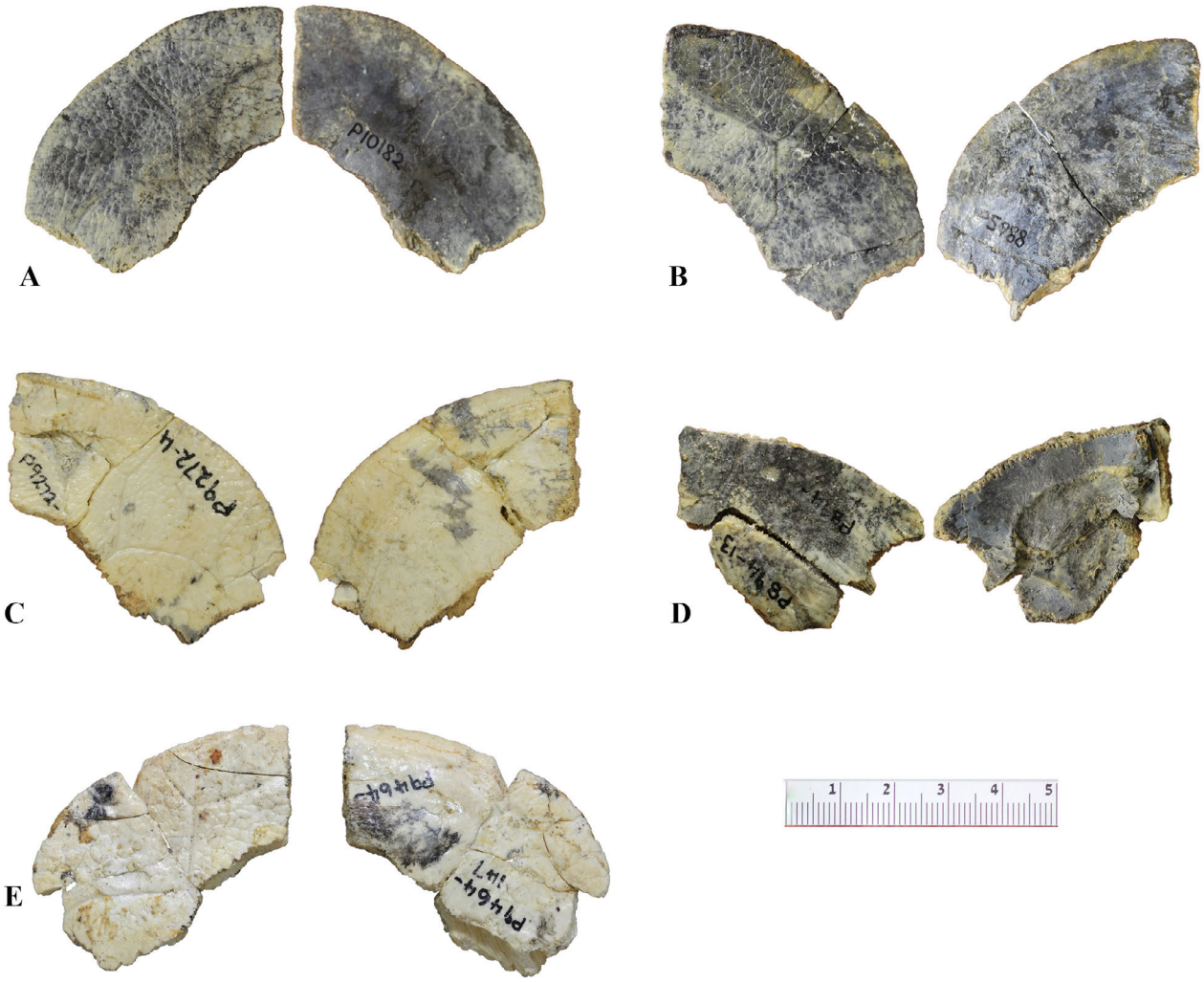


Figure 1. *Chelodina (Chelodina) aquanimare* **sp. nov.**, hypodigm: a) NTM P10182, holotype, complete right epiplastron; b) NTM P5988, paratype, complete left epiplastron; c) NTM P9272, paratype, partial left epiplastron; d) NTM P894-13, referred specimen, complete articulated right costal 7 and costal 8; e) NTM P9464-147, referred specimen, a right epiplastron. All to scale.

genera *Macrochelodina* and *Chelydera* (except *C. (Chely.) parkeri*) by the placement of the intergular-humeral-pectoral scute sulcus conjunction on the epiplastron, far from the entoplastron. It can be distinguished from *C.* (*Chely*.) *parkeri* and all other members of the subgenus *Chelodina* by the autapomorphic shape of the humero-pectoral scute sulcus which is strongly recurved and forms an almost perfect quarter circle.

The holotype specimen NTM P10182 (Blast Site) consists of a complete and undamaged fossil right epiplastron. All scute sulci are distinct and strongly preserved. The specimen is relatively squat (robust) with the greatest straight-line length being only two times the greatest width and the inter-epiplastral suture accounting for about 65% of the straight-line length of the anterior-most point of the entoplastron to the posteriormost point of the epiplastron. The gular-intergular scute sulcus is two times the length of the humeral-intergular scute sulcus. The intergular-humeral-pectoral sulcus conjunction occurs on the epiplastron and strongly exterior to the entoplastron. The gular-intergular scute sulcus crosses the midline plastron at the anterior 1/3rd point of the inter-epiplastral suture. An autapomorphy is present, that of a strongly posteriorly recurved humero-pectoral scute sulcus, forming almost a perfect quarter circle of the posterior epiplastron such that the pectoral scute accounts for nearly 20% percent of the surface area of the epiplastron. A surface texture of fine scale-like sulci are preserved on the entire ventral face. The humeral-pectoral scute sulcus crosses the epiplastral-hyoplastral suture at the exterior 2/5th point.

NTM P5988 (Blast Site), a complete but damaged left epiplastron, here declared as paratype; NTM P9272-4 (Blast Site), a complete but damaged left epiplastron; NTM P9464-147 from Top Site, a right epiplastron, NTM P894-13 (Blast Site), complete and articulatable right 7thand 8th costal bones;all shown in Figure 1. These latter two specimens were allocated by Megirian & Murray to their *Chelodina* sp. B. (our *C. (C.) aquanimare* sp. nov.); all Camfield Station, Northern Territory (Latitude 17 00'S. Longitude 131 30'E.), Bullock Creek Local Fauna, mid-Miocene.

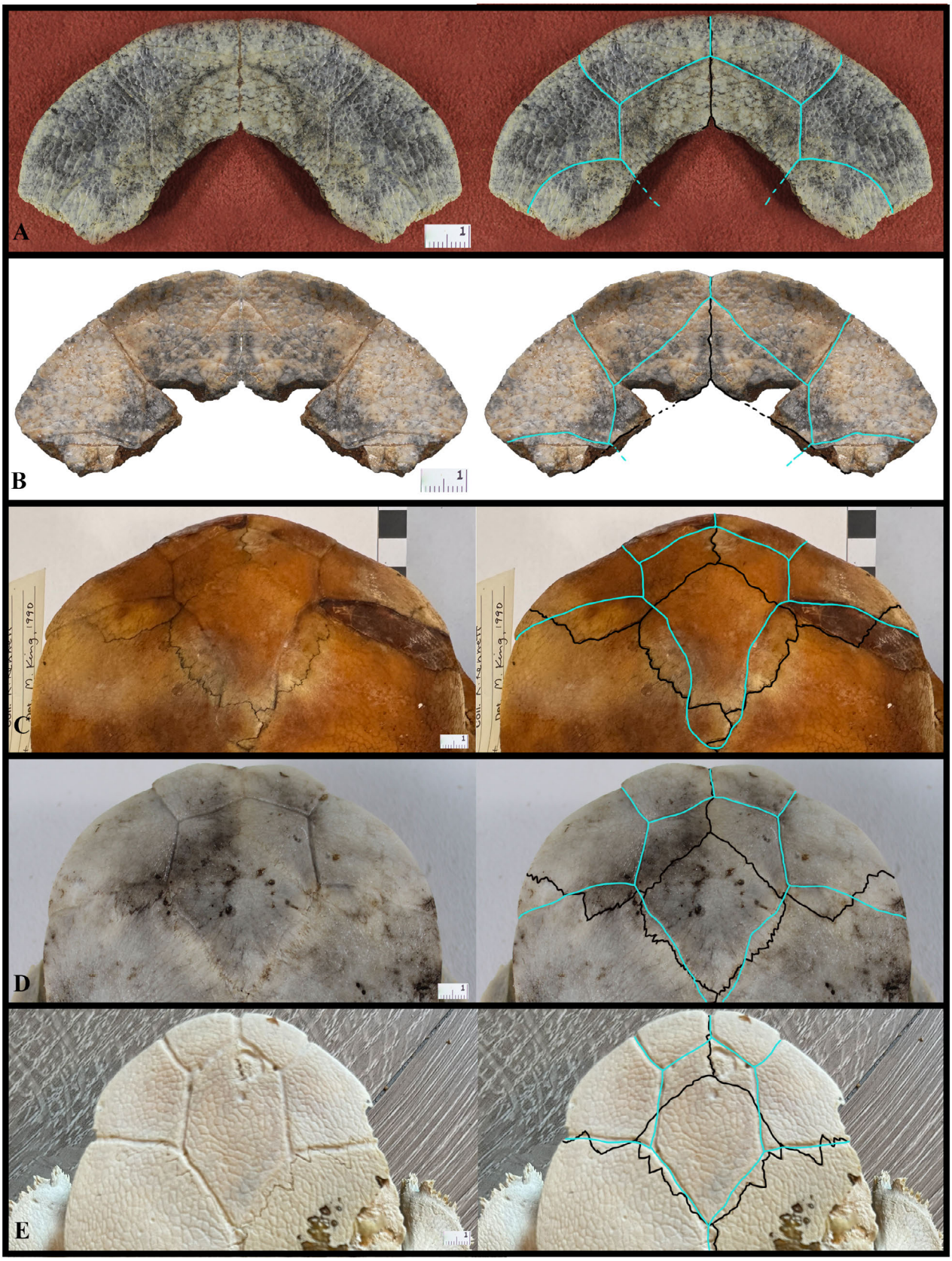


Figure 2. Typical character states of *Chelodina (Chelodina)* plastral forelobes showing the size and shape of the epiplastra and entoplastron, bone sutures, surface bone texturing and scute sulci. Raw image in left column, interpretive sulci in blue and sutures in black in right column. All currently described species illustrated over Figures 2-4. Row A: *C. (C.) aquanimare* **sp. nov.** holotype NTM P10182; Row B: *C. (C.) murrayi* holotype NTM P5364: Row C: *C. (C.) canni* NTM R16234); Row D: *C. (C.) longicollis*: Row E. *C. (C.) steindachneri*. Images by authors, or courtesy of G. Marshall, J.Cann and I.Smales.

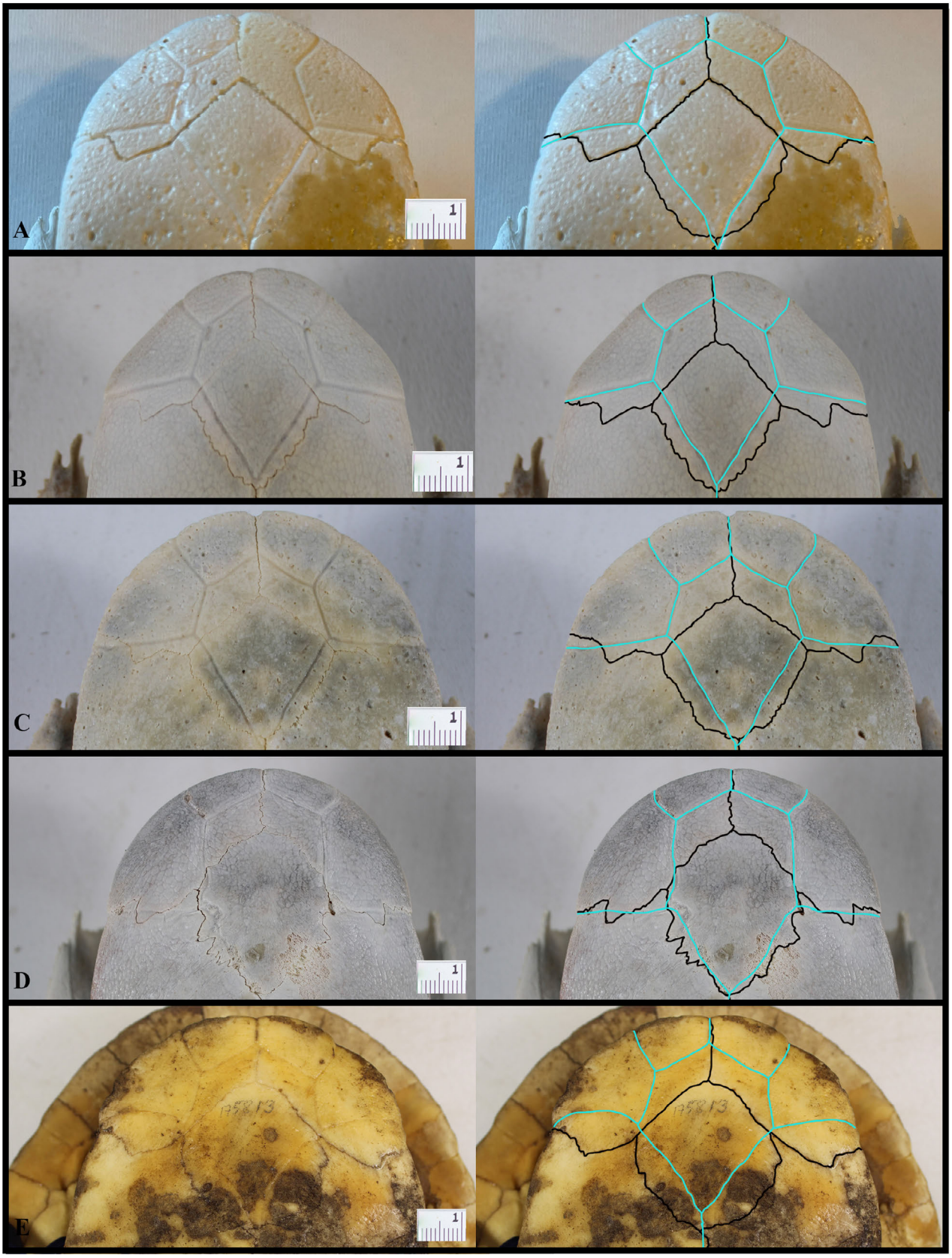


Figure 3. Typical character states of *Chelodina (Chelodina)* plastral forelobes showing the size and shape of the epiplastra and entoplastron, bone sutures, surface bone texturing and scute sulci. Raw image in left column, interpretive sulci in blue and sutures in black in right column. All currently described species illustrated over Figures 2-4. Row A: *C. (C.) novaeguineae*; Row B:*C. (C.) ipudinapi*: Row C: *C. (C.) gunaleni*; Row D: *C. (C.) reimanni*; Row E. *C. (C.) pritchardi* paratype MCZ R17813. Images by authors.

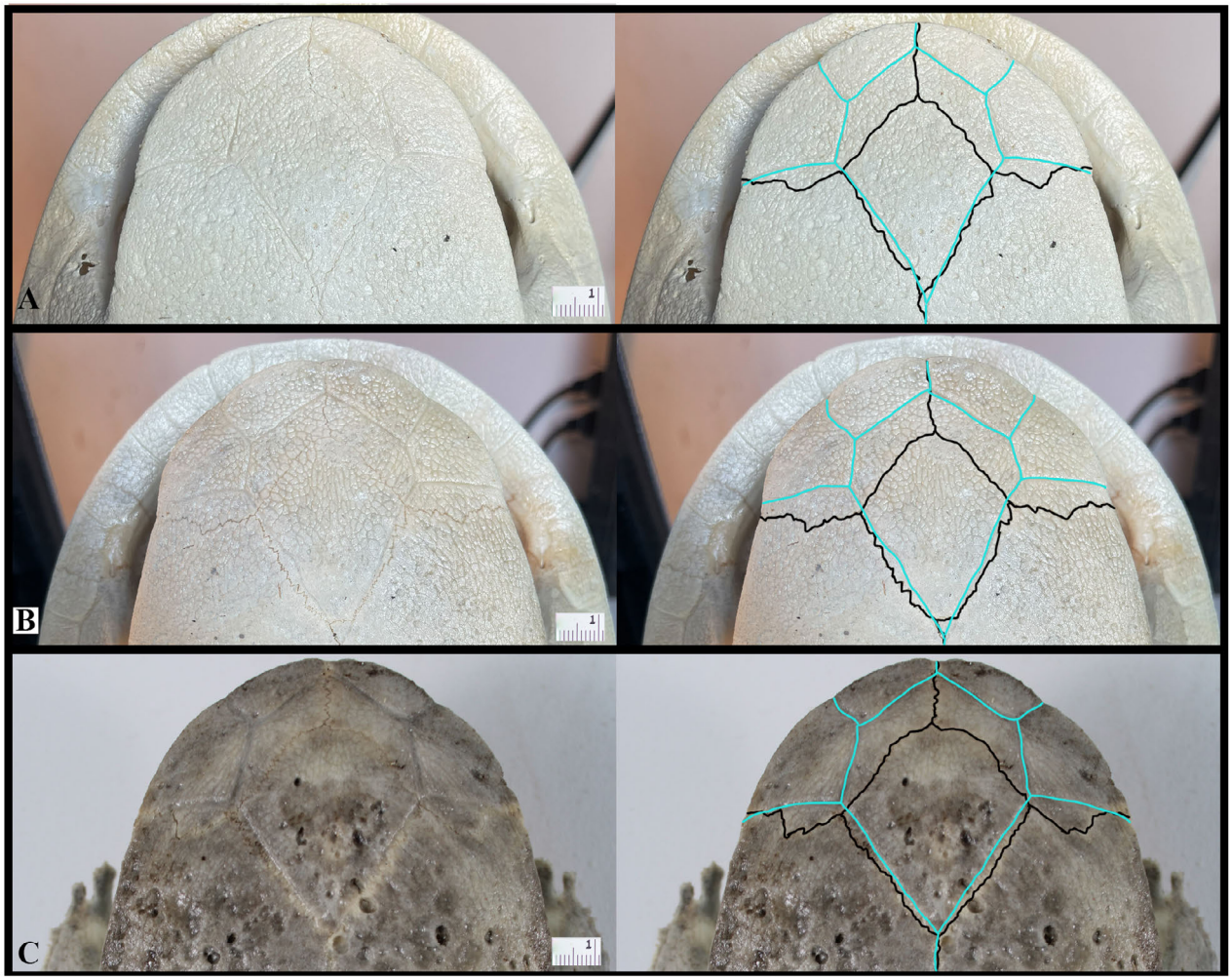


Figure 4. Typical character states of *Chelodina (Chelodina)* plastral forelobes showing the size and shape of the epiplastra and entoplastron, bone sutures, surface bone texturing and scute sulci. Raw image in left column, interpretive sulci in blue and sutures in black in right column. All currently described species illustrated over Figures 2-4. Row A: *C. (C.) mccordi mccordi*; Row B:*C. (C.) mccordi roteensis*: Row C: *C. (C.) mccordi timorensis*. Images by authors.

Etymology. The species epithet is derived from the Latin 'aqua' = water and 'animare' =animating, enlivening, in allusion to snake-necked turtles' spiritual presence in waterways.

Remarks. Some specimens of *C. canni* display a recurved humeral-pectoral scute sulcus that bears some resemblance to the strongly curved sulcus seen in *C. aquanimare*, but this is shallow and crosses the epiplastral-hyoplastral suture at the exterior 1/3rd point, restricting the pectoral scute to cover only approximately 15% of the surface area of the epiplastron. *Chelodina aquanimare*further differs from *C. canni* in having a narrower, more elongated epiplastron (the inter-epiplastral suture accounting for 50% of the straight-line length of the anteriormost point of the entoplastron to the posteriormost point of the epiplastron). Figures 2 – 4 illustrate comparative material of all pertinent *Chelodina (Chelodina)* taxa.

Chelodina (Chelodina) aquanimare sp. nov. differs from the fossil species *C. (C.) murrayi* by the absence of a distinct epiplastral lip in the former which is an autapomorphy present for the latter species (Yates, 2013). The Plio-Pleistocene fossil *Chelodina (C.) insculpta* De Vis, 1897 was described from non-overlapping material with this new species.

The combination of character states that diagnoses *Chelodina (Chelodina) aquanimare* sp. nov. can be seen on all four known specimens, demonstrating their consistency as opposed to singularity or aberrancy.

Referred specimen NTM P9272-4, an epiplastron, was chosen by Megirian & Murray (1999) to represent their concept of *Chelodina* sp. B, in a direct effort to comparatively illustrate the presence of two types of *Chelodina* amongst the Camfield fossil fauna (their *Chelodina* sp. A also being represented by an epiplastron). Those authors only referred two other specimens to their *Chelodina* sp. B, NTM P9464-147 and P895-72. We concur with those referrals.

In addition to other specimens referred here, we refer NTM P894-13 (Blast Site), complete and articulating right

7th and 8thcostal bones to the subgenus *Chelodina* on the basis of the reduced iliac suture scar surface on the visceral side as well as the reduced 8thcostal bone wherein the posterior elongation of the 7th costal prevents midline contact of the 8th costals (a feature strangely seen, and currently known only to us, in some *C. (C.) reimanni* specimens).

Lastly, it is highly likely, though not recovered together, that the holotype right epiplastron NTM P10182 and paratype left epiplastron NTM P5988 are from the same single adult individual, as they are congruently complementary in all regards.

Chelodina (Chelydera) nerophis

Fig. 5

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Holotype:. NTM P908-49 (Figure 5), a complete and undamaged right epiplastron; excavated from the 'Blast Site', Camfield Station, Northern Territory (Latitude 17 00'S. Longitude 131 30'E.), Bullock Creek Local Fauna, mid-Miocene.

A mid-Miocene fossil species of long-necked turtle of the family Chelidae, assigned to the genus *Chelodina* based on the morphology of the shape of the epiplastron with clear intergular sulci showing the anterior border encapsulated by the presence of gular scutes (in medial contact), and further to the subgenus *Chelydera* based on the indicative placement of the conjunction of the humeral, pectoral and intergular sulci on the entoplastron as well as the proportionally smaller and narrower footprint of the intergular scute on the epiplastron; distinguished from all currently known fossil and extant species by the following combination of characters: presence of an autapomorphy amongst *Chelodina (Chelydera)*, being the placement of the gular, humeral and intergular scute intergular scute sulcus conjunction well anterior of the level of the anteriormost portion of the epiplastral-entoplastral suture; relatively small portion of the epiplastral surface; humero-intergular scute sulcus longer than the gular-humeral scute sulcus, three times the length of the inter-gular scute sulcus and equal to the gular-intergular sulcus; humeral-intergular scute sulcus parallel to midline of plastron; the greater anterior occurrence of the humero-pectoral sulcus on the epiplastron and the indicative placement of the conjunction of the humeral, pectoral and intergular sulci on the entoplastron.

The holotype specimen consists of a whole and undamaged right epiplastron. The ventral surface contains well-defined scale-like sculpture that is larger distally from the midline of the plastron and grading to a smaller size on the proximally portion, all conforming to *Chelodina* (Joseph-Ouni *et al.* 2023). It contains indications of the inter-gular scute sulcus, the entirety of the gular-intergular scute sulcus and gular-humeral scute sulcus. It also contains the humeral-intergular scute sulcus that normally occurs in subgenus *Chelydera* as well as the correct portion of the humeral-pectoral scute sulcus. This latter sulcus posteriorly crosses the epiplastral-hyoplastral suture at the mid-point; the epiplastral-hyoplastral sutural edge contains a posterior projection typically of Chelidae. The inter-epiplastral sutural edge is approximately 1.5 times the straight length of the epiplastral-entoplastral sutural edge. The humero-pectoral sulcus occurs almost entirely on the epiplastron, making this placement much more anterior than all other described taxa.

NTM P895-66 (Blast Site), a partial right epiplastron, here declared as paratype; P10858 (Blast Site), an almost complete left hyoplastron (Figure 5); NTM P8692-24 (Blast Site), a partial right 1st costal bone (Figure 5); NTM P908-48 (Figure 5), a complete and undamaged left 1st costal bone (Blast Site), all from Camfield Station, Northern Territory (Latitude 17 00'S. Longitude 131 30'E.), Bullock Creek Local Fauna, mid-Miocene.

Etymology. The species epithet is derived from the Greek, 'nero' = water and 'ophis' = snake, in reference to the long snake-like necks of *Chelodina*.

Remarks. Chelodina (Chelydera) nerophis sp. nov. is readily distinguished from all other described fossil and extant species of the subgenus *Chelydera* by the presence of an autapomorphy amongst *Chelydera* (gular, humeral and intergular scute intergular scute sulcus conjunction well anterior of the level of the anteriormost portion of the epiplastral-entoplastral suture) and the greater anterior occurrence of the humero-pectoral sulcus on the epiplastra (occurring posteriorly on all other species such that the majority of this sulcus occurs across the epi-hyoplastral suture) as well as by the following: from *C. (C.) burrungandjii C. (C.) kuchlingi* and *C (C.) walloyarrina* by a narrow, laterally straight-sided intergular scute, the humero-pectoral sulcus lying mostly anterior of the suture and by the conjunction of the intergular, humeral and pectoral sulcus conjunction lying anterior of the widest portion of the entoplastron (versus anteriorly wider intergular scute, the humero-pectoral sulcus lying along the epi-hyoplastral suture and the conjunction sulcus level lying at the widest point); from the *C. (C.) rugosa* group of taxa (*C. rugosa*, *C. siebenrocki*, and *C. kurrichalpongo*) by shorter lateral intergular scute sulci, the humero-pectoral sulcus lying mostly anterior of the suture and by the conjunction of the intergular, humeral and pectoral sulcus conjunction lying anterior of the widest portion of the entoplastron (versus longer sulci, the humero-pectoral sulcus lying along the epi-hyoplastral suture and the conjunction sulcus level lying at the widest point); from *C. parkeri* by the short, diverging lateral intergular scute sulci in *C. parkeri* (this latter taxon is the only member of *Chelydera*in which the conjunction of the humeral, pectoral and intergular sulci occurs on the epiplastron); and from the monotypic subgenus *Chelodina (Macrochelodina) oblonga* by the short lateral intergular scute sulci, the humero-pectoral sulcus lying mostly anterior of the

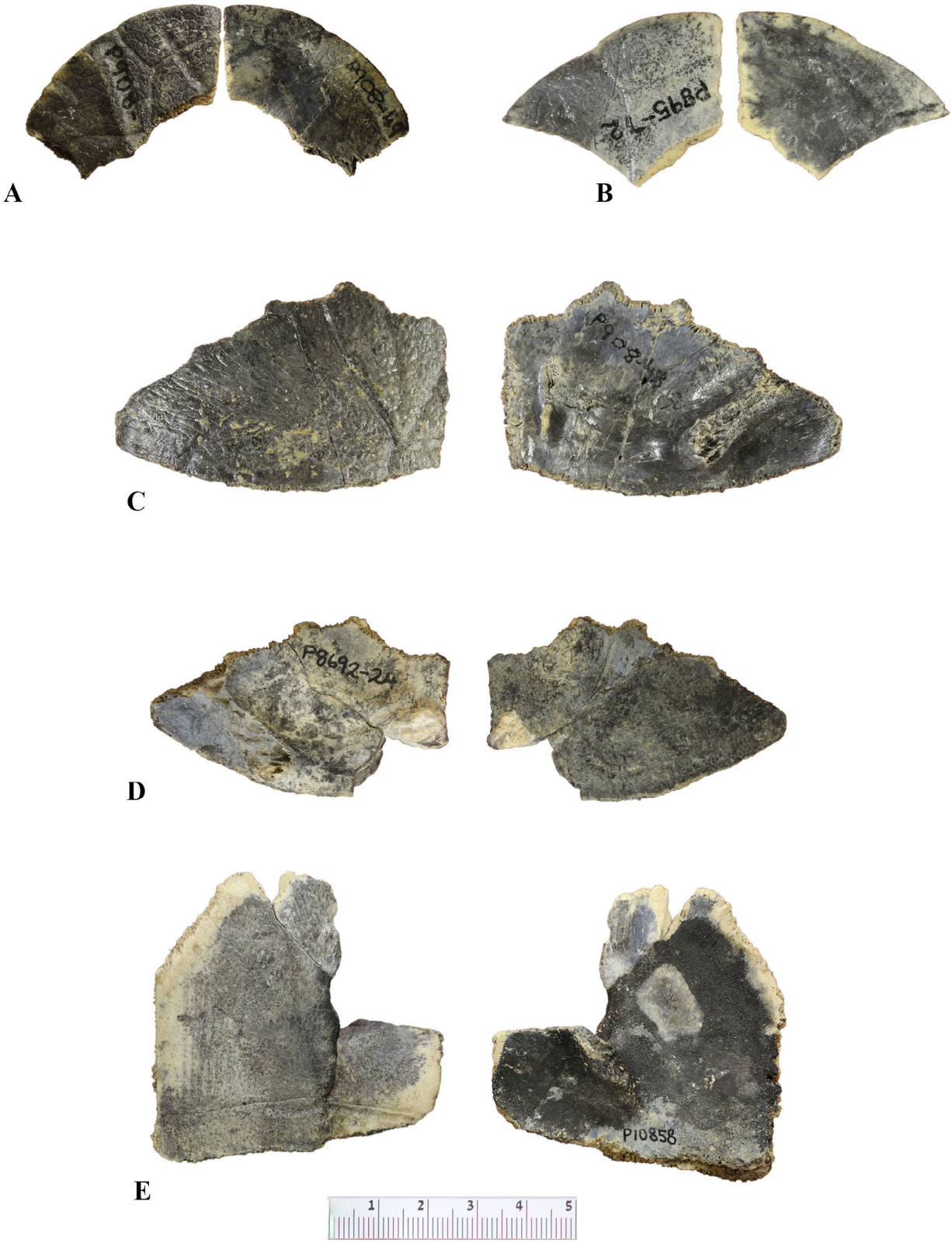


Figure 5. *Chelodina (Chelydera) nerophis* **sp. nov.**, hypodigm: a) NTM P908-49, holotype, complete right epiplastron; b) NTM P895-72, paratype, partial right epiplastron; c) NTM P908-48, referred specimen, complete left costal 1; d) NTM P8692-24, referred specimen, partial right costal 1; e) NTM P10858, referred specimen, partial left hyoplastron. All to scale.

suture and by the conjunction of the intergular, humeral and pectoral sulcus conjunction lying anterior of the widest portion of the entoplastron (versus longer intergular lateral sulci, the humero-pectoral sulcus lying along the epi-hyoplastral suture and the conjunction sulcus level lying at the widest point). Figures 6 – 7 illustrate comparative material of all pertinent *Chelodina (Cheydera)* and *Chelodina (Macrochelodina)* taxa.

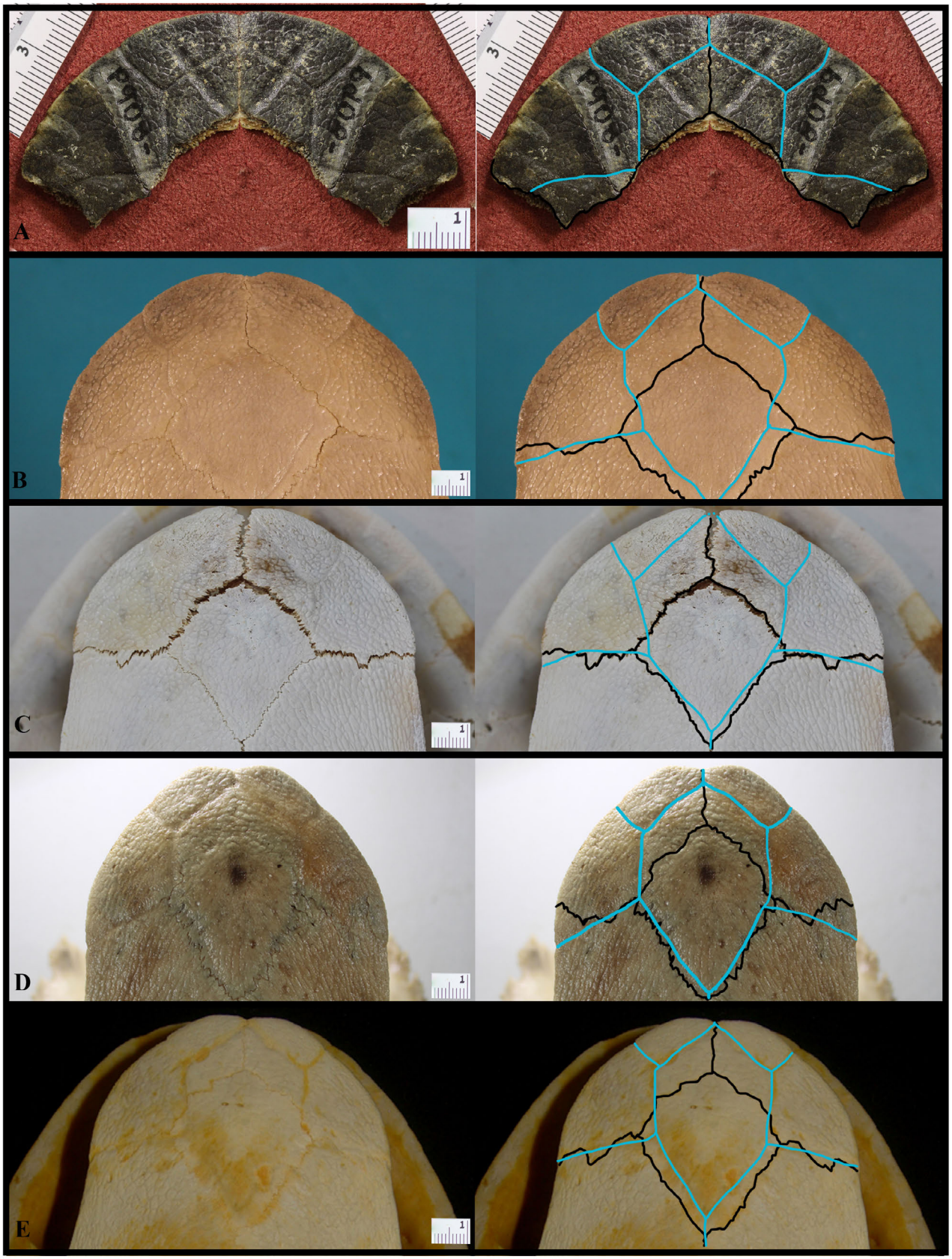


Figure 6. Typically character states of *Chelodina (Chelydera)* plastral forelobes showing the size and shape of the epiplastra and entoplastron, bone sutures, surface bone texturing and scute sulci. Raw image in left column, interpretive sulci in blue and sutures in black in right column. All currently described species illustrated over Figures 6 and 7. Row A: *C. (C.) nerophis* **sp. nov.** holotype NTM P908-49; Row B: *C. (C.) walloyarrina*: Row C: *C. (C.) kuchlingi*: Row D: *C. (C.) kurrichalpongo*: Row E. *C. (C.) burrungandjii*. Images by authors, or courtesy of J.Cann and I.Smales.

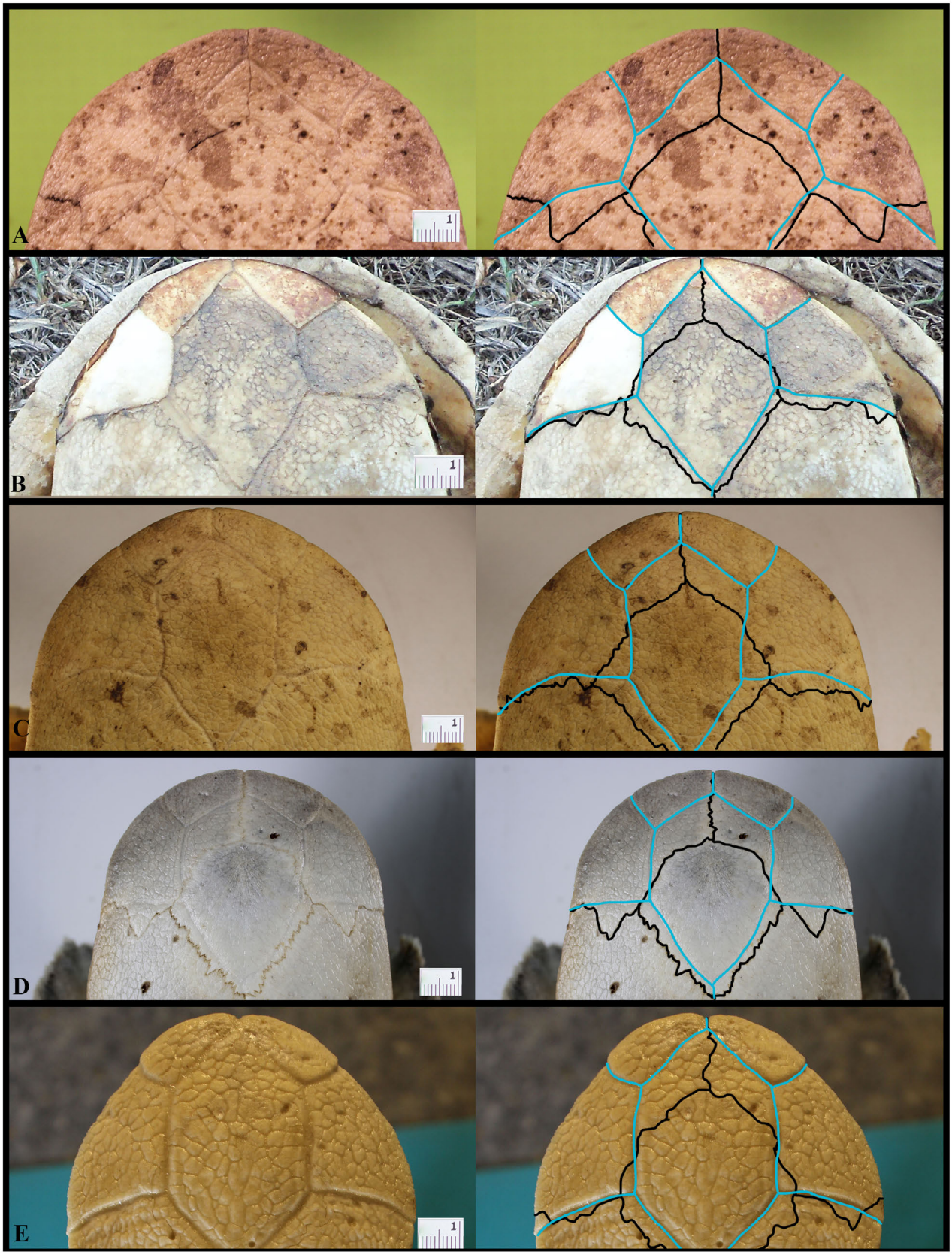


Figure 7. 1) Typically character states of *Chelodina (Chelydera)* and *Chelodina (Macrochelodina)* plastral forelobes showing the size and shape of the epiplastra and entoplastron, bone sutures, surface bone texturing and scute sulci. Raw image in left column, interpretive sulci in blue and sutures in black in right column. Row A: *C. (C.) parkeri*: Row B: *C. (C.) rugosa rugosa*; Row C: *C. (C.) rugosa siebenrocki* (MCZ R153043); Row D:*C. (C.) expansa*: Row E: *C. (M.) oblonga.* Images by authors, or courtesy of J.Cann and I.Smales.



Figure 8. Artistic life recreations of *Chelodina (Chelodina) aquanimare sp. nov.* (left) and *Chelodina (Chelydera) nerophis sp. nov.* (right) with respective holotype epiplastron superimposed. Illustrations by M. Joseph-Ouni.

We note that Kehlmaier *et al.* (2025) recently placed *C. walloyarrina*in the synonymy of *C. kuchlingi* and *C. burrungandjii* into the same synonymy as a valid subspecies, taxonomic acts with which we disagree (a forthcoming publication in preparation by the senior author that examines the osteology of all extant Northern Australian and New Guinea extant *Chelydera*species will lay out the continued recognition of these taxa based on the strongly differential morphology of the skull, suture scars, coloration and scutation and bone sutures).

The Plio-Pleistocene fossil *Chelodina (Chelydera)* taxa *C. (C.) taracreek*, *C. (C.) rugosa peregrina, C. (C.) expansa piscis* and *C. (C.) expansa flammafera* all were described from non-overlapping material (Joseph-Ouni *et al.,* 2023) with this new species. All of these latter taxa occur spatially and temporally separate (by millions of years) from *C. (C.) nerophis* sp. nov.

NTM P985-66, a referred specimen for *C. (C.) nerophis* sp. nov., a right epiplastron, also contains the observed autapomorphy and other characters confirming that the holotype epiplastron NTM P908-49 is not an aberrance.

The holotype specimen of *Chelodina (Chelydera) nerophis* sp. nov. NTM P908-49 was referred to as *Chelodina* sp. A by Megirian & Murray (1999), and it was the single specimen of all collected from Camfield Station attributed by them to that taxon. Those authors correctly observed the presence of two fossil *Chelodina* here, and noted that their *Chelodina* sp. A can be distinguished from their *Chelodina* sp. B (the taxon described here as *Chelodina (Chelodina) aquanimare* sp. nov.) by its "rounded as opposed to squared off marginal profile of the anterior plastral lobe in ventral view; proportionally long inter-epiplastral contact; and proportionally narrower intergular".

A second fossil specimen, NTM P10858, a left hyoplastron, included as a referred specimen, offers further confirmation of the presence of the subgenus *Chelydera*at Camfield Station. It can be identified as *Chelodina* by the absence of the humeral-pectoral sulcus on the anterior hyoplastron (present in *Elseya*and *Birlimarr*, the only other species known) as well as by the reception pit on the epiplastral-hyoplastral sutural edge which receives the epiplastral process when in articulation. It can be further identified to *Chelydera*by the proportion of the length of the inter-hyoplastral suture edge being 1.5 times the length of the epiplastral-entoplastral sutural edge (1 to 1 in the subgenus *Chelodina* and 3 times longer in *Elseya/ Birlimarr* – see Joseph-Ouni *et al.,* 2023) for further description and illustration).

A third specimen, NTM P908-48, a complete and undamaged left 1stcostal bone is also referred here. Though this specimen is isolated and we cannot link it directly to the holotype, it is highly distinct and belongs to the subgenus *Chelydera* based on shared characters (see Joseph-Ouni et al., 2023 for these character states). We work from the assumption that only a single species of the subgenus *Chelydera* was present at this site and therefore confidently include it in the hypodigm of *Chelodina (Chelydera) nerophis* sp. nov. If so it helps strengthen the distinctiveness of this new species in that it differs from all known fossil and extant Chelodina in the following combination of characters: an autapomorphy in having the suture scar of the 1stdorsal rib laterally reach the anterior to posterior level of the joint nuchal-1st peripheral-1st costal suture conjunction; an axillary bridge buttress suture scar (ABBSS) not constricted but evenly broad along the length and becoming broader at the terminus into a rounded spoon head shape; ABBSS terminus ending anterior of the posterior bone suture edge of costal one (thereby being confined entirely to the 1st costal); ratio of the V1 scute surface present on the 1st coastal being more than 7 times that of the V2 scute surface.

Disclosures

None.

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