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PO Box 3300, South Brisbane 4101, Australia
Phone 06 7 3840 7555
Fax 06 7 3846 1226
Email qmlib@qm.qld.gov.au
Website www.qm.qld.gov.au

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Further evidence in support of the recognition of the Freshwater Turtle *Elseya oneiros* (Testudines: Chelidae) from the Nicholson and Gregory rivers of Northern Queensland

Mehdi JOSEPH-OUNI[1], Arthur WHITE[2], Ian SMALES[3], Ross SADLIER[4], John CANN[5], William P. MCCORD[6], Patrick COUPER[7], Andrew AMEY[7] & Alastair FREEMAN[8]

1. South Glastonbury, CT 06073 USA (elseyaman@netscape.net) corresponding author
2. BEES, University of New South Wales, Sydney, NSW, 2052 Australia
3. Birregurra, Victoria, 3242 Australia
4. Outwest Reptile Consulting Services, Wellington, New South Wales, 2820 Australia
5. Phillip Bay, Sydney, NSW, 2036 Australia
6. Hopewell Junction, NY 12533 USA
7. Biodiversity Program, Queensland Museum, South Brisbane, Queensland, 4101 Australia
8. Aquatic Species Program, Dept. of Environment and Science, Atherton, Queensland, 4883 Australia

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ABSTRACT

Thomson *et al.* (1997) proposed that the extant *Elseya* from the Nicholson-Gregory drainages in northwestern Queensland was conspecific with the holotype of *Elseya lavarackorum,* which comprised a fossil carapace and associated plastron excavated from the late Pleistocene Terrace Site at Riversleigh. Analysis of additional fossil material, and examination of a suite of 16 scute characters (eight for each of the carapace and plastron) by Joseph-Ouni *et al.* (2020) concluded that the two species were distinct and represented separate *Elseya* lineages and proposed the new name *Elseya oneiros* for the extant lineage. Recently, the Turtle Taxonomy Working Group (TTWG) in their 9th edition Checklist of Turtles of the World (TTWG 2021) questioned the status of *E. oneiros* and placed it in the synonymy of *E. lavarackorum,* making the claim, amongst others, that the skeletal characters of Thomson *et al.* (1997) were not addressed. Here we fully address the claims made and evaluate those skeletal characters. We also assess an additional nine thoracic skeletal characters of the pertinent *Elseya* species, including *E. dentata* sensu stricto. The results again do not support the conclusions of Thomson *et al.* (1997) of the holotype of *Elseya lavarackorum* being conspecific with the extant *Elseya* from the Nicholson-Gregory Rivers, reaffirms the proposal offered by Joseph-Ouni *et al.* (2020) for the placement of *E. lavarackorum* in the subgenus *Elseya,* and the status of *E. oneiros* in the Nicholson-Gregory drainages as a distinct species.

❑ *Elseya lavarackorum; Elseya oneiros; Queensland; Australia; skeletal characters; fossils.*

In 1994, White and Archer described a "giant" fossil species of chelid turtle, *Emydura lavarackorum*, on the basis of associated plastron, carapace and pelvic fragments, excavated from the late Pleistocene Terrace Site, Riversleigh, northwestern Queensland. Soon after, in revisiting that taxonomic assignment, Thomson *et al.* (1997) demonstrated its relationship to the genus *Elseya* and assigned the species to that genus. Further, the latter authors concluded that in the absence of any diagnosable difference between the fossil material of *E. lavarackorum* and the living population of *Elseya* snapping turtles in the Nicholson River (then formally undescribed) the two be regarded as a single species. Hence, *Elseya lavarackorum* has been recognised as including both the late Pleistocene and extant populations of *Elseya* of the Nicholson and Gregory rivers region.

Since then, considerable progress has been made in the understanding of morphological characters and interspecies relationships of Australian chelids, especially within the genus *Elseya* (Thomson *et al.* 2015, Thomson and Georges 2016). In 2020, Joseph-Ouni *et al.* proposed an alternative interpretation to that of conspecificity between the living species of *Elseya* in the Nicholson-Gregory drainages and the Riversleigh fossil turtle, utilizing a suite of 16 scutation characters (eight for each of the carapace and plastron) to assess differences between the fossil and extant populations.

Joseph-Ouni *et al.* (2020) concluded that the fossil holotype *E. lavarackorum* (QM F24121) differed markedly from the living population of *Elseya* in the Nicholson-Gregory, sharing only four carapace characters and a single plastron character. By contrast, the fossil holotype of *E. lavarackorum* was found to be more similar in morphology to extant *E. dentata* of the Northern Territory, sharing up to five of the eight carapace characters and up to six of the eight plastron characters. On this basis, Joseph-Ouni *et al.* (2020) concluded that the living population of *Elseya* in the Nicholson-Gregory drainage was different from the fossil holotype of *E. lavarackorum* and represented an undescribed species. This new species was recognised as having its closest affinities with other extant Queensland *Elseya* species assigned to the subgenus *Pelocomastes* by Thomson *et al.* (2015), and therefore, Joseph-Ouni *et al.* (2020) described it as *Elseya* (*Pelocomastes*) *oneiros*. By virtue of its closer affinities to *Elseya* (*Elseya*) *dentata* s.s., the fossil holotype of *E. lavarackorum* was regarded as belonging to the subgenus *Elseya*.

In addition to the fossil holotype of *E. lavarackorum*, two other fossil specimens from Riversleigh, QM F30817, and QM F30818, were examined by Joseph-Ouni *et al.* (2020) and by Thomson *et al.* (2015). Both are partial plastrons excavated contemporaneously with the holotype of *E. lavarackorum* from the same stratum at the Terrace Site, but not mentioned in the description of that species. Specimen QM F30817 had at least five of the plastron characters (out of the six that were able to be evaluated) in common with the holotype and was regarded as conspecific with *E. lavarackorum*. However, QM F30818 had only two characters (out of the eight that could be evaluated) in common with the holotype of *E. lavarackorum* and seven characters of the eight in common with *E. oneiros*, strongly suggesting it was synonymous with that species. As such, it appears two sympatric species of *Elseya* were present at Riversleigh in the late Pleistocene, one represented by two fossils (QM F24121 and QM F30817), that we regard as *E. lavarackorum* s.s., and one represented by a single fossil (QM F30818) considered conspecific with the extant populations in the Nicholson-Gregory drainages described as *E. oneiros*.

Recently, the Turtle Taxonomy Working Group (TTWG) in their 9th edition Checklist of Turtles of the World (TTWG 2021) questioned the status of *E. oneiros* and placed it into the synonymy of *E. lavarackorum*. In doing so, the TTWG made several claims in Annotation 30 of their checklist. We find the rationale for the synonymy presented by the TTWG was not well-founded and contained errors of fact. We present the claims made by the TTWG below in italic text in order of appearance (bold text is ours for emphasis), along with our responses. Their citations of Joseph-Ouni *et al.* (2021) refers to Joseph-Ouni *et al.* (2020).

> TTWG: That *'Joseph-Ouni et al. (2021) described apparent shell scutation differences between two late Pleistocene fossils (one partial carapace and one plastron) of E. lavarackorum from the Riversleigh site* ***and several living specimens of E. lavarackorum*** *from the Nicholson and Gregory River drainages, and concluded that the living specimens were not the same species as the fossils, in contradiction to the earlier conclusion by Thomson et al. (1997) that the fossil and living specimens belong to the same species.'*

The statement by the TTWG is incorrect in that it does not take into account the extent of all of the material examined by Joseph-Ouni *et al.* (2020) in describing *Elseya oneiros.* Reference to Appendix B 'Specimens Examined and Character Scoring' of that publication clearly identifies six museum specimens, one fossil specimen, and four live specimens of *Elseya oneiros* that were scored for comparison with the fossil holotype of *Elseya lavarackorum* and lists an additional eight museum and living specimens under 'Additional Specimens Examined' and an extensive array of comparative material of other *Elseya* species. The museum specimens are held by public institutions and are available for scrutiny.

> TTWG: That *'Thomson et al. (1997) had based their conclusions of* ***conspecificity*** *on* ***several*** *skeletal characters and* ***a single scutellation character*** *that demonstrated a close relationship between the fossil and living specimens, yet Joseph-Ouni et al. (2021) did not address or describe any of the skeletal characters, focusing instead on a variety of other apparently variable scutellation differences.'*

While TTWG did not specify which osteological and scutellation characters were used by Thomson *et al.* (1997) for this purpose, the paper by Thomson *et al.* only provided character state scores for five characters (identified by them as A-E), of which the first three were osteological and the remainder scutellation. Of these, the condition for two (characters A & C) was shared broadly across all the species of *Elseya* and *Emydura* (using the current concept of *Elseya*, excluding the species in the *latisternum* complex subsequently transferred to *Wollumbinia*). The condition for character D was shared across all *Elseya* species examined, and character E showed a difference only in one species, *Elseya novaeguineae,* making all four uninformative in inferring relationships of *lavarackorum*, or conspecificity of the *lavarackorum* holotype with the extant species. Only a single skeletal character (Character B) in that study, pertaining to the anterior bridge suture shape, was shared between the holotype of *E. lavarackorum* and the living species from the Nicholson and Gregory River drainages to the exclusion of species in the *Elseya dentata* group s.s. and *E. novaeguineae.* This character was also shared with two other species of *Elseya* in Queensland not formally described at that time (since described as *E. albagula* Thomson *et al.* 2006 and as *E. irwini* Cann 1997 / *E. stirlingi* Wells 2007). Thomson *et al.* (1997) also stated that the holotype of *E. lavarackorum* and the extant species from the Nicholson and Gregory River drainages were indistinguishable in the indentation of the anterior margin of the carapace, but that this feature was also 'variable among the Queensland forms of *Elseya dentata.'* As such, and by default, the three extant Queensland *Elseya* species (presumably those listed under *E. lavarackorum* (Nicholson – Gregory), *E.* sp. aff. *dentata* (Johnstone) = *E. irwini / E. stirlingi*, and *E.* sp. aff. *dentata* (Burnett) = *E. albagula*) were equally indistinguishable from the fossil holotype of *E. lavarackorum* on the basis of shared character states across the three skeletal characters and two scutellation characters scored in the data matrix by Thomson *et al.* (1997). However, it should be noted that Thomson and coauthors subsequently recognised two of these taxa as distinct from the fossil holotype of *E. lavarackorum* in describing one (*E.* sp. aff. *dentata* (Burnett) as *E. albagula* Thomson *et al.* 2006 and treating another (*E.* sp. aff. *dentata* (Johnstone) as the species *E. irwini* (Georges & Thomson 2010).

In reality, the evidence presented by Thomson *et al.* (1997) for conspecificity of the holotype of *E. lavarackorum* and the living species of the Nicholson and Gregory Rivers, to the exclusion of all other *Elseya* species, rests on one plastron scutellation character, the 'sigmoidal shape of the sulcus between the humerals and pectorals on the plastron'. This character state was examined by Joseph-Ouni *et al.* (2020) and identified as representing two separate conditions (see Character 4 of Joseph-Ouni *et al.*, 2020 – their plate 5a). In the first condition, found in the fossil holotype of *E. lavarackorum,* the humeral-pectoral sulcus could be interpreted as 'sigmoidal' (approximating an S-shaped) with its lateral extremity (on the edge of the plastron) and its medial extremity (at its intersection with the midline sulcus) on the same anterior-posterior level or plane. In extant *Elseya oneiros*, the humeral-pectoral sulcus is not sigmoidal, rather its lateral extremity (on the edge of the plastron) has a more anterior position to its medial extremity (at its intersection with the midline sulcus) i.e. in a different plane. These conditions represent characters 3 and 4 in Joseph-Ouni *et al.* (2020) and were shown to be consistent across the specimens of the extant species assigned to *Elseya oneiros,* and clearly diagnostic with regard to the holotype of *E. lavarackorum*, and to other species in the subgenus *Pelocomastes*.

While the details of the plastron that characterise and separate *Elseya oneiros* and the holotype of *E. lavarackorum* were qualitatively examined and illustrated in Joseph-Ouni *et al.* (2020), we here offer a quantitative assessment of plastral sulcus ratios (Figure 1) as further evidence for their recognition as two distinct species.

> TTWG: That '*basing these variable differences on only single carapacial and plastral fossil specimens* ***without regard to the extent of variation in living specimens*** *does not, in our opinion, constitute adequate demonstration of significant enough specific differences to warrant recognition of separate taxa, and as such most of us consider E. oneiros to be a junior synonym of E. lavarackorum.*'

Again, this statement by the TTWG misrepresents both the variation documented and the extent of material of the extant species from the Nicholson and Gregory River drainages examined by Joseph-Ouni *et al.* (2020) in describing *Elseya oneiros*. The effort of these authors in that regard has been addressed above.

> TTWG: That '*Joseph-Ouni et al. (2021) erroneously placed E. lavarackorum in the subgenus Elseya, despite the clear allocation of that species to the subgenus Pelocomastes, as demonstrated by its skeletal morphology (Thomson et al. 1997, 2015).*'

The placement of *E. lavarackorum* by Thomson *et al.* (1997) within the 'Queensland *Elseya* group' (subgenus *Pelocomastes*) vs the *Elseya dentata* group (subgenus *Elseya*) rests on a single character difference (Character B of Thomson *et al.* 1997: – Table 1) pertaining to the shape of the axillary bridge suture with the carapace, given that the states for all other characters (four of five) in the data matrix are also present in the *Elseya dentata* group. While this single character state was not discussed by Joseph-Ouni *et al.* (2020), the reallocation of the holotype of *E. lavarackorum* to the subgenus *Elseya* was intentional (not mistakenly as implied by TTWG) and was based on the extent of concordance of five of the eight carapace characters and up to six of the eight plastron characters they investigated (and fossil specimen QM F30817 in five of six plastral characters able to be scored).

We note also that Thomson *et al.* (2015) offered no further evidence in terms of character states applicable to the fossil holotype of *E. lavarackorum* in support of their formal placement of it within the subgenus *Pelocomastes*, to the exclusion of the subgenus *Elseya* (see also Joseph-Ouni *et al.* 2022, in press for a full review of the lectotype of *Pelocomastes* and the type species' character states and nomenclature).

The TTWG criticism of the character states and variability comes down to a few sweeping statements. They did not specify which character states they considered to be so variable as to dismiss all other characters evaluated from further consideration, nor did they provide or give reference to any conclusive contrary

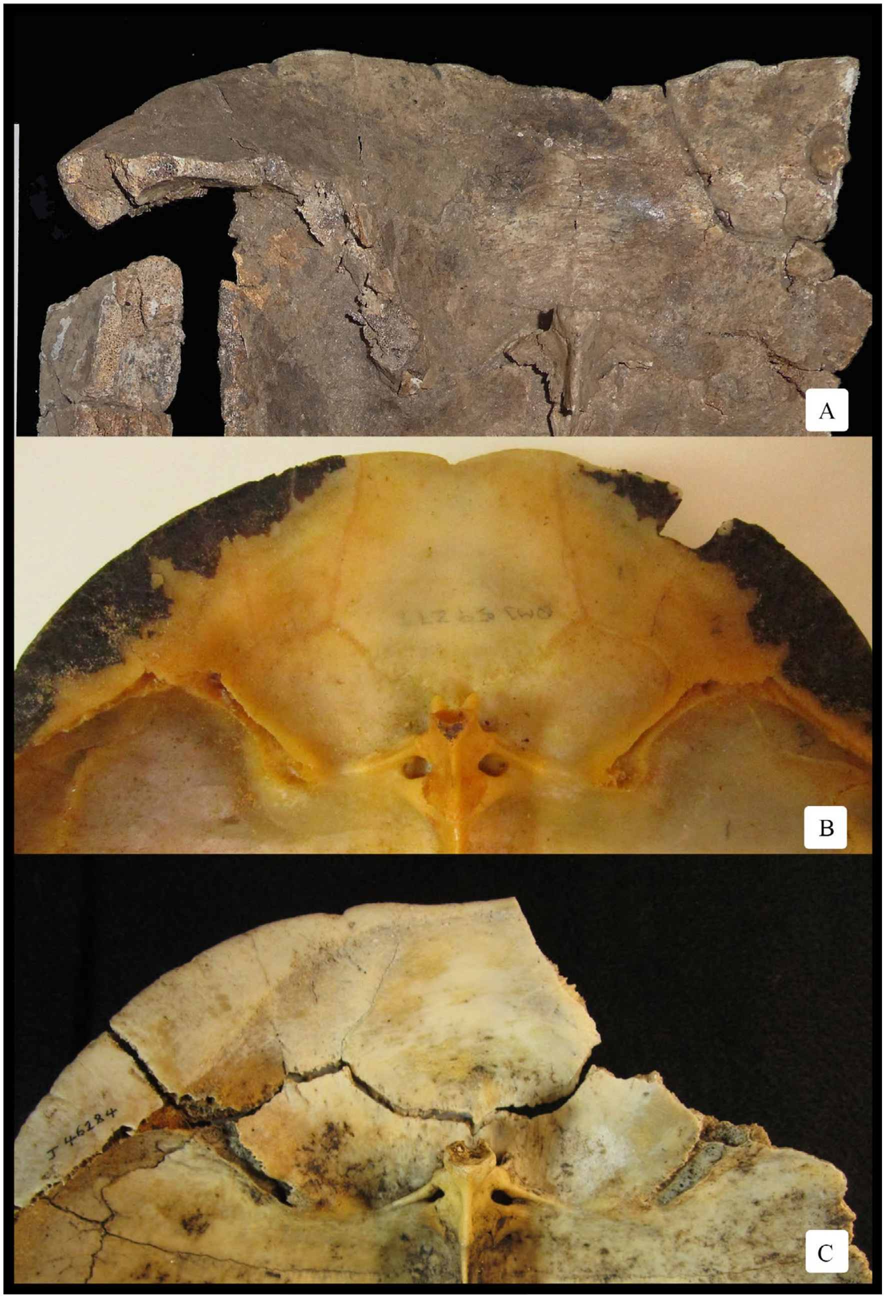

PLATE 1. Comparison of the anterior ventral carapace surfaces of **A**) holotype of *Elseya lavarackorum* (QM F24121); **B**) *E. dentata* (QM J59277, Daly River, Northern Territory); **C**) *E. oneiros* (QM J46284, Nicholson River, Qld.). See Plate 2 for explanatory differences.

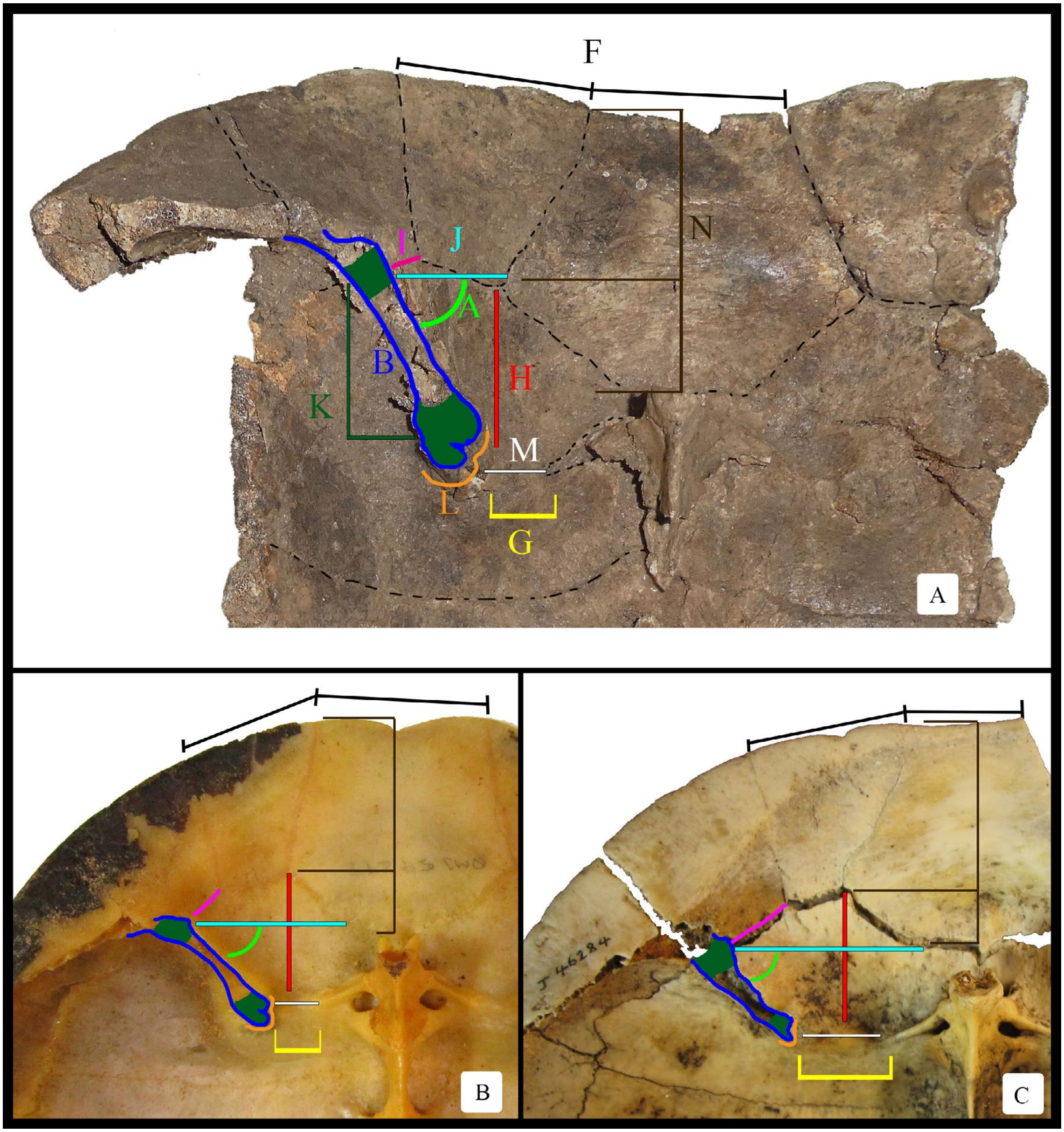

PLATE 2. Above: Visual guide to skeletal characters A, B in Thomson *et al.* (1997) and F - N, added in this current study, demonstrated on the internal anterior carapace of **A**) the holotype of *Elseya lavarackorum* (QMF24121). Same characters on that of **B**) *E. dentata* (QM J 59277 - below left) and **C**) *E. oneiros* (QM J46284, below right). See text for definitions of characters and comparative descriptions.

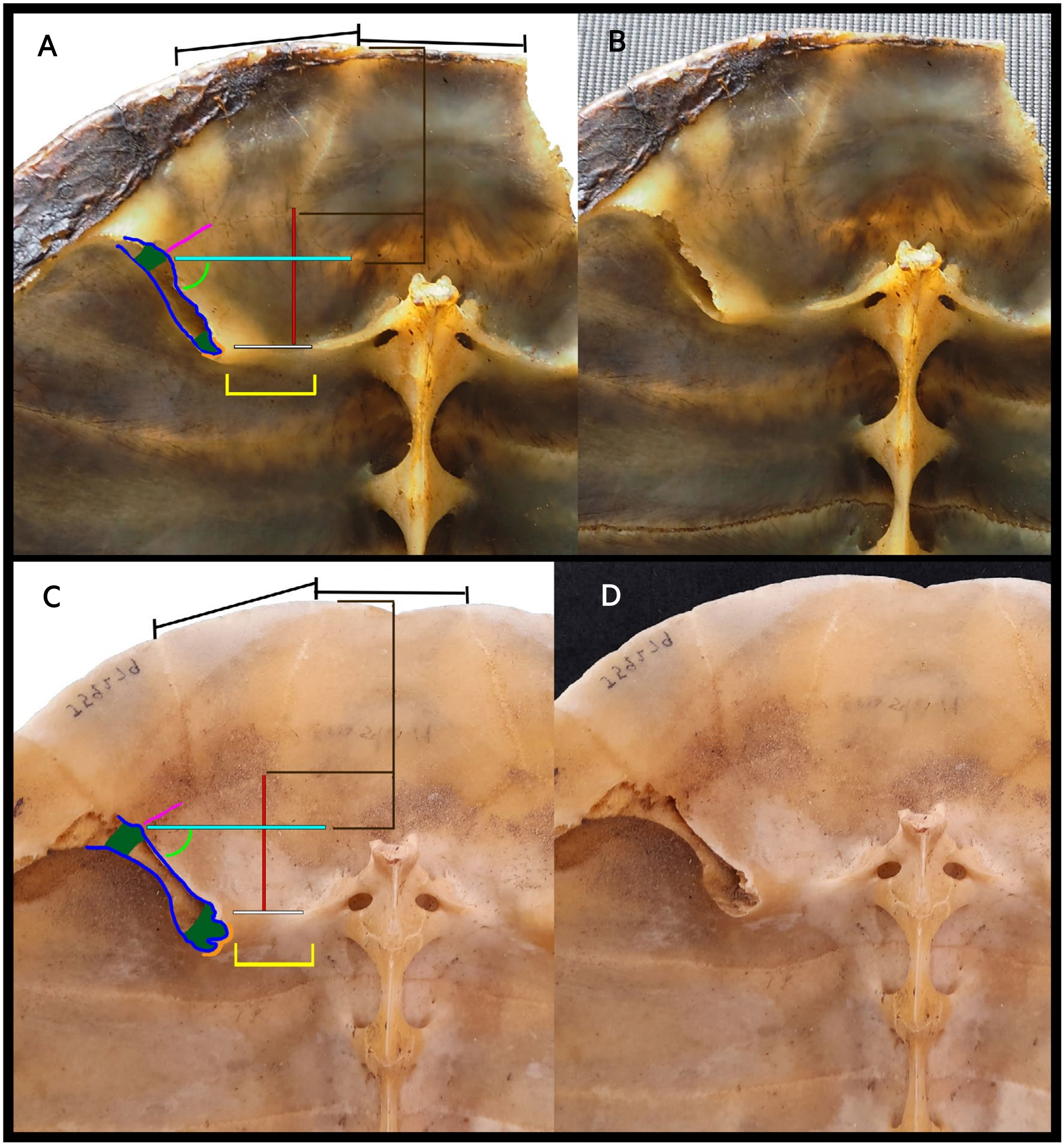

PLATE 3. Interior (visceral) views of the anterior carapaces: a second specimen of *E. oneiros*, **A**) Gregory River, JC collection, (image of actual specimen is mirror-reversed for ease of comparison) and a second specimen of *E. dentata;* **B**) - Douglas River, QM J59279, (image of actual specimen is mirror-reversed for ease of comparison and suture clarity), both with the labelling of the same characters in Plate 2.

PLATE 4. New images of the holotype of *Elseya (Elseya) lavarackorum* QM F24121, **A**) in its current state, in external and, **B**) internal carapace; (**C-D**) and plastron. The medially constricted axillary buttress suture scar and 'bulb' terminus are easily discernible (B).

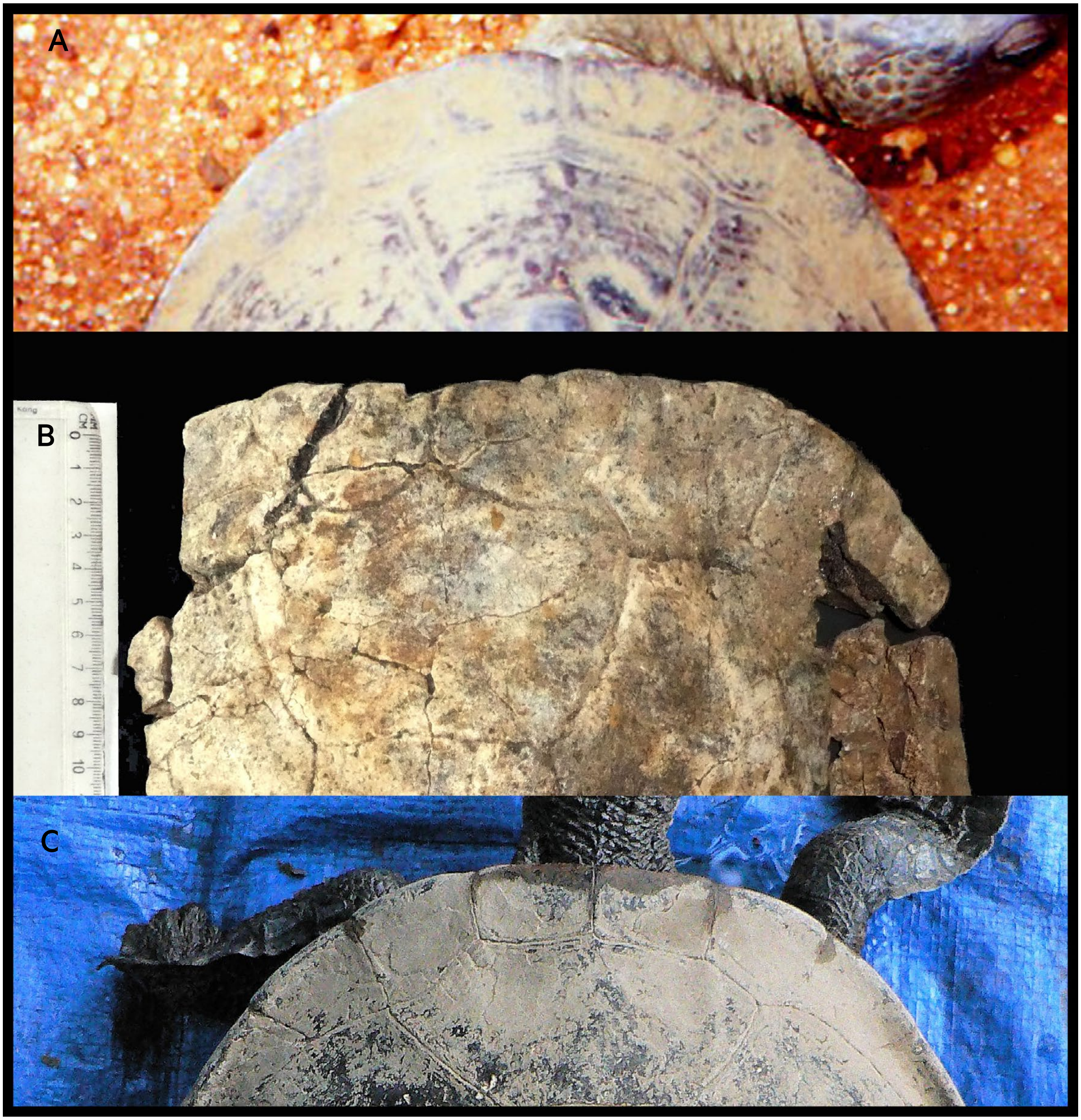

PLATE 5. (A-C) Comparison of the scute sulci, anterior carapace and nuchal emargination of: **B**) holotype of *Elseya lavarackorum* (QMF24121) with, **A**) a live *E. dentata* from Katherine River, Northern Territory and, **C**) a live *E. oneiros* from Gregory River.

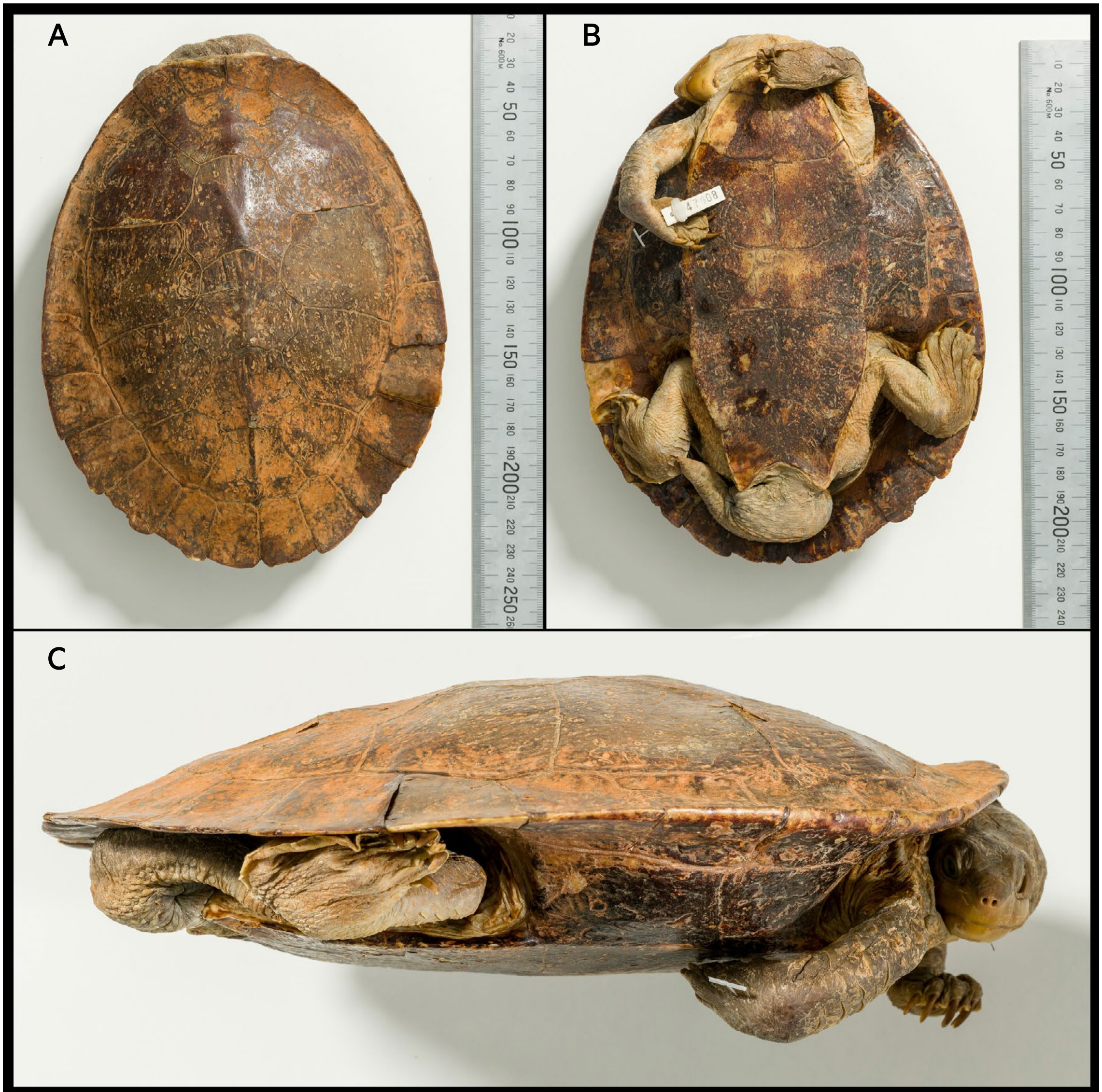

PLATE 6. Holotype of *Elseya oneiros* QMJ 47908 in dorsal **A**), ventral; **B**) and lateral views; **C**), and view of the gular-intergular scutes with repositioning of the left forelimb; **D**). All images © Queensland Museum, Peter Waddington.

evidence for such alleged variability. Contrary to the assertions made by TTWG, variation in these characters was covered by Joseph-Ouni *et al.* (2020) and was based on multiple specimens of all described and known undescribed species of *Elseya*, and the additional fossil specimens. On these points future researchers will have to come to their own conclusions after impartial consultation of the publications and referenced material.

Regarding the criticism by the TTWG that Joseph-Ouni *et al.* (2020) did not consider the skeletal morphology of Thomson *et al.* (1997, 2015) we contend that the analysis of skeletal morphology as presented by Thomson *et al.* (1997) identified (erroneously) no differences between the fossil holotype of *E. lavarackorum* and the 'Queensland *Elseya* group' which included *E. oneiros, E. stirlingi/irwini* and *E. albagula*. The carapace and plastron characters examined by us in 2020 identified diagnosable differences.

We take the opportunity here to rectify our omission identified by the TTWG with regard to assessing the skeletal morphology of the fossil holotype of *E. lavarackorum* and *E. oneiros*.

SKELETAL AND SCUTELLATION CHARACTERS ASSESSED

We have reviewed the three thoracic skeletal characters, A to C, and the two scutellation characters, D and E, reported by Thomson *et al.* (1997), and here present a further nine skeletal characters evaluated by us in assessing differences among the three key taxa under discussion: *E. oneiros, E. dentata* and the holotype of *E. lavarackorum.* These characters are here labelled Character F to N for continuity of presentation with the characters identified by Thomson *et al.* (1997).

Examination of relevant internal skeletal characters of extant taxa was reliant on disarticulated shells. For *E. oneiros* we have examined the same specimen (QM J46284 – Plate 1, 2) used by Thomson *et al.* (1997 – Fig 2E, 2F), and an additional skeletal carapace (JC collection – Plate 3) to ascertain the condition of bony characters in that species. For *E. dentata* s.s. we have examined the same specimen (QM J59277 from the Daly River, Northern Territory – Plate 1, 2) as used by Thomson *et al.* (1997: – Fig 2C, 2D), and a second specimen (QM J59279, from the Douglas River, Northern Territory - Plate 3) to account for variation in that species.

It is important to note that until the current paper, assessment of the visceral osteological characters applicable to the extant species *E. oneiros* via disarticulated shells was limited to a single specimen in the Queensland Museum (QM J46284) for both Thomson *et al.* (1997) and Joseph-Ouni *et al.* (2020). The specimens listed by Thomson *et al.* (1997) in the Queensland Museum from the Nicholson-Gregory rivers are either articulated shells or 'whole' animals (additional juvenile specimens were figured in Plate 12d in Joseph-Ouni *et al.* (2020).

Terminology. Regarding the terminology used for carapace bones, Thomson *et al.* (1997) state in their 'Materials and Methods' that "Throughout this paper, names of the bony elements of the shell and the overlying scutes follow those of Zangerl (1969)'. However, they use the term 'pleural' for carapace bones, in contrast to Zangerl (1969), who described these as 'costals' and used 'pleural' for carapace scutes that overlie them. Here, we have followed Zangerl (1969).

Thoracic Skeletal Characters. To avoid ambiguity, we present the thoracic skeletal characters used by Thomson *et al.* (1997) verbatim, noting that their '*gomophosisis*' is correctly spelled '*gomphosis*'.

> ANTERIOR BRIDGE STRUTS Character A
> Contact with Pleural I
>
> A0. In the primitive state, the posterior edge of the bridge-carapace suture runs parallel and adjacent to the rib/gomophosisis of pleural 1 (Fig. 1A-F).
>
> A1. In the derived state, the posterior edge of this suture contacts the rib/gomophosis is at its anterior end, but is set at a forward divergent angle of between 15 and 50°. This

angle is most pronounced in *Emydura*, least in *Rheodytes* (Figs. 2A-F, 3A-D).

Character B. Bridge suture shape.

Bl. The anterior and posterior edges of the bridge-carapace suture diverge from their point of congruence closest to the vertebral column. The widest extent of the suture is distal to the vertebral column and there is no medial constriction (Fig. 1A-F).

B2. The anterior and posterior edges of the bridge-carapace suture are parallel or closely so with a prominent suture surface between them. There is no medial constriction (Figs 2A-B, E-F, 3A-B).

B3. The bridge-carapace suture is expanded for its full length, but more so at extremes, there being an obvious medial constriction (Fig. 2B).

B4. The bridge-carapace suture narrows from its widest point proximal to the vertebral column and constricts completely to form a ridge confluent with the edge formed by the ventral suture of the peripheral bones (Fig. 3C-D).

RIB/GOMOPHOSISIS OF PLEURAL 1.
Character C. Rotation of the Rib/Gomophosisis.

C0. The ventral surface of the distal extent of the rib/gomophosisis is rotated obliquely, to face ventrally but with posterior inflection (Figs 1A-F, 2A-B).

C1. The rib/gomophosisis shows no such torsion distally (Figs 2C-F, 3A-D).

Characters A and B relate to morphology of the suture between the bridge strut, or buttress process of the hyoplastron with the thoracic surface of costal 1. This character is most clearly observed from morphology of the sutural scar on the thoracic surface of the carapace. In the holotype of *E. lavarackorum* broken remnants of the hyoplastron axillary buttress remain attached to the carapace, but the shape and configuration of the suture between these elements is readily seen.

For Character A the anterior edge of the bridge-carapace suture is set at a forward divergent angle to the rib/gomphosis of costal 1. The derived state (A1) cited by Thomson *et al.* (1997), occurs in *E. oneiros, E. dentata,* and the holotype of *E. lavarackorum*. However, the angle of the anterior edge of the bridge suture relative to the rib/gomphosis in the fossil holotype of *E. lavarackorum* is at an angle of 60-70° (character A1 of Thomson *et al.* 1997), i.e. close to parallel with the longitudinal axis of the animal. In *E. dentata* and *E. oneiros* the anterior edge of the bridge suture is oblique to the rib/gomphosis at an angle of 45-50°. In support of our reassessment of this character we illustrate the state of the anterior bridge suture scar (Plates 1 & 2) in the *E. lavarackorum* holotype, *E. oneiros* and *E. dentata* for Character A of Thomson *et al.* (1997).

Our assessment of Character B, the shape of the axillary bridge suture and degree of medial constriction of the suture in the fossil *E. lavarackorum* holotype is not in agreement with that of Thomson *et al.* (1997). From our examination of the thoracic surface of the carapace the correct state for this character in the holotype of *E. lavarackorum* is a medial constriction of the bridge-carapace sutures (character state B3 of Thomson *et al.* 1997), not parallel or closely so (character state B2) as presented by Thomson *et al.* (1997). As such, the condition found in the holotype of *E. lavarackorum* is in agreement with that found in the *Elseya dentata* group s.s. and not the 'Queensland *Elseya* group' (now the subgenus *Pelocomastes*), of which *E. oneiros* is a member. As evidence of our reassessment of this character we illustrate the state of the anterior bridge suture scar (Plate 1, 2) in the holotype of *E. lavarackorum*, and specimens of *E. oneiros* and *E. dentata* for Character B of Thomson *et al.* (1997), and again in Plate 4 (upper right) in which this constriction can be clearly observed in new images we provide of the holotype of *E. lavarackorum*.

Character C, which assesses the extent to which the ventral surface of the distal extent of the rib/gomphosis is rotated obliquely, to face ventrally but with posterior inflection, is regarded as the same in the holotype of *E. lavarackorum*, *E. oneiros* and *E. dentata*, in agreement with Thomson *et al.* (1997).

The two scute characters assessed by Thomson *et al.* (1997), and labelled characters D (Relative width of Vertebral 1) and E (Cervical Scute) were both addressed in Joseph-Ouni *et al.* (2020), and need not be discussed further as there was agreement with the determination of the state presented by Thomson *et al.* (1997), and they provide no differentiation between the fossil holotype of *E. lavarackorum* and extant *E. oneiros* or *E. dentata* s.s.

Hence, the entirety of the case for conspecificity of the holotype of *E. lavarackorum* with that of the extant Nicholson-Gregory *Elseya* species (*E. oneiros*) presented by Thomson *et al.* (1997) rests on the characterization of a single scute character (qualitatively described by Thomson *et al.* 1997 in the text, that being the nature of the sinuosity of the humeral-pectoral sulcus) and a single skeletal character (Character B). The scute character was shown to have been incorrectly assessed (Joseph-Ouni *et al.* 2020), and the skeletal character is shown here to have been incorrectly assessed.

Further, reliance on the five skeletal and scutellation character states presented by Thomson *et al.* (1997) as the basis of conspecificity between the holotype of *E. lavarackorum* with the extant Nicholson-Gregory *Elseya* species would equally place *E. albagula* and *E. irwini* / *stirlingi* (sensu Georges & Thomson 2010 for Johnstone River, Queensland population) into the synonymy of *E. lavarackorum*.

The additional nine skeletal characters are presented here (Plates 2, 3) for the fossil holotype of *E. lavarackorum* and specimens of extant *E. oneiros* and *E. dentata* s.s., and we evaluate their condition in assessing differentiation between these three taxa. These characters, labelled Characters F to N for continuity of presentation with the characters utilised and labelled by Thomson *et al.* (1997), are initially described, and the various states observed listed. Note – 'ABSS' = Axillary bridge suture scar.

Character F - Nuchal-Peripheral 1: Relationship of the length of the anterior border of the nuchal bone in relation to that of the 1st peripheral bone, measured straight. This occurs in three typical conditions:

> F0. Anterior edge of nuchal wider than anterior edge of peripheral 1 (some *dentata*).
>
> F1. Anterior edge of nuchal not as wide as anterior edge of peripheral 1 (some *oneiros*).
>
> F2. Anterior edge of nuchal and anterior edge of peripheral 1 subequal in width (some *dentata*, some *oneiros*, *lavarackorum*).

Character G – Proximity of ABSS to rib 1: Proximity of the medial extremity of the ABSS terminus to the distal extremity of rib 1.

> G0. Distance between the medial extremity of ABSS terminus and distal extremity of rib 1 is substantially less than half the length of the ABSS (*lavarackorum, dentata).*
>
> G1. Distance between the medial extremity of ABSS terminus and distal extremity of rib 1 is substantially more than half the length of the ABSS (*oneiros*).

Character H – Medial extremity of ABSS relative to intersection of the nuchal, peripheral 1 and costal 1: This character is determined by observing the position of the medial extremity of ABSS terminus relative to a longitudinal line posterior from the sutural intersection of the nuchal, peripheral 1 and costal 1.

> H0. The medial extremity of ABSS terminus lies almost directly posterior to the sutural intersection of the nuchal, peripheral 1 and costal 1 (*lavarackorum*).
>
> H1. The medial extremity of ABSS terminus lies substantially lateral to a longitudinal line running posterior from the sutural intersection of the nuchal, peripheral 1 and costal 1 (*dentata*, *oneiros*).

Character I – Portion of the internal width of peripheral 2 occupied by the ABSS:

This character relates to the proportion of peripheral 2 occupied by the hyoplastron suture with the carapace. It is measured by the shortest distance between the anterior edge of ABSS and the suture of peripherals 1 and 2.

I0. Distance between the anterior edge of ABSS and the suture of peripherals 1 and 2 is less than half the width of peripheral 2 (*dentata, lavarackorum).*

I1. Distance between closest anterior edge of ABSS and suture of peripherals 1 and 2 is equal to, or greater than half the interior width of peripheral 2 (*oneiros*).

Character J - ABSS-Nuchal: The position of the orthogonal level of the nuchal suture in relation to that of where the ABSS (base) first crosses the Peripheral 2-1st costal suture, pinned at the center point of that crossing on the suture.

J0. Line orthogonal contacts the nuchal suture at the lateral extremity of nuchal (*lavarackorum).*

J1. Line orthogonal contacts the nuchal suture at the posterior extremity of nuchal (*dentata, oneiros*).

Character K - ABSS Terminus-Base: An assessment of the size of the ABSS terminus relative to the size of the ABSS base at the point where peripheral 2 is immediately adjacent to the 1st costal.

K0. ABSS terminus is larger than base (*lavarackorum, dentata).*

K1. ABSS terminus is smaller than base (*oneiros*).

K2. ABSS terminus is subequal to base.

Character L – Shape of the medial extremity of ABSS:

L0. Medial extremity of ABSS has a rounded, lobed and bulbous shape (*dentata, lavarackorum).*

L1. Medial extremity of ABSS terminates with a tapered, finger-like projection (*oneiros*).

Character M - ABSS Terminus-Level: The position of the ABSS terminus at an orthogonal level relative to the distal-most portion of the 1st dorsal vertebra rib suture (rib one). In this condition the terminus lies in three conditions: anterior to, medial to, or posterior to the rib suture.

M0. Terminus lies anterior to rib one (*lavarackorum).*

M1. Terminus lies medial to rib one (*dentata, oneiros*).

M2. Terminus lies posterior to rib one.

Character N - Nuchal shape:

N0. Greatest width of the nuchal is at a point slightly posterior to half its length (*lavarackorum).*

N1. Greatest width of the nuchal is at a point substantially posterior to half its length (*dentata*, *oneiros*).

DISCUSSION

The distribution of character states for the nine additional thoracic skeletal characters assessed are described and illustrated for the three species of *Elseya* that are the focus of our investigation.

Character F - Nuchal-Peripheral 1: In the holotype of *E. lavarackorum* the width of the anterior border of the nuchal is subequal to that of the adjacent peripheral 1 (F2). In *E. dentata* the nuchal may be wider than (F0), or subequal (F2) to peripheral 1, while the nuchal is not as wide as peripheral 1 (F1) or subequal (F2) in *E. oneiros*.

Character G – Proximity of ABSS to rib 1: In the holotype of *E. lavarackorum* and in *E. dentata* the distance between the medial extremity of the ABSS terminus and distal extremity of rib 1 is substantially less than half the length of the ABSS (G0). In *E. oneiros* the distance is substantially greater than half the length of the ABSS (G1). As such, the condition in the holotype of *E. lavarackorum* is more similar to that in *E. dentata* than it is to the condition in *E. oneiros*. The specimen of *E. dentata* QM J59277, examined and illustrated here (Plate 1), is the specimen illustrated as Fig 2C-D by Thomson *et al.* (1997). In their photograph rib 1 cannot be discerned and in their schematic drawing rib 1 is shown significantly shorter than it is in reality.

Character H – Medial extremity of ABSS relative to intersection of the nuchal, peripheral 1 and costal 1: In the holotype of *E. lavarackorum* the medial extremity of the ABSS is almost directly posterior to the sutural intersection of the nuchal, peripheral 1 and costal 1, and the condition in *E. dentata* QM J59277 is similar (H0). This state is incorrectly portrayed in the schematic drawing of the specimen of *E. dentata* (QM J59277) presented by Thomson *et al.* (1997: - Fig. 2D). In *E. dentata* QM J59279, a longitudinal line running posterior to the nuchal-peripheral 1-costal intersection is positioned further medially, relative to the ABSS terminus (H1), than it is in QM J59277. In *E. oneiros* the character also conforms to H1. Thus, while the position of the medial extremity of the ABSS relative to the sutural junction of the nuchal, costal 1 and peripheral 1 serves to distinguish *E. oneiros* from the fossil holotype of *E. lavarackorum*, its use in inferring relationship between the holotype of *E. lavarackorum* and *E. dentata* s.s. is equivocal.

Character I – Portion of the internal width of peripheral 2 occupied by the ABSS: In the holotype of *E. lavarackorum* the distance between the anterior edge of ABSS and the suture of peripherals 1 and 2 is less than half the interior width of peripheral 2 (I0). In *E. dentata* this distance is variable but in both QM J59277 and QM J59279 it is greater than half the interior width of peripheral 2 (I1). The extent to which the ABSS extends across peripheral 1-costal 1 junction in QM J59277 (Plates 1 & 2) is more extensive than presented in the schematic drawing of that specimen in Thomson *et al.* (1997: Fig 2D) and is more similar to that of the fossil holotype of *E. lavarackorum*. In *E. oneiros* the extent of the ABSS across the peripheral 2-costal 1 suture is minimal, so that the distance between the anterior edge of ABSS and the suture of peripherals 1 and 2 is also greater than half the interior width of peripheral 2 (I1). In *E. oneiros* QM J46284 the anterior peripherals are partially disarticulated from costal 1 and this may have affected this measurement. The *E. oneiros* specimen shown in Plate 3 is entire and the distance is substantially greater than it is in either the *E. lavarackorum* holotype or in E. *dentata*. Hence, while the extent to which the ABSS extends along the peripheral 2 - costal 1 suture amply serves to distinguish *E. oneiros* from the fossil holotype of *E. lavarackorum*, its use in inferring relationship between the holotype of *E. lavarackorum* and *E. dentata* s.s. is equivocal.

Character J - ABSS-Nuchal: The fossil holotype of *E. lavarackorum* (Plates 1 & 2) has the ABSS first contacting costal 1 ('pleural 1' of Thomson *et al.* (1997) – see above) at the conjunction of posterior peripheral 2 and anterior peripheral 3 (as in all known *Elseya*), but this conjunction occurs at the same level as the junction of the lateral-most point of the nuchal (J0), at a point substantially more anterior of the costal/ nuchal than it is in either *E. dentata* or *E. oneiros* (J1).

Character K - ABSS Terminus-Base: In the fossil holotype of *E. lavarackorum* the ABSS terminus is marginally larger than the base (K0), and as large or marginally larger in *E. dentata* (K0), whereas in *E. oneiros* the ABSS terminus is noticeably smaller than the base and ends truncated (K1).

Character L - Shape of the medial extremity of ABSS: In the fossil holotype of *E. lavarackorum* the ABSS on costal 1 has a distinct medial constriction and terminates in an inflated, rounded bulb (L0) (see also our discussion of character B above), and is the condition also seen in E. *dentata*, whereas in *E. oneiros* the medial portion of the ABSS on costal 1 has minimal to no medial constriction and terminates in a reduced, non-inflated, finger-like truncated end (L1).

Character M - ABSS Terminus-Level: In the fossil holotype of *E. lavarackorum* the ABSS terminus lies just anterior to the 1st rib suture (M0), but lies medial-posterior orthogonally in

TABLE 1. Distribution of the character states (A-E = Thomson *et al.* (1997); F-N = this study) for specimens of *Elseya lavarackorum*, *E. oneiros* and *E. dentata*. Boldened character states differ from that scored by Thomson *et al.* (1997).

Taxon & Specimen	**Character State**													
E. lavarackorum QM F24121	A1	B3	C1	D2	E0	F2	G0	H0	I0	K0	J0	L0	M0	N0
E. oneiros QM J46284	A1	B2	C1	D2	E0	F1	G1	H1	I1	K1	J1	L1	M1	N1
E. oneiros JC collection	A1	B2	C1	D2	E0	F2	G1	H1	I1	K1	J1	L1	M1	N1
E. dentata QM J59277	A1	B3	C1	D2	E0	F0	G0	H0	I1	K0	J1	L0	M1	N1
E. dentata QM J59279	A1	B3	C1	D2	E0	F2	G0	H1	I1	K0	J1	L0	M1	N1

E. *dentata*, and medially-anterior orthogonally in *E. oneiros* (M1).

Character N - Nuchal shape: The greatest width of the nuchal of the *E. lavarackorum* holotype is slightly posterior to a point halfway along the length of the bone (N0). In *E. dentata* and *E. oneiros* the greatest width of the nuchal is at a point significantly greater than halfway along the length of the bone (N1).

The results of our analysis of characters A - E utilised by Thomson *et al.* (1997) and of the additional characters F - N presented here are summarised in Table 1 above.

The fossil holotype of *E. lavarackorum* differs from *E. oneiros* in nine to ten of the 14 characters assessed and shares only four to five character states. The extent of these differences strongly supports the two as representing distinct species.

The fossil holotype of *E. lavarackorum* agrees with *E. dentata* (QM J59277; QM J59279) in nine of the characters assessed and differs in five character states. Of the skeletal character states shared between these two taxa, the morphology of the axillary bridge suture in the holotype of *E. lavarackorum* indicates it is best assigned to the subgenus *Elseya* based on the criteria of Thomson *et al.* (2015).

Of the fourteen character states, the two skeletal specimens of *E. oneiros* examined shared 13 character states and differed in one, and the two skeletal specimens of *E. dentata* shared 12 character states and differed in two, indicating that multiple specimens should be investigated where possible to assess for any additional intraspecific variation.

Two features of the anterior carapace rim of the *E. lavarackorum* holotype (Plate 5) that also mark it as distinct from *E. oneiros* are revisited here. In the holotype of *E. lavarackorum* the anterior carapace rim is much broader than that of either extant *E. dentata* or *E. oneiros* and it has a distinct nuchal emargination (the shallow concave notch at the midpoint of the anterior carapace edge, previously assessed by Joseph-Ouni *et al.* 2020) that is present in some specimens of *Elseya dentata*, but which was not observed in any of the specimens of *E. oneiros* listed as examined by Joseph-Ouni *et al.* (2020) (11 in Appendix B, and eight additional specimens listed).

The presence of nuchal emargination in the holotype of *E. lavarackorum* was also addressed by Thomson *et al.* (1997) in support of a close (conspecific) relationship between the fossil *Emydura lavarackorum* and the extant form of *Elseya* from the Nicholson River, as follows:

> 'A significant feature of *Emydura lavarackorum*, though difficult to quantify, was an indentation of the carapace margin in the area of the cervical cleft and first marginal scutes. This feature is held in common with turtles in the *Elseya latisternum* group and *Pseudemydura*, is variable among the Queensland forms of *Elseya dentata*, and never present in the Northern Territory and New Guinea forms

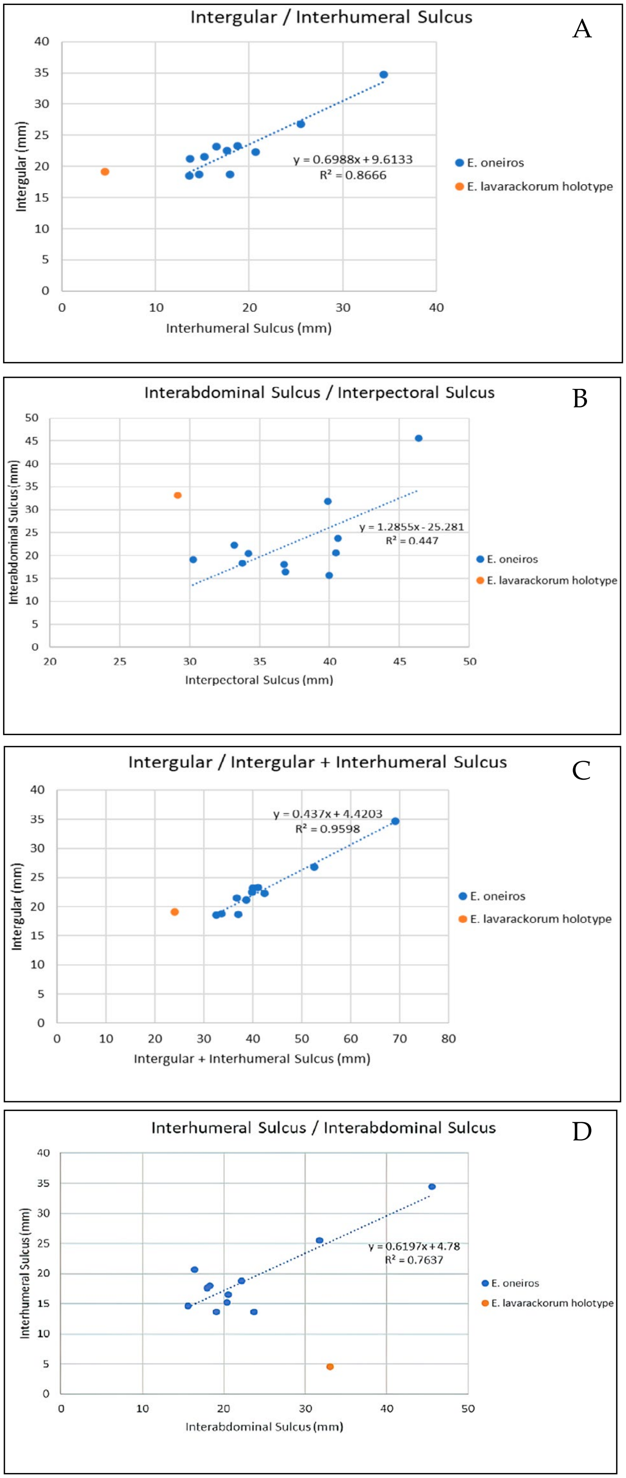

FIG. 1. *Elseya oneiros* is readily diagnosed from *E. lavarackorum* by the intergular length / interhumeral sulcus length ratio (d) (1.01-1.55 for *E. oneiros* n =11 vs 4.17 for *E. lavarackorum* holotype); the interabdominal sulcus length / interpectoral sulcus length ratio (e) (.39-.98 in *E. oneiros* n= 11 vs 1.13 in *E. lavarackorum* holotype); the intergular sulcus length / intergular + interhumeral sulcus length ratio (e) (0.50-0.58 in *E. oneiros* n= 11 vs 0.80 in *E. lavarackorum* holotype); the interhumeral sulcus length / interabdominal sulcus length ratio (e) (0.58 – 1.26 in *E. oneiros* n= 11 vs 0.14 in *E. lavarackorum* holotype). It is diagnosed from the northern Australian *Elseya dentata* group by the interhumeral sulcus length / interabdominal sulcus length ratio (0.58-1.26 in *E. oneiros* vs 0.11-0.20 in the *E. dentata* group) and from the Queensland *Elseya (Pelocomastes)* group by the genetic data presented in Georges & Adams, 1996 and Todd *et al.*, 2014.

FIGS 2A-D. **A)** Scatterplot showing the intergular length / interhumeral sulcus length ratio for *E. oneiros* and *E. lavarackorum*. **B)** Scatterplot showing the interabdominal sulcus length / interpectoral sulcus length ratio for *E. oneiros* and *E. lavarackorum*. **C)** Scatterplot showing the intergular sulcus length / intergular + interhumeral sulcus length ratio for *E. oneiros* and *E. lavarackorum*. **D)** Scatterplot showing the interhumeral sulcus length / interabdominal sulcus length ratio for *E. oneiros* and *E. lavarackorum*.

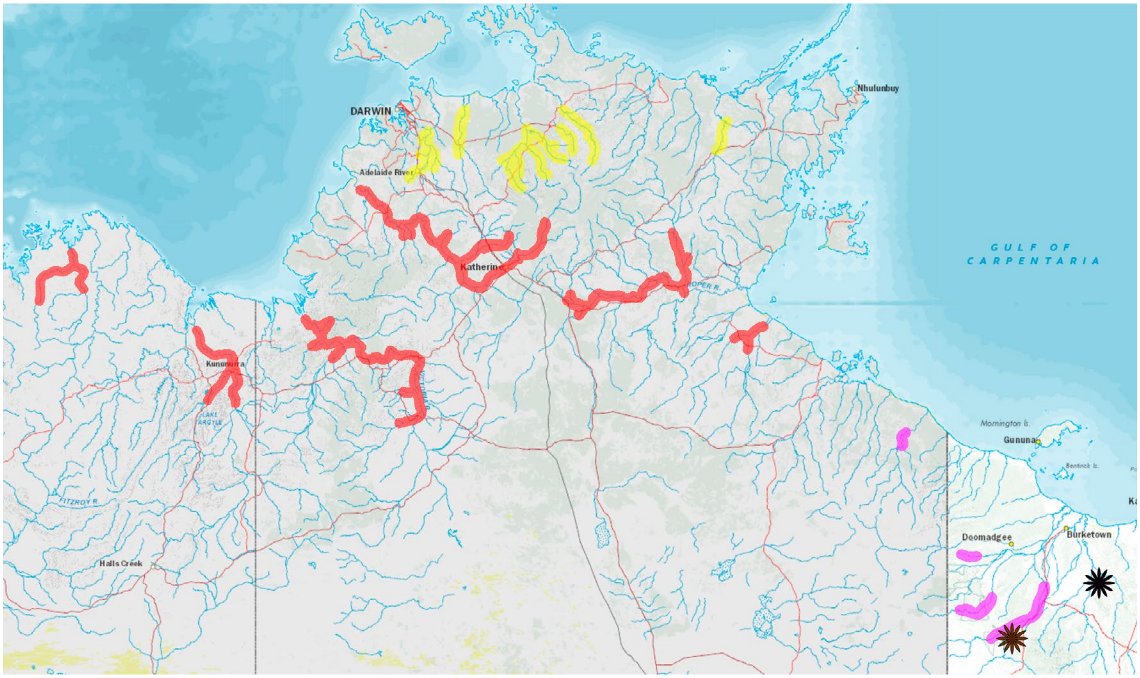

FIG. 3. Distribution of *Elseya* species in northern Australia: the species *E. dentata* (red) and *E. flaviventralis* (yellow) in the extant subgenus *Elseya*; the Pleistocene fossils, *E. lavarackorum* (brown star) and *E.* sp. Leichhardt (black stars); and *E. oneiros* (purple) in the extant subgenus *Pelocomastes*. Extant species distributions are restricted to confirmed museum and/or photographic identification with the exception of the populations of Western Australia and the Roper and Limmen rivers (Northern Territory which are under investigation (also see TTWG 2021), and also include field identifications by J. Cann and A. Freeman; distributions assumed to eventually be broader with further data. *E. (E.)* sp. Leichhardt refers to a new Pleistocene fossil species (description *in. prep.* by A. White). Base map © State of Queensland 2020.

> of *Elseya dentata* nor in *Elusor, Rheodytes* and *Emydura*. Although not considered a useful character at generic level, we will use it in combination with other similarities to establish a close relationship between the fossil *Emydura lavarackorum* and an extant form of *Elseya* from the Nicholson River.’

We agree that nuchal emargination is difficult to quantify (although it has been used repeatedly as a key character in the diagnosability of fossil chelonian species - MJO, AW pers. obs., see also Joyce and Lyson (2015) and Maniel and de la Fuente (2016). However, our observations on this feature (Joseph-Ouni *et al.*, 2020) are not in concordance with those presented by Thomson *et al.* (1997). We do not regard it as providing evidence in support of a close relationship between the fossil holotype of *E. lavarackorum* and the extant *Elseya* from the Nicholson River, *E. oneiros* (Plate 5). The observation offered by Thomson *et al.* (1997) that the nuchal emargination is “never present in the Northern Territory and New Guinea forms of *Elseya dentata*” is incorrect for the Northern Territory, as illustrated for *E. dentata* by Joseph-Ouni *et al.* (2020). As nuchal emargination does indeed occur invariably in *E. dentata*, we point to this shared occurrence with the holotype of *E. lavarackorum* as indicative of a closer relationship with that extant taxon, not with *E. oneiros*. As *E. dentata* does not occur in New Guinea, our assumption for the ‘New Guinea’ form is in reference to the

New Guinea endemic *E. branderhorsti*, and we confirm here that nuchal emargination is absent in that species (pers. obs. MJO).

Lastly, we note that the TTWG (2021), citing an unpublished, private report by Georges *et al.* (2021), extended the range of *E. oneiros* (under the nomen *E. lavarackorum*) into the upper reaches of the Roper River, Northern Territory. Additionally, that same report concluded that the *Elseya dentata* population of the Roper and Limmen rivers (the two species being found in microsympatry in the Roper) constituted a distinct species based on genetic analysis. The taxonomy of *Elseya* species in northern Australia is currently under investigation (Joseph-Ouni *et al.*, in prep.), and a distribution map of the current taxonomy of *Elseya* in northern Australia (Figure 3) is presented here pending further data.

CONCLUSION

The diagnostic scute characters presented in Joseph-Ouni *et al.* (2020) in combination with the differentiation in skeletal characters presented here confirm the distinction made between the fossil holotype of *E. lavarackorum* and *E. oneiros*, and that the two species are not conspecific. We again validate *Elseya* (*Pelocomastes*) *oneiros* as the only extant *Elseya* occurring in the Nicholson-Gregory drainages, as represented by the holotype (QMJ 47908, an adult male collected from Elizabeth Gorge, Bowthorn Station, Queensland, Australia on the 23 April 1988) lodged in the herpetological collection of the Queensland Museum (Plate 6).

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