RE-EVALUATION OF *EMYDURA LAVARACKORUM*: IDENTIFICATION OF A LIVING FOSSIL

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Post-cranial osteological characters can be used to diagnose Australian short-necked chelid turtles to genus. Morphological examination of the Pleistocene fossil *Emydura lavarackorum*, from Riversleigh, shows that it is aligned with the genus *Elseya* not *Emydura* and should be referred to as *Elseya lavarackorum* (White & Archer, 1994). Furthermore, the fossil specimen is not distinguishable from an undescribed extant form of *Elseya* from the Nicholson drainage, with which it shares one unique feature so this name should apply also to this extant form, identified to date only from electrophoretic data. It is Australia's first living fossil turtle, an extant population of a Pleistocene taxon. ☐ *Chelonia, Chelidae, Pleistocene, fossil, turtle.*

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The taxonomy of Australian chelid turtles is poorly known and in dire need of review (Cogger et al., 1983). Recent electrophoretic surveys (Georges & Adams, 1992; 1996) have revealed that in some instances, currently accepted species boundaries are difficult to justify and in others, what are currently regarded as single species are in fact two or more. The detailed morphological analyses required to verify these findings have not been conducted (but see Thomson & Georges, 1996), and until recently it was not possible to distinguish even between extant short-necked genera on the basis of osteological characters (Gaffney, 1977). This paucity of osteological data suitable for distinguishing the extant genera makes the identification of fossil forms, most of which are incomplete specimens, difficult. In many instances, chelid fossils have been assigned to either *Chelodina* or *Emydura*, with little or no evidence presented to eliminate the possibility that the short-necked forms among them may be *Elseya*, *Rheodytes* or *Elusor*.

In 1994 a partial carapace and associated plastron from Riversleigh was described as a new species, *Emydura lavarackorum*, by White & Archer (1994). The fossil specimen was from Terrace Site, a fluviatile site on the Gregory River. These authors interpreted the sediments as being Pleistocene in age because of the presence of remains of *Diprotodon optatum* (White & Archer, 1994). The holotype consists of the anterior half of the carapace with some anterior peripherals and an essentially complete plastron with some pelvic material present. The length of the plastron is 390mm (White & Archer, 1994) which corresponds to a carapace length of approximately 420mm. Two other plastra from the same site were also collected but not described.

White and Archer (1994) assigned the specimen to *Emydura* on the mode of the insertion of the anterior bridge into the ventral surface of the carapace. They found that in the derived state, the anterior bridge is angled steeply backwards towards the rib/gomophosisis (called transverse process in White & Archer, 1994), whereas in all other chelids the anterior bridge was found to form a continuous line with the rib/gomophosisis.

In this paper, we reassess the generic assignment of the fossil by comparing the fossil material with post-cranial character states we have found useful in separating extant genera of Australian short-necked chelid turtles. We also propose that the fossil taxon is extant, a distinctive, undescribed form closely aligned with *Elseya dentata*.

MATERIALS AND METHODS

Specimens of each of the short-necked species identified using electrophoresis by Georges and Adams (1996) were obtained from museums, the Conservation Commission of the Northern Territory and the University of Canberra. Where forms have not been included in published keys or descriptions, the specimens were selected from those lodged as vouchers to accompany the elec-

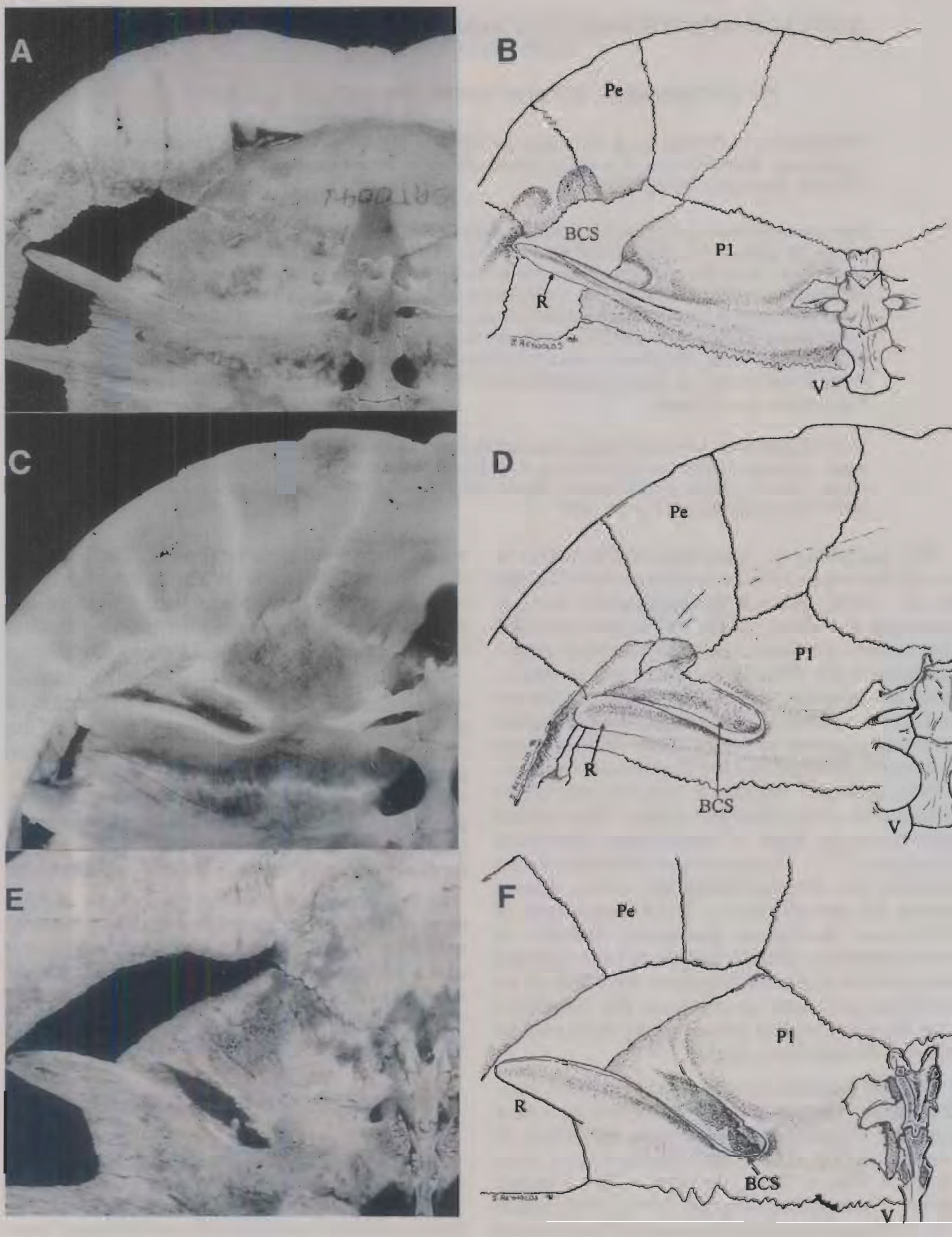

FIG. 1. Ventral view of the anterior carapace of short-necked turtles showing the bridge-carapace suture (BCS) the rib/gomophosisis (R) on pleural 1 (Pl) and their relationship to the vertebral column (V) and the peripherals (Pe). A-B, *Pseudemydura* (UC0178). C-D *Elseya* sp. aff. *E. latisternum* (Manning) (QM59289); E-F, *Elusor macrurus* (UC0184).

trophoretic data. The specimen collection was supplemented by limited field sampling.

Each specimen was skeletonised by removing excess soft tissue and feeding the remaining carcase to dermestid beetles. The skeletal material was bleached in 5% sodium hypochlorate solution, and the process stopped by immersion in 100% ethanol. Plastra were separated from carapaces by disarticulating the plastral-carapacial suture between the hyo- and hypoplastra of the plastron and the lateral peripherals of the carapace. This was done by the carefully heating the carapace until the sutures become mobile and the plastron was then gently prised off. This also required disarticulation of the pelvis from the carapace. Characters potentially diagnostic at the generic level were examined to establish their consistency across a range of specimens within the polytypic genera *Elseya* and *Emydura*, and across a range of specimens within each species.

The fossil specimens of *Emydura lavarackorum* were examined to determine the presence of character states which are generically diagnostic in extant taxa. The fossil specimen was then assigned to genus.

Throughout this paper, we refer to a generic group as a group of species that are sufficiently distinct collectively to warrant recognition at the level of genus, though this has not yet been formally established. These groups were first identified by Legler (1981), have a foundation in electrophoretic studies (Georges & Adams, 1996), and have been referred to since several times in the literature. In contrast, a species complex is a group of species, all but one of which are undescribed, which together presumably represent a distinct clade but which are not considered distinctive enough to warrant recognition at the level of genus.

We refer to the *Elseya dentata* species complex as comprising the distinctive forms of *Elseya* from coastal Queensland currently assigned to *Elseya dentata*, and the Northern Territory forms including *Elseya dentata* (sensu stricto) and *Elseya* sp. aff. *E. dentata* from the Alligator Rivers region (Georges & Adams, 1996). The *Elseya dentata* generic group (sensu Legler, 1981) comprises the *Elseya dentata* species complex plus *Elseya novaeguineae* and *Elseya branderhorsti* from New Guinea. The *Elseya latisternum* generic group comprises *Elseya latisternum* (sensu stricto), a related form from the headwaters of the Darling River drainage and a sibling species pair from coastal New South Wales (Georges & Adams, 1996; Thomson & Georges, 1996). The later three are currently undescribed. It is not the purpose of this paper to describe new genera, so for consistency, we use the nomenclature of Georges & Adams (1992) and Legler (1981) and recognise six groups of Australian short-necked chelid at generic level: *Elusor*, *Emydura*, *Rheodytes*, *Pseudemydura*, the *Elseya latisternum* generic group and the *Elseya dentata* generic group.

Throughout this paper, names of the bony elements of the shell and the overlying scutes follow those of Zangerl (1969). A complete list of the specimens examined in this study will be found in Appendix A.

RESULTS

Five characters were identified as diagnostic at generic level. Where polarity is indicated, it was determined by comparison with South American chelids and African pelomedusids in a cladistic analysis (Thomson & Georges, unpublished data). Only those characters relevant to the identification of the fossil specimen are presented.

ANTERIOR BRIDGE STRUTS. Character A. Contact with Pleural 1.

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/gomophosisis 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.

B1. 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).

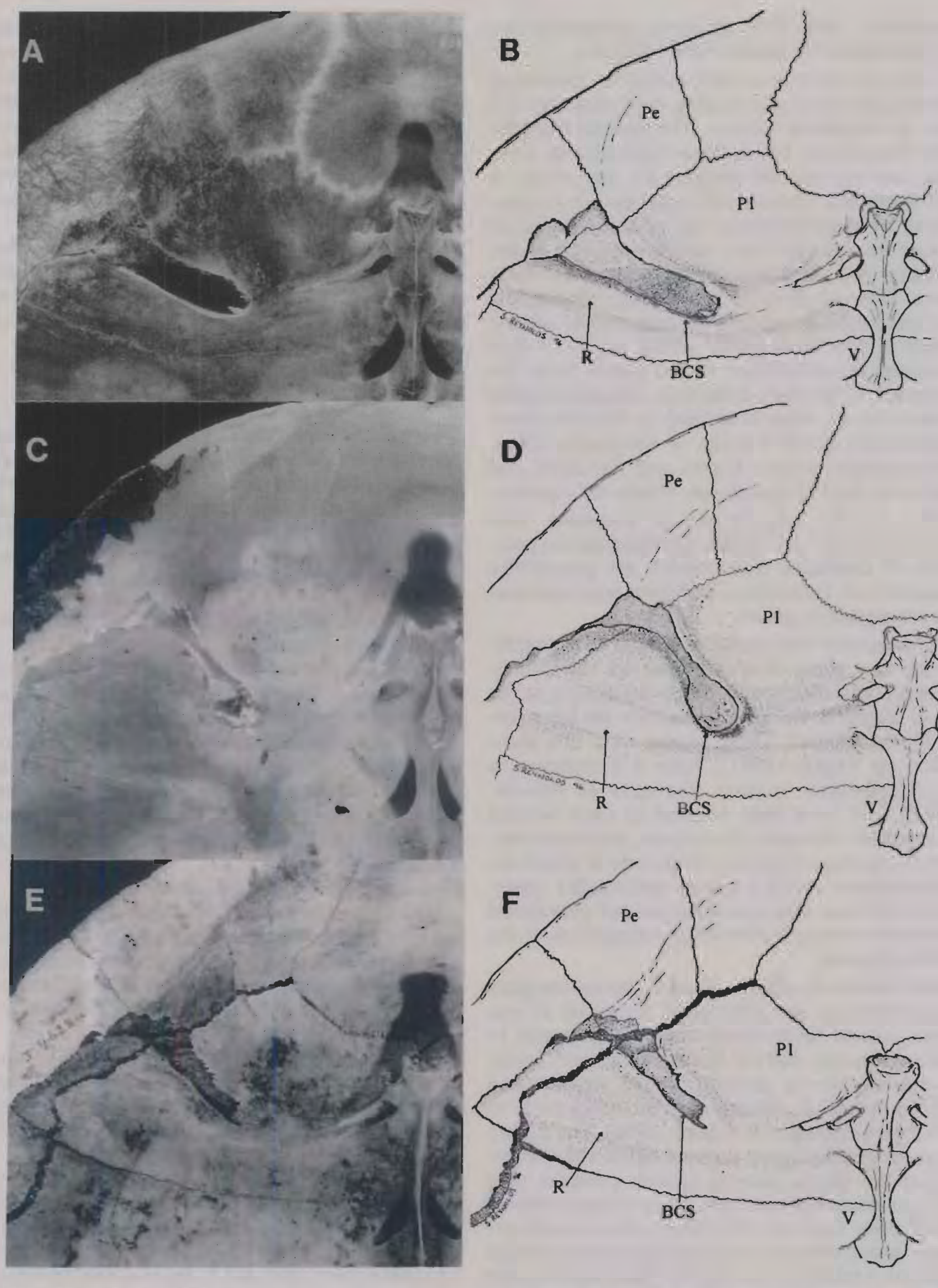

FIG. 2. Ventral view of the anterior carapace of short-necked turtles showing the bridge-carapace suture (BCS) the rib/gomophosisis (R) on pleural 1 (Pl) and their relationship to the vertebral column (V) and the peripherals (Pe). A-B, *Rheodytes leukops* (UC0173). C-D, *Elseya dentata* (QM59277). E-F, *Elseya lavarackorum* (extant) (QM46284).

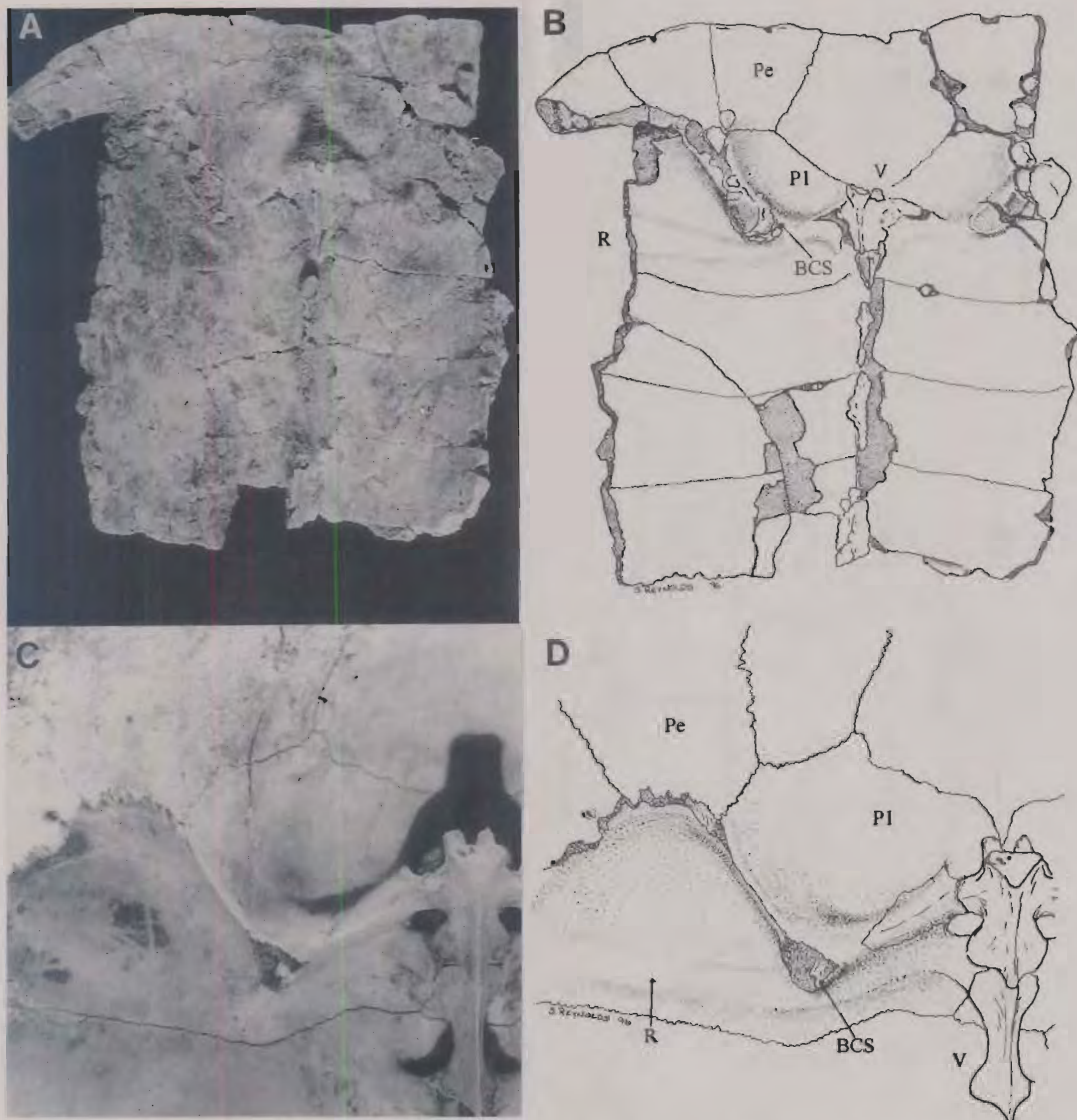

FIG. 3. Ventral view of the anterior carapace of short-necked turtles showing the bridge-carapace suture (BCS) the rib/gomophosisis (R) on pleural 1 (Pl) and their relationship to the vertebral column (V) and the peripherals (Pe). A-B,*Elseya lavarackorum* (fossil) (QM24121). C-D, *Emydura subglobosa* (UC0172).

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).

DORSAL CHARACTERS. Character D. Relative width of Vertebral 1.

D1. 1st 3 vertebral scutes equal or subequal in width (Figs 4A-D, 5B).

D2. 1st vertebral scute wider than 2nd and 3rd (Figs 4E-F, 5A).

Character E: Cervical Scute.

E0. Cervical scute typically present (Fig. 5B).

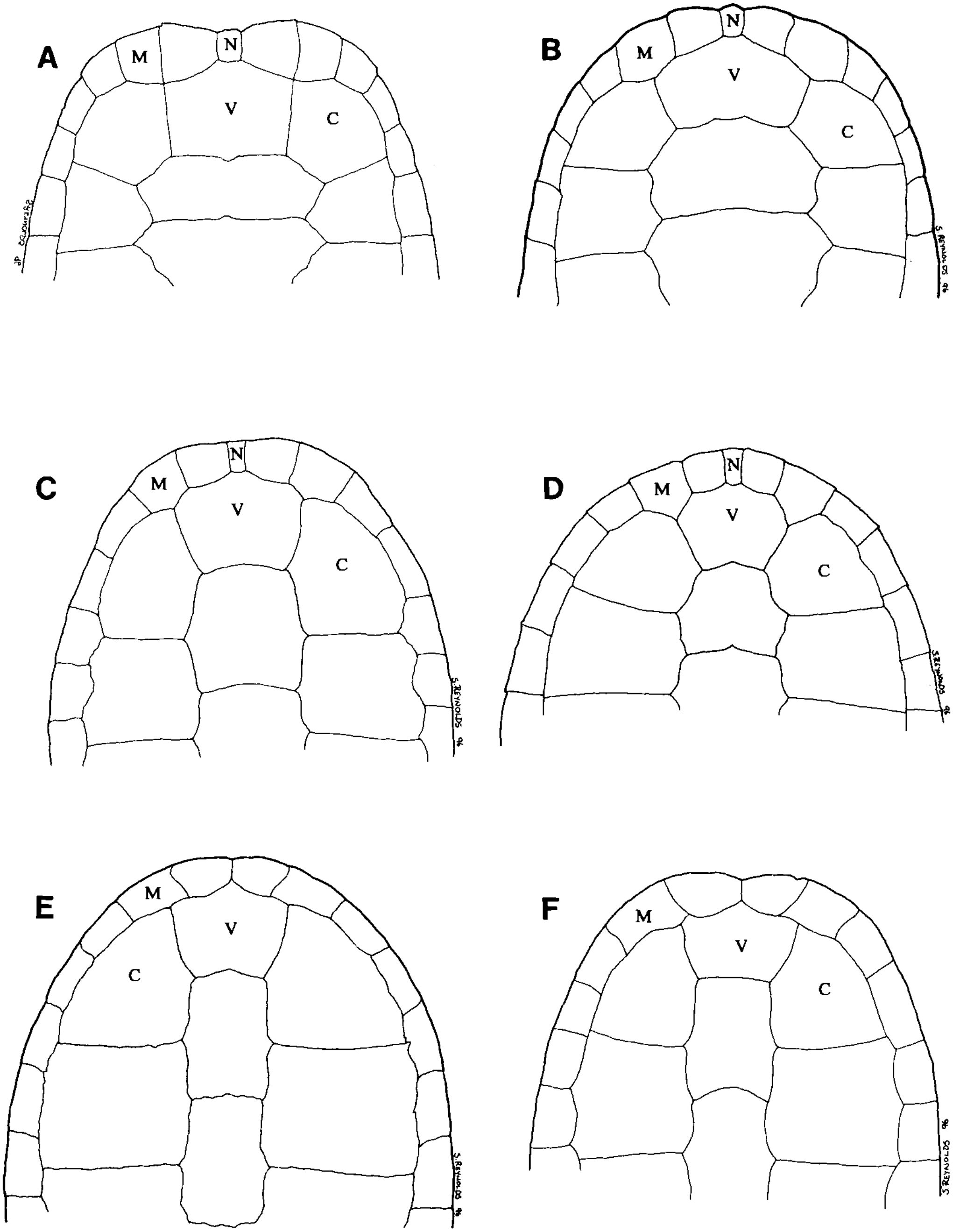

FIG. 4. Dorsal view of the anterior carapace of short-necked turtles showing the relative size between the vertebral scutes (V) and the presence or absence of the cervical scute (N) their relationship to the costal scutes (C) and marginals (M). Note the indentation at the anterior of some taxa. A, *Pseudemydura* (UC0178). B, *Elseya* sp. aff. *E. latisternum* (Manning) (QM59289). C, *Elusor macrurus* (UC0344). D, *Rheodytes leukops* (UC0173). E, *Elseya dentata* (QM59277). F, *Elseya lavarackorum* (extant) (QM46284).

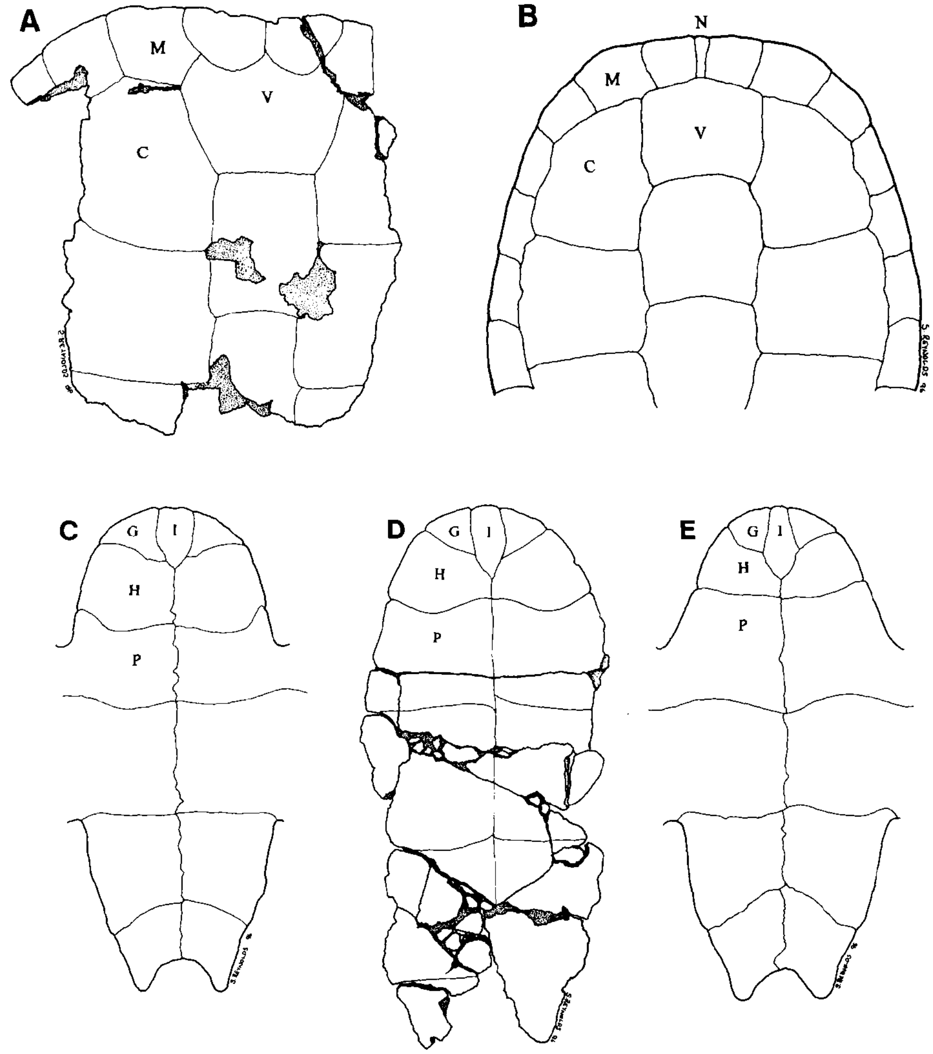

FIG. 5. A-B, Dorsal view of the anterior carapace of short-necked turtles showing the relative size between the vertebral scutes (V) and the presence or absence of the cervical scute (N) their relationship to the costal scutes (C) and marginals (M). Note the indentation at the anterior of some taxa. A, *Elseya lavarackorum* (fossil) (QM24121). B, *Emydura subglobosa* (UC0172). C-E, Ventral view of the plastrons showing the arrangement of the sulci between the humeral (H) and pectoral (P) scutes, also shown are the gular scutes (G) and the intergular (I). C, *Elseya lavarackorum* (extant) (QM46284); D, *Elseya lavarackorum* (fossil) (QM24121). E, *Elseya dentata* (QM59277).

E1. Cervical scute typically absent (Figs 4E-F, 5A).

The distribution of the character states for each taxon is provided in Table 1. The holotype *Emydura lavarackorum* had a combination of a widely divergent angle (45°) between the anterior bridge suture and the rib/gomophosisis of pleural one; parallel anterior and posterior edges of the bridge-carapace suture throughout their length, widely spaced, with no medial constriction; no distal rotation of the gomophosisis of pleural one;

TABLE 1. Character matrix. Distribution of the key character states among taxa. Abbreviations (s = no. of species examined in group, n = no. of specimens), polymorphic characters shown: Pseud, *Pseudemydura*; Elat, *Elseya latisternum* group; Elus, *Elusor*; Rheo, *Rheodytes*; Else, *Elseya dentata* group; Elno, *Elseya novaeguineae*; EQld, Queensland *Elseya* group; Elav, *Elseya lavarackorum* (holotype); Emyd, *Emydura*.

Taxa	Pseud (s=1) (n=2)	Elat (s=4) (n=20)	Elus (s=1) (n=18)	Rheo (s=1) (n=1)	Else (s=2) (n=25)	Elno (s=1) (n=2)	EQld (s=3) (n=10)	Elav (s=1) (n=1)	Emyd (s=4) (n=28)
Character A	0	0	0	1	1	1	1	1	1
Character B	1	1	1	2	3	3	2	2	4
Character C	0	0	0	0	1	1	1	1	1
Character D	1	1	1	1	2	2	2	2	1
Character E	0	01	0	0	1	0	1	1	0

a first vertebral scute that was markedly wider than vertebrals 2 and 3; and no cervical scute.

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 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.

DISCUSSION

The bridge carapace suture runs parallel and adjacent to the rib/gomophosisis in species of the *Elseya latisternum* group, *Pseudemydura* and *Elusor* and so can be clearly distinguished from the fossil *Emydura lavarackorum* (Table 1). Rotation of the rib/gomophosisis of Pleural 1 eliminates *Rheodytes* as a possible identification for the fossil, leaving only the *Elseya dentata* generic group and *Emydura* as possibilities.

Two sub-groups within the *Elseya dentata* generic group can be distinguished. The first comprises *Elseya dentata* (sensu stricto), *Elseya novaeguineae*, *Elseya branderhorsti*, and *Elseya* sp. (Vogelkopf Region, PNG; Anders Rhodin, pers. comm) and *Elseya* sp. (South Alligator River, NT; Georges & Adams, 1996). The second sub-group is restricted to Queensland (Queensland *Elseya dentata* sub-group) and comprises *Elseya* sp. (Nicholson), *Elseya* sp. (Johnstone), and *Elseya* sp. (Burnett) (Georges & Adams, 1996). Generic recognition of these sub-groups is not suggested.

Emydura lavarackorum possesses all characters that are consistent across species of the *Elseya dentata* generic group (Table 1) and, more significantly, all characters uniquely possessed by the Queensland *Elseya dentata* sub-group (Table 1). Of those characters which separate *Emydura* from the *Elseya dentata* generic group, the fossil consistently possessed character states which distinguished it from *Emydura*. Therefore, we assign *Emydura lavarackorum* to the genus *Elseya* as *Elseya lavarackorum* (White & Archer, 1994).

Since the description of *Elseya lavarackorum*, specimens of the extant *Elseya* sp. (Nicholson drainage, Georges & Adams, 1996) have become available. The two forms are indistinguishable in every diagnostic character, including the indentation of the anterior margin of the carapace. A unique feature of the Nicholson population, when only extant forms are considered, is the sigmoidal shape of the sulcus between the humerals and pectorals on the plastron (Fig. 5C), this sulcus is straight in all other species of the *Elseya dentata* generic group (Fig. 5E). This feature is present in the holotype of *Elseya lavarackorum* (White & Archer, 1994) and in one (QM30818) of the additional fossil specimens now available (Fig. 5D). The anterior plastron is absent from the third fossil specimen (QM30817).

In contrast, the fossil has strongly embossed, rounded peripherals in the region adjacent to the bridge, a feature not present in the 15 specimens from the Nicholson population. This is a similar condition to that found in aged, adult individuals in a number of species, i.e., individuals which are large for their species, such as *Elusor macrurus* (specimens over 400mm), *Elseya* sp. aff. *E. dentata* from the Burnett River (specimens over 380mm) and *Emydura subglobosa* from the Gregory and Reynolds Rivers (specimens over 250mm). We consider this trait to be essentially a feature of large aged specimens in a range of chelid turtles. None of the turtles examined from the Nicholson drainage had carapace lengths in excess of 320mm, well below the maximum size for species in the *Elseya dentata* generic group.

In species level taxonomy, the onus is on differential diagnosis. The shell of the fossil holotype is adequately preserved for diagnostic purposes. We therefore propose that, in the absence of any diagnosable difference and the relatively young age of the fossil material, *Elseya lavarackorum* and the Nicholson *Elseya* sp. aff. *E. dentata* be regarded as a single species. It is Australia's first living fossil freshwater turtle, an extant population of a Pleistocene taxon. We do not propose that allochronic subspecies be recognised.

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APPENDIX A

Specimens Examined: All names used for undescribed species are from Georges & Adams (1992, 1996). Abbreviations used: AM, Australian Museum; NTM, Museum and Art Galleries of the Northern Territory; QM, Queensland Museum; WAM, Western Australian Museum; UC, University of Canberra; UM, University of Michigan Field Series; UU, University of Utah.

Elusor macrurus: UC0184-93, 0225-29, 0344, UU19488, 19508; *Elseya dentata*: NTM13319, 13521, 16330, QM59265, 59277-80, UC0307-18; *Elseya latisternum*: AM123037, 123039, 125474-75, QM48054-55; *Elseya novaeguineae*: AM42662, 125038; *Elseya lavarackorum*: QMF24121, F30817-18 (fossil), QM31939, 31942, 31944, 31946-47, 31949-50, 31952, 46284, 47908, 47911, 48544, 48547, 60255, UC0201 (extant); *Emydura macquarii*: QM48016, 48034, 48050-51, 59275-76, UC0175-76, 0303; *Emydura subglobosa*: NTM5028, 8206, 13428, 13433, 16332, UC0171-72, 0177; *Emydura victoriae*: NTM13513-14, 32917, 32976, UC 0165; *Elseya* sp. aff. *E. dentata* (Burnett): UC 0305-6, QM2966, 28449, 36036, 36039, 36041-42, 36044-47, 37933, 38533, 59269-71; *Elseya* sp. aff. *E. dentata* (Johnstone): QM22694, 23175, 23299, 23300, 23322, 24938, 28449, 48060, 48068; *Elseya* sp. aff. *E. dentata* (South Alligator): AM128002, 128004, QM59285-89, NTM5097, 13512, 13985, UC0304; *Elseya* sp. aff. *E. latisternum* (Gwyder): AM123028-29, QM 48028, 48038; *Elseya* sp. aff. *E. latisternum* (Bellingen): AM138387-88, UM02016-17; *Elseya* sp. aff. *E. latisternum* (Manning): AM123040, 123042, QM-59289-90; *Emydura* sp. aff. *E. victoriae* (Daly Mission) AM125470-71, 125491, NTM8211, 8213, 17339; *Pseudemydura umbrina*: UC0178, WAM29337; *Rheodytes leukops*: UC0173.