



***Myuchelys* gen. nov. —a new genus for *Elseya latisternum* and related forms of Australian freshwater turtle (Testudines: Pleurodira: Chelidae)**

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Abstract

Myuchelys, a new genus, is erected for a well supported clade of Australasian freshwater turtles; its establishment resolves an unacceptable paraphyly in relationships among species of the genus *Elseya*. Molecular and morphological evidence indicates that the closest relationship of the new genus is with *Emydura*, not the redefined *Elseya*.

Key words: Phylogeny; paraphyly; side-necked turtle; sawshelled turtle

Introduction

The genus *Elseya* has had a long and confused history. It was erected by Gray (1867) for the species *Chelymys* [now *Elseya*] *dentata* Gray, 1863 and *Elseya latisternum* Gray 1867. *Elseya dentata* was later designated as the type species (Lindholm, 1929). The genus was diagnosed by the presence of a horny shield on the dorsal surface of the head; flat polygonal plates on the temples, cheeks and throat; prominent tubercles on the dorsal surface of the neck; a pair of tubercles on the chin; and the usual absence of a cervical scute (Gray, 1867; Gray, 1872). Boulenger (1889) redefined the genus, placing significance on the alveolar ridge (a longitudinal ridge on the triturating surface of the maxillary sheath and underlying bone) as a character, then known to be present only in *Elseya dentata*. *Elseya latisternum* and *Elseya novaeguineae* (Meyer, 1874) lack the alveolar ridge, and so Boulenger placed them in the genus *Emydura*. Later, Goode (1967) disagreed with the importance placed on the alveolar ridge, noting that well-established cryptodiran genera displayed considerable variation in this character, and returned *E. latisternum* and *E. novaeguineae* to the genus *Elseya*.

Elseya novaeguineae, *Emydura signata* Ahl, 1932 and *Emydura subglobosa* (Krefft, 1876), as defined in 1980, were virtually indistinguishable using total serum protein electrophoresis and were very closely related to *Elseya latisternum* (Frair, 1980). Their karyotypes are identical, with a diploid number of 50 (Bull & Legler, 1980), and Gaffney (1977) could not consistently differentiate the various taxa using skull morphology. McDowell (1983) considered a wide range of morphological characters and concluded that the closest relatives of *Elseya dentata* are among the species of *Emydura*, not *Elseya latisternum*. Frair (1980), Gaffney (1977), and McDowell (1983) all argued for synonymising *Emydura* and *Elseya*, but that recommendation has not gained wide acceptance. The paraphyletic arrangement of species within *Elseya* was well established with the addition of molecular evidence (Georges & Adams, 1992; Seddon, *et al.*, 1997; Georges, *et al.*, 1998) and the descriptions of *Elusor* (Cann and Legler 1994) and *Rheodytes* (Legler and Cann 1980) (see Megirian & Murray, 1999).

The purpose of this paper is to resolve the unacceptable paraphyletic relationship among the species of *Elseya* by splitting them into two monophyletic genera.

***Myuchelys*, gen. nov.**

Type species. *Elseya latisternum* Gray, 1867 designated herein.

Etymology. The name is a combination of a contraction of the Aboriginal word for clear water, Myuna, and the Greek word for tortoises, *chelys*. It is a generalised reference to the types of habitat often preferred by the species of this genus.

Diagnosis. A member of the short-necked chelid turtles of the Australasian region which, excluding *Pseudemydura umbrina* (Siebenrock, 1901), together form a well-established clade (Georges & Adams, 1992; Georges, *et al.*, 1998). Differs from other short-necked turtles of the clade in possessing the following combination of characters (Table 1): Absence of a well-developed alveolar ridge on the triturating surfaces and underlying bones of the jaw (Fig. 1B) (present only in the redefined *Elseya*, Fig. 1A); parietal arch of skull wide, nearly as wide as tympanum (Fig. 2) (narrower than the tympanum in *Elseya* and *Emydura*); large distinctive head shield, entire, that extends in part down the parietal arch toward the tympanum (absent in *Emydura*, not extending down the parietal arch in *Elseya*, *Rheodytes* and *Elusor*); ilium-carapace suture involves pleurals 7–8 and the pygal (as in *Elusor* but distinct from the condition in *Elseya* and *Emydura*); anterior bridge strut is confluent with the rib-gomphosis of pleural one; no angle of intersection between these two bony units when viewed ventrally (as in *Elusor*, but unlike *Elseya*, *Emydura* and *Rheodytes* – see Fig. 1 and 2 of Thomson, *et al.*, 1997).

Description. Medium-sized turtles with a broadly oval carapace that is dorso-ventrally flattened and dark brown to black in colour, depending on species. Cervical scute typically present, though present only as a rare variant in most populations of *M. latisternum* north of the NSW–Queensland border (Legler & Cann, 1980). Plastron narrow, anterior lobe distinctly wider than posterior lobe. Plastron grey, light cream or yellow often with dark streaking or blotching, especially at the leading growth edge of plastral scutes and ventral surfaces of the marginal scutes. Intergular scute highly variable, but typically as wide as the adjacent gulars. Bridge carapace suture is narrowest medially and at its widest on the peripheral edge of the bridge strut region. Rib-gomphosis of pleural five inserts into the centre of peripheral seven; ilium-carapace suture involves pleurals seven, eight and the pygal bone. Parietal arch of skull is wide, nearly as wide as tympanum; crista supraoccipitalis short does not extend past crista paroccipitalis. Lingual ridge small, unmodified.

Species. *Myuchelys latisternum* (Gray, 1867), *M. georgesi* (Cann, 1997; *Elseya* [var. Bellinger] in Georges & Adams, 1992;1996), *M. purvisi* (Wells & Wellington, 1985; *Elseya* [var. Manning] in Georges & Adams, 1992;1996) and *M. bellii* (Gray, 1844; *Elseya* [var. Gwydir] in Georges & Adams, 1992;1996, resurrected by Cann, 1998) are assigned to the new genus. Molecular analyses by Georges and Adams (1992; 1996) verified the validity of each of these as biological species and showed that they formed a distinct clade. *Myuchelys purvisi* and *M. georgesi* are cryptic species (Georges & Adams, 1996; Thomson & Georges, 1996) differing overtly only in intensity of colouration.

Distribution. Species of *Myuchelys* are found in the coastal rivers of northern New South Wales north to Cape York and west to the Arnhem Land plateau of the Northern Territory (Georges & Thomson, 2009). *Myuchelys bellii* is restricted to the tributaries of the Murray-Darling drainage basin that flow west from the Great Dividing Range in northern New South Wales. *Myuchelys georgesi* and *M. purvisi* are restricted to the Bellinger and Manning Rivers of coastal New South Wales, respectively. *Myuchelys latisternum* is the most widespread, ranging from the Richmond River (NSW) in the south to the Jardine River of Cape York in the north (Qld). Its distribution includes also the rivers that flow into the Gulf of Carpentaria and the headwater tributaries that drain the Arnhem Land plateau into the Roper, South Alligator and Daly Rivers of the Northern Territory. An isolated population is known from the headwaters of the Mary River in the Northern Territory in Kakadu National Park.

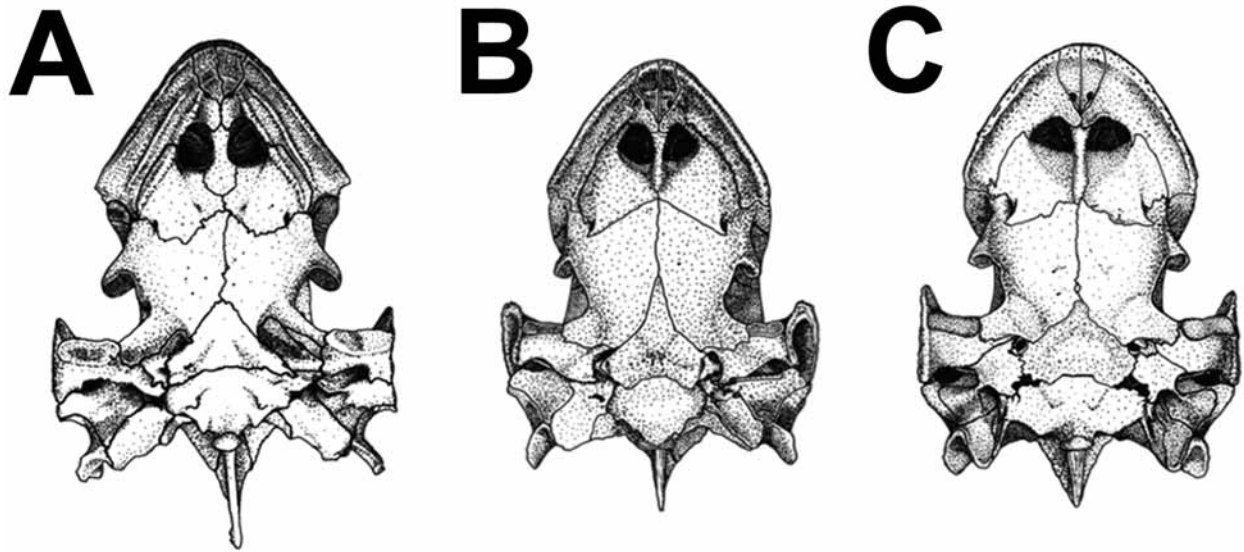


FIGURE 1. Ventral view of the skulls of **A.** *Elseya dentata* (UC0302); **B.** *Myuchelys latisternum* (AM 125475) and **C.** *Emydura macquarii* (QM48034). Note the alveolar ridge on the maxillary surface of *Elseya dentata*.

Habitat. Known from the middle reaches of the rivers they occupy, but greatest abundances for all species of *Myuchelys* occur in the upper reaches and tributaries of the drainage basins they occupy, often above escarpments that exclude other riverine species.

Relationships. Georges and Adams (1992) established the relationships among the four species of *Myuchelys*. Despite being a cryptic species pair, *Myuchelys georgesii* and *M. purvisi* are not sister species, and indeed their common ancestor has all species of *Myuchelys* as its descendents. This suggests that many of the characters jointly possessed by these two species are plesiomorphic for the genus.

Relationships between *Myuchelys* and the other short-necked genera are less clear, so we undertook a morphological analysis to complement the prior analyses of molecular data (Georges & Adams, 1992; Georges, *et al.*, 1998). Cladistic analysis of 45 characters (Appendix) from the extant genera of short-necked Australian chelids yielded a phylogeny with strong bootstrap support for all major nodes (Fig. 2). One tree of 69 transitions in length was shorter than all others, with the next shortest trees (n=3) 71 transitions in length. Genera received at least 74% bootstrap support. The paraphyly of the genus *Elseya*, as previously defined, is clearly evident.

Specimens examined. Abbreviations: AM, Australian Museum; NHM, Natural History Museum (BMNH); NTM, Museum and Art Gallery of the Northern Territory; NWC, National Wildlife Collection; QM, Queensland Museum; UC, University of Canberra; UM, University of Michigan Field Series.

Chelodina expansa*:** UC 2099, Albury (36°05'S, 146°55'E); UC 2074, 2190-94, Mungabareena Reserve, Albury (36°06'S, 147°00'E). ***Chelodina longicollis*:** QM 59266, UC 0199, Hawkesbury River (33°45'S, 150°42'E); QM 59267-68, 59281-2, Jervis Bay (35°08'S, 150°42'E); QM 59274, UC 0134, 0164, 0169, Canberra (35°17'S, 149°08'E); UC 0166, Oasis Creek, Dubbo (32°15'S, 148°36'E); UC 0174, Mumbar, Near Rockhampton (23°23'S, 150°31'E). ***Chelodina colliei*:** QM 59272-73, 59283, Perth (31°56'S, 115°50'E); UC 0161-63 Perth, (31°56'S, 115°50'E). ***Elseya albagula*:** QM 48012, 48046, Burnett River, near Gayndah (25°37'S, 151°37'E). QM 47987, 47998, 48002, 48010, Dawson River, Theodore (24°57'S, 150°05'E); AM 123067, Grey's Waterhole, Burnett River (25°32'S, 151°39'E); UC 0305-06 Mary River. ***Elseya branderhorsti*:** UC 0334, Maurauke River, Irian Jaya. ***Elseya dentata*:** AM 72692-94, 72934-46, 73346, 79160, Bullo River at crossing of Katherine-Kununurra Road (15°42'S, 129°38'E); NTM 17201, 17205-06, 17210, UC 0309-19, 0328, Douglas River (13°47'S, 131°17'E); ***Elseya dentata [var. South Alligator, sensu

Georges & Adams, 1992;1996]: UC 0304, Corroboree Billabong, Mary River; NWC 0531, Deaf Adder Creek (13°04'S, 132°58'); AM 128001-04, Magela Creek; NTM 13985, Pul Pul Billabong, South Alligator River (13°34'S, 132°35'); NTM 13512, South Alligator River (13°30'S, 132°28'). *Elseya dentata* [var. Johnstone,

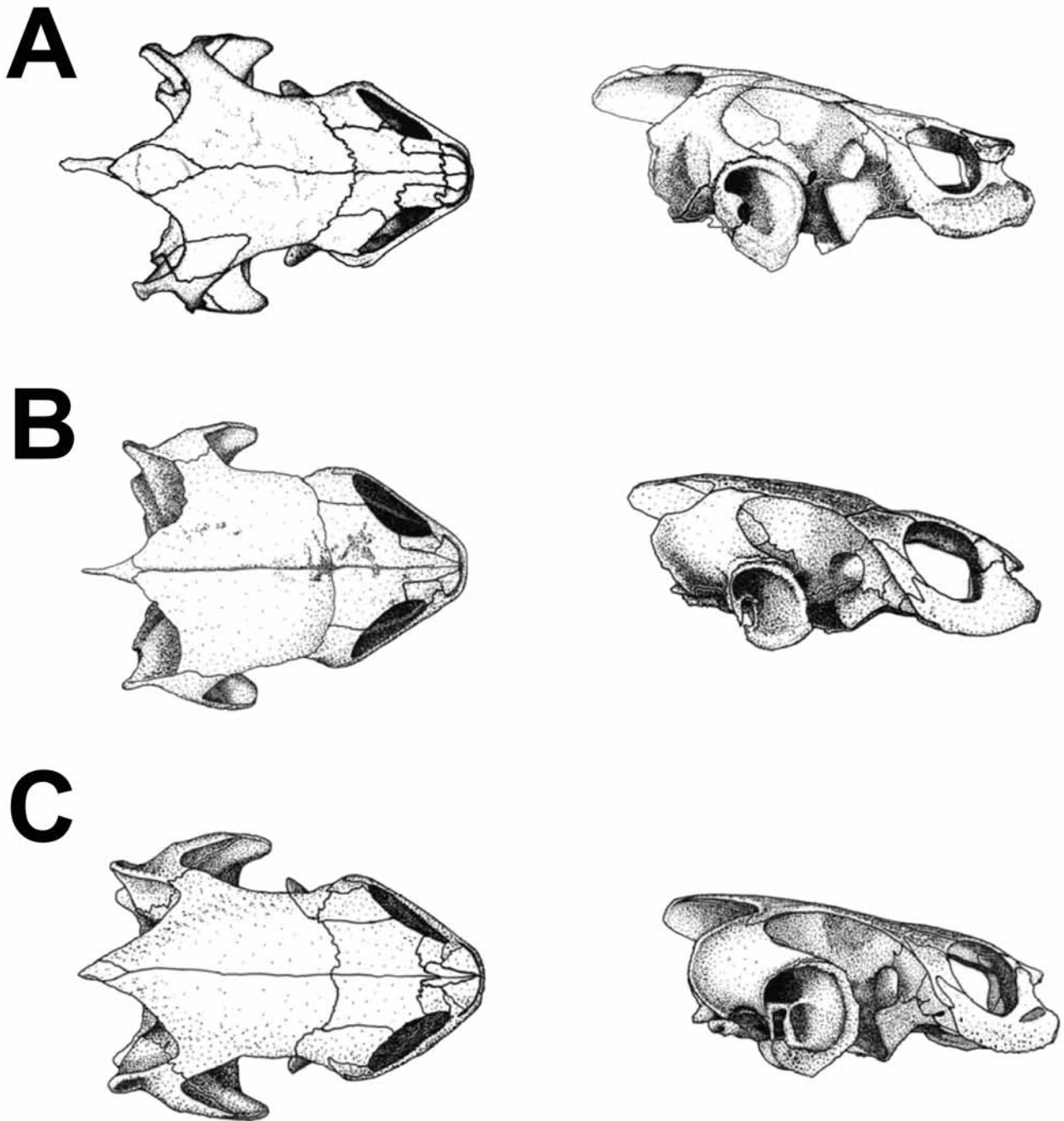


FIGURE 2. Dorsal and lateral views of the skulls of **A.** *Elseya dentata* (UC0302); **B.** *Myuchelys latisternum* (AM 125475) and **C.** *Emydura macquarii* (QM48034).

sensu Georges & Adams, 1992;1996]: QM 48068, Hartley Creek (15°46'S, 145°19'E); QM 48060, near Cairns (16°55'S, 145°46'E); QM 48059, 48064-65, South Johnstone River (17°38'S, 145°05'E). *Elseya irwini* NWC 0520, Townsville (19°16'S, 146°49'E); *Elseya lavarackorum* QM 47908, 47911, 48547, 48564, Elizabeth Gorge, Bowthorn Station (18°13'S, 138°2'E); QM 31939, 31942, 31944, 31946-47, 31949-50,

31952, Gregory River, Riversleigh Station, north of Mt Isa (19°02'S, 138°45'E); UC 0201, QM 48544, Lawn Hill Gorge (18°46'S, 138°25'E); QM 46284 Lawn Hill National Park (18°35'S, 138°35'E). *Elseya novaeguineae*: AM 42662, 125038, Sepik River, New Guinea (6°47'S, 146°46'E). *Elusor macrurus*: NHM 1890.2.26.2, UC 170, 184-93, 195-197, 225-229, Mary River, Queensland 26°21'S, 152°41'E. *Emydura macquarii*: UC 176, Hastings River (31°26'S, 152°28'E); UC 2063-73, Mungabareena Reserve, Albury (36°06'S, 147°00'E). *Emydura subglobosa*: UC 389, 391, 394-95, Bahunia Springs, Limmen Bight River (16°00'S, 139°05'E); UC 177, Batten Creek, McArthur (15°54'S, 136°40'E); UC 2083-84, Goyder River (12°56'S, 135°01'E); UC 171-72, Gregory River (19°12'S, 137°54'E); UC 2059, 2091, 2095-97, Ooloo Crossing, Daly River (14°04'S, 131°15'E); *Emydura tanybaraga*: UC 2195, Mareeba Wetlands (17°00'S, 145°26'E); UC 464, 468, 469, Ooloo Crossing, Daly River (14°04'S, 131°15'E); *Emydura victoriae*: UC 461, 463, 468, 473, 2055-58, Ooloo Crossing, Daly River (14°04'S, 131°15'E); UC 222, *Myuchelys bellii*: AM123028-29, QM 48028, 48038, billabong on Roumalla Creek, 3 km downstream from bridge at Kingston (30°30'S, 150°07'E); *Myuchelys georgesi*: UM 02016-17, Bellinger River; AM 138387-88, Bellinger River, vicinity of sawmill 1 km from Thora on the Upper Thora Road (30°25'S, 152°46'E); *Myuchelys latisternum*: AM 123037, 123039, Lismore Lake, Lismore, Richmond River Drainage (26°50'S, 153°16'E); UC 470, Richmond River, NSW; AM 125474-75, South Alligator River, Gimbat Station (13°34'S, 132°35'E); QM 48054-55, no data; UC 2094, South Pine River, Bunya crossing (27°21'S, 152°57'E); *Myuchelys purvisi*: QM 59289-90, Barnard River; AM 123040, 123042, Barnard River Natmap 1:250000, Hastings SH56-14 488075 (31°44'S, 151°51'E). *Phrynops geoffroanus*: UC 274, no data, pet trade. *Phrynops hilarii*: UC 330, 336, no data, pet trade. *Phrynops williamsi* UC 298-99, 333, no data, pet trade. *Phrynops tuberosus* UC 328, 332, 337, no data, pet trade. *Batrachemys raniceps*: UC 2043, no data, pet trade. *Pseudemydura umbrina*: UC 178, WAM 29348, Twin Swamps Reserve, Perth. *Rheodytes leukops*: UC 173, 2053, Fitzroy River, Queensland.

Discussion

Evidence for the paraphyletic arrangement of species in the former genus *Elseya* is very strong. It derives from morphological data (McDowell, 1983), electrophoretic data (Georges & Adams, 1992), gene sequencing data (Seddon, *et al.*, 1997; Georges, *et al.*, 1998) and the combined analysis presented in this paper. We have chosen to split the genus *Elseya* to resolve the paraphyly (see Legler & Cann, 1980; Legler, 1981; Georges & Adams, 1992), rather than to combine *Elseya* into an expanded single genus *Emydura* (Gaffney, 1977; McDowell, 1983). The closer affinities of *Elseya dentata* to *Emydura australis* (including *Emydura krefftii* and *Emydura subglobosa*) rather than to *Myuchelys latisternum* (McDowell, 1983) are fully consistent with this new arrangement. It also explains the apparent lack of skull characters that consistently distinguish *Elseya* and *Emydura*, as in making these comparisons (Gaffney, 1977), since Gaffney did not have available skeletal material for *Myuchelys* (then *Elseya latisternum*). The inclusion of *Rheodytes* and *Elusor* in the clade containing *Elseya* and *Myuchelys* (Megirian & Murray, 1999) would preclude the alternative of merging the former *Elseya* with *Emydura* to resolve the paraphyly, as this would require subsuming *Rheodytes* and *Elusor* into *Emydura* also. In our view, this would create a taxonomy that did not adequately represent the variation present in this group, and would not serve the interests of nomenclatural stability by overturning the well established names *Emydura*, *Elseya*, *Elusor* and *Rheodytes*.

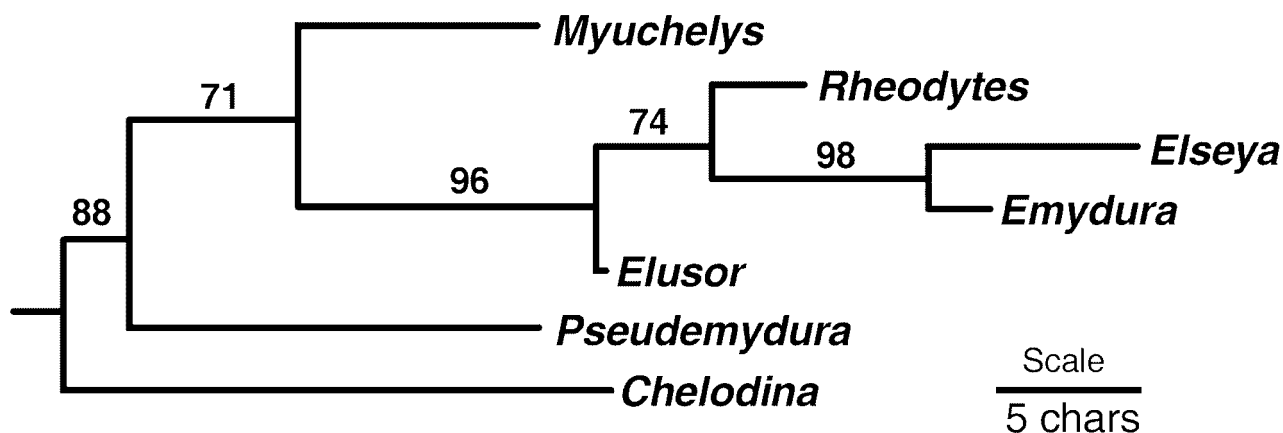


FIGURE 3. A phylogeny for the extant genera of the Australian short-necked Chelidae generated using PAUP* (v64d) as the single most parsimonious tree from the character data presented in Table 1. Values on the branches are bootstrap percentages—nodes for which values exceed 70% are considered robust. *Phrynops* was used as the outgroup taxon. Note that the genus *Elseya*, as defined prior to this paper (i.e. *Elseya* + *Myuchelys*), was clearly paraphyletic.

TABLE 1. Distribution of character states among taxa utilised in the cladistic analysis. Characters are described in the Appendix.

Character	<i>Myuchelys</i>	<i>Pseudemydura</i>	<i>Rheodytes</i>	<i>Elusor</i>	<i>Elseya</i>	<i>Emydura</i>	<i>Chelodina</i>	<i>Phrynops</i>
1	0	0	0	0	1	0	0	0
2	0	0	1	1	1	2	2	0
3	0	0	0	0	1	0	0	0
4	0	0	0	0	1	1	2	0
5	0	1	0	0	0	0	0	0
6	0	0	0	0	2	1	0	0
7	1	1	1	1	1	1	0	0
8	0	0	0	0	1	1	0	0
9	0	0	0	0	0	0	1	0
10	0	1	0	0	0	0	0	0
11	0	0	0	0	0	0	1	0
12	0	0	0	0	0	0	1	0
13	0	0	0	0	0	0	1	0
14	0	1	0	0	0	0	0	0
15	1	2	1	1	1	1	3	0
16	0	1	0	0	0	0	0	0
17	0	1	0	0	0	0	0	0
18	0	1	0	0	0	0	0	0
19	0	0	0	0	0	0	1	0
20	1	1	1	1	1	1	0	0
21	0	0	0	0	0	0	1	0
22	1	0	1	1	1	1	0	0

to be continued

TABLE 1. (continued)

23	0	1	0	0	0	0	0	0
24	0	0	0	0	0	0	1	1
25	0	0	1	0	1	1	0	0
26	1	1	0	1	2	3	0	0
27	0	0	0	0	1	1	0	0
28	0	0	0	0	1	0	1	1
29	0	1	0	0	1	0	0	0
30	0	0	1	0	2	1	0	0
31	0	0	2	1	1	1	0	0
32	0	1	1	1	1	1	0	0
33	0	1	0	0	0	0	1	1
34	0	0	0	0	0	0	1	0
35	0	0	1	1	1	1	0	0
36	0	0	0	0	1	1	0	0
37	0	0	0	0	0	0	1	0
38	0	0	0	0	0	0	1	0
39	0	0	0	0	0	0	1	0
40	1	0	1	1	1	1	0	0
41	0	0	0	0	0	0	1	0
42	0	0	0	1	1	1	0	0
43	1	?	0	0	0	0	0	?
44	0	?	1	0	0	1	0	?
45	1	?	0	0	1	1	0	?

Appendix. Description of Characters and Character analysis.

Specimens of all species of the *Elseya latisternum* (n = 20) and *Elseya dentata* generic groups (n = 68) defined by Legler (1981) were examined. These were compared with specimens of *Elusor* (n = 20), *Rheodytes* (n = 2), *Emydura* (n = 38, 4 species), *Phrynops/Batrachemys* (n = 10, 5 species), *Pseudemydura* (n = 2) and *Chelodina* (n = 23, 3 species). Character states were assigned and polarised (where possible), and primitive characters assigned the code 0 unless otherwise specified. A character analysis was performed using maximum parsimony (PAUP* version 64d, default settings), with *Phrynops/Batrachemys* as the outgroup (Georges, *et al.*, 1998). Defining characters for each genus were used in the diagnosis. Note that 20 of the 45 characters presented here are autapomorphic and not phylogenetically informative at the genus level. Morphological characters were obtained from the literature or devised in the present study as indicated by an appropriate citation.

Skull characters

1. **Alveolar ridge** (medial alveolar ridge between the lingual and maxillary ridges of the triturating surface of the upper jaw): 0—Absent; 1—Present. Absent in all but specialised herbivorous forms; its presence a derived state within the Australian Chelidae.
2. **Head shield**: 0—Present as a cap on the dorsal surface of the head, with lateral extensions down parietal arch toward the tympanum; 1—Present, but restricted to the dorsal surface of the head; 2—Absent, occasionally present in older individuals but without discrete border or highly fragmented. Cap present in Pelomedusidae and most Chelidae, regarded as primitive, absence a derived loss.

3. **Crista supraoccipitalis**: 0—not elongated beyond the foramen magnum; 1—elongated beyond the foramen magnum. State 0 the most common state for turtles, considered the primitive state.
4. **Parietal arch**: 0—Wide; 1—Narrow; 2—Absent. Present in all chelids except *Chelodina*, so complete loss is considered derived. Narrow parietal arch associated with relocation of digastricus masticus muscles of the jaws, derived.
5. **Posterior emargination of skull**: 0—Present; 1—Absent. Absence is an autapomorphy in *Pseudemydura*, regarded as secondary expansion of the skull roof (Gaffney, 1977).
6. **Lingual ridge**: 0—narrow not enlarged; 1—enlarged to form crushing plates; 2—enlarged and serrated for shearing plates. Simple narrow structure of triturating surfaces of the jaw sheath, primitive; specialisation for crushing or shearing, derived.
7. **Medial symphysis of lower jaw**: 0—rami not fused; 1—rami fused to form single unit. Most turtles have a sutural surface between the rami of the lower jaw, primitive; fusion derived.
8. **Rhamphotheca of upper jaw**: 0—thin, without modification; 1—thickened and enlarged to form a crushing plate. Simple narrow structure of triturating surfaces of the jaw sheath, primitive; specialisation for crushing or shearing, derived. Functionally correlated to Character 6, but not always coincident states.
9. **Vomer**: 0—contacts pterygoids; 1—does not contact pterygoids. Exclusion of vomer-ptyergoid contact and medial contact between the pterygoids, derived based on conditions in outgroup taxa.
10. **Anterior process of frontal** (Gaffney, 1977): 0—present; 1—absent. Absence in *Pseudemydura*, a derived autapomorphy.
11. **Nasals** (Gaffney, 1977): 0—not completely separated by frontal process; 1—completely separated. Complete separation of nasals, derived synapomorphy for *Chelodina*.
12. **Prefrontals** (Gaffney, 1977): 0—not exposed along dorsal margin of apertura narium externa; 1 exposed. *Chelus* has character state 1, but Gaffney (Gaffney, 1977) also considers it as being narrowly present for *Chelodina*, hence we include it here. Functionally correlated to presence/ absence and form of nasals, so no characters defined for nasals.
13. **Frontals** (Gaffney, 1977): 0—not fused, 1—fused. Well defined synapomorphy for *Chelodina*, fusion is considered derived.
14. **Dorsal portion of postorbital** (Gaffney, 1977): 0—small; 1—large. Broad ventrolateral expansion of postorbital a defined autapomorphy for *Pseudemydura*.
15. **Dorsal portion of parietal** (Gaffney, 1977): 0—covers little of adductor fossa; 1—covers central area of adductor fossa; 2—broadly covers adductor fossa; 3 absent, does not cover adductor fossa. Functionally correlated with character 24, but not always coincident states.
16. **Supraoccipita- parietal contact**: 0 narrow, 1—broad. Expansion of the supraoccipital an autapomorphy in *Pseudemydura* (but see Gaffney, 1977)
17. **Quadrate-parietal contact** (Gaffney, 1977): 0—absent; 1—present. Quadrate excluded from parietal, derived autapomorphy in *Pseudemydura*.
18. **Dorsal horizontal portion of supraoccipital** (Gaffney, 1977): 0—not expanded; 1—broadly expanded. Autapomorphy for *Pseudemydura*, forming part of expanded roofing of skull.
19. **Medial portions of jugal and postorbital** (Gaffney, 1977): 0—not facing more laterally than posteriorly; 1—facing more laterally than posteriorly. Complex homology, depends on degree of flattening of skull. State 1 present in *Phrynops*, *Chelus* and the *Chelodina expansa* group, to a lesser degree in *Hydromedusa*. We agree with Gaffney on the polarity, present only in species with strike-and-gape behaviour.
20. **Dorsal processes of exoccipitals** (Gaffney, 1977): 0—do not meet above the foramen magnum; 1—meet above the foramen magnum. In most turtles the exoccipitals fail to meet above the foramen magnum, primitive state for the Chelidae.
21. **Quadrate basisphenoid contact**: 0—absent; 1—present. In most chelid turtles the basisphenoid and quadrate are separated on the ventral surface by the prootic; in *Chelodina*, the basisphenoid extends laterally, anterior to the foramen posterior canalis caracoti interni, to meet the quadrate; derived.
22. **Symphyseal hook** (Gaffney, 1977). 0—absent; 1 present. Most short necked species in Australia have a pronounced symphyseal hook, with the exception of *Pseudemydura*. Absent in the South American forms, derived.
23. **Prearticular separates coronoid and splenial** (Burbidge, *et al.*, 1974; Gaffney, 1977): 0—absent; 1—present. In all turtles that retain the splenial, including fossils, the coronoid and splenial have an extensive contact; State 1 autapomorphic for *Pseudemydura*. Splenial is usually absent in *Rheodytes* (Legler & Cann, 1980), scored as 0.
24. **Temporal emargination**: 0—emargination minor, not extending deeply into parietal; 1 parietal is significantly narrowed.

Shell characters

Anterior Bridge Struts

25. **Contact with Pleural 1** (Thomson, *et al.*, 1997): 0—posterior edge of bridge-carapace suture runs parallel and adjacent to rib-gomphosis of pleural one; 1—posterior edge of suture contacts rib-gomphosis at anterior end, set at a forward divergent angle between 15 and 50 degrees. Angle most pronounced in *Emydura*, least in *Rheodytes*. Bridge strut parallel to the rib-gomphosis in almost all turtles, even many Cryptodires, State 1 derived.
26. **Bridge suture shape** (Thomson, *et al.*, 1997): 0—anterior and posterior edges of bridge-carapace suture parallel or closely so, with prominent suture surface between them, no medial constriction. 1—anterior and posterior edges of bridge-carapace suture diverge from their point of congruence closest to the vertebral column, widest extent of suture distal to vertebral column, no medial constriction; 2—bridge-carapace suture expanded for full length, more so at extremes, obvious medial constriction; 3—bridge-carapace suture narrows from widest point proximal to vertebral column, constricts completely to form a ridge confluent with edge formed by ventral suture of peripheral bones. One of the most difficult characters to polarise. Primitive state shared by most chelids and pelomedusids that are unmodified in this region (by plastral hinges).

Rib/Gomphosis of Pleural 1

27. **Rotation of Rib/Gomphosis** (Thomson, *et al.*, 1997): 0—ventral surface of distal extent of rib/gomphosis rotated obliquely to face ventrally but with posterior inflection; 1—rib/gomphosis shows no such torsion distally. Rotation of the gomphosis is found in almost all chelids, primitive. Functionally it would appear to have strengthened the juncture of the first pleural to the peripherals in this region. It also allows for kinesis and is necessary if that were present. Only *Pseudemydura* has mild plastral kinesis.

Dorsal characters

28. **Relative width of Vertebral 1** (Gaffney, 1977, Thomson, *et al.*, 1997): 0—first vertebral scute wider than second and third; 1—first three vertebral scutes equal or sub-equal in width. Gaffney (Gaffney, 1977) identified the wider first scute as primitive, possibly secondarily derived in *Pseudemydura*.
29. **Cervical scute** (Gaffney, 1977; Legler & Cann, 1980; Thomson, *et al.*, 1997): 0—cervical scute typically present; 1—cervical scute typically absent. This character has been well analysed and the presence of this scute is clearly primitive for turtles.

Posterior internal carapace characters

30. **Carapace pelvis suture** (Thomson & Mackness, 1999): 0—ilium sutures to pleurals 7 and 8 and pygal; 1—ilium sutures to pleural 8 and pygal only, but directly adjacent to the suture between pleurals 7 and 8; 2—ilium sutures to pleural 8 and pygal only but widely separated from suture between the pleurals 7 and 8. Most chelids examined possess State 0, primitive, including the outgroups *Phrynops/Batrachemys* and other South American Chelids.
31. **Location of rib gomphosis of Pleural 5**; 0—inserts between peripherals 7 and 8; 1—inserts into middle of peripheral 7; 2—inserts into peripheral 6. Minor differences in the location of the gomphosis between pleural 5 and the peripherals have been found. These are probably correlated to differences in shell length ratios. State 0 present in the majority of species, many of which are not closely related, primitive.
32. **Exposed neural bones present** (contiguous series): 0—Present, 1—Absent. Thomson and Georges Thomson & Georges, 1996 demonstrated that neural bones are present in a reduced form in all chelids. This explains their occasional appearance in species that do not generally have a contiguous series of neurals, particularly in older animals. This is an ontogenetic condition and its occurrence is more or less correlated to the thickness of the shell. Some species normally have a large exposed series of neurals – *Chelodina oblonga* (Burbidge *et al.*, 1974); *Myuchelys purvisi* (Thomson & Georges, 1996) and *Chelodina burrungandjii* (Thomson, *et al.*, 2000). In the *Chelodina* this is associated with the expansion of the rib heads to make room for enlarged musculature, hence is considered derived. In *M. purvisi* this is considered a retained primitive condition.
33. **Intergular scute** (Gaffney, 1977): 0—intergular large extends between and separates the humerals, 1—intergular small does not separate the humerals. In most chelids, the intergular scute is small and extends back to only partially separate the humeral scutes, primitive condition. In the derived state, intergular scute large, completely separates the humerals and separates the anterior of the pectoral scutes.
34. **Gular scutes** (Gaffney, 1977): 0—separated by intergular; 1—contact each other excluding intergular from anterior edge. A well defined synapomorphy for the *Chelodina*, useful for the identification of fossil *Chelodina* (Gaffney, 1981 Thomson, 2000).

35. **Anterior plastron lobe:** 0—large, squared at anterior; 1—small, narrow, tapered at anterior. In most chelids the anterior plastron is square in general shape, primitive; in *Emydura* and *Elseya* the anterior is tapered, derived.
36. **Generalised shell shape** 0—dorso-ventrally flattened; 1—high domed. In most chelids the shell is flattened.

Other characters

37. **Number of clawed toes (manus)** (Gaffney, 1977): 0—five; 1—four. Primitive state for number of toes on the manus of most tetrapods 5; hence 4 derived.
38. **Cervical vertebrae length** (Gaffney, 1977): 0—same length as thoracic vertebrae or shorter, 1 longer than the thoracic vertebrae. Elongation of the cervical vertebrae considered derived.
39. **Atlas-axis complex structure** (Williams, 1950). 0—not fused to single unit; 1—fused to single unit. In the primitive state the atlas-axis complex consists of a number of separate units held together by ligaments and cartilage; in the derived state this complex fuses into a single inseparable bony structure, e.g. *Chelodina*.
40. **Skin contact with carapace:** 0—skin of ventral surface of carapace does not extend to anterior margin in cervical P1 region; 1—skin extends to approach anterior margin. In most turtles there is a gap between the skin carapace contact at the anterior and the anterior margin, primitive.
41. **Hyoids:** 0—hyoid complex small; 1—hyoid complex large. Expansion of the hyoid structure is found in turtles that employ the suck and gape feeding strategy, derived.
42. **Neck tubercles:** 0—present, large and cornified; 1—absent or small, not cornified. Pelomedusids, South American Chelids, *Chelonia*, many fossil taxa have large scales on the head and neck that are fully cornified, primitive.
43. Allozyme AK-1 (Georges & Adams, 1992). 0-a, 1-b. Unordered.
44. Allozyme AK-2 (Georges & Adams, 1992). 0-a, 1-e. Unordered.
45. Allozyme Glo-1 (Georges & Adams, 1992). 0-b, 1-a. Unordered.

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