

ARTICLES

Chelonian Conservation and Biology, 2000, 3(4):675–685
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A New Species of Long-Necked Turtle (Testudines: Chelidae) from the Arnhem Land Plateau, Northern Territory, Australia

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ABSTRACT. – A new species of long-necked freshwater turtle of the family Chelidae is described from the Arnhem Land Plateau in the Northern Territory of Australia. The taxon is included within the *Chelodina expansa* group of species and is the smallest member of that group. First collected by scientists some 20 years ago, research on the species has been hampered by its isolation — it is restricted to sparsely inhabited, rugged sandstone country of tropical northern Australia. It can be diagnosed by its broad, shortened and flattened skull, by the possession of a contiguous neural series, and by contact of the vomer and the pterygoids. It is clearly distinct from *Chelodina rugosa* in a canonical discriminant analysis. Preliminary data on natural history are also presented. Males examined in October–November had enlarged vascularized testes and epididymes distended with sperm. Females examined at the same time had regressed corpora lutea and atretic follicles from the previous nesting season, presumably in the immediately preceding dry season. The diet is primarily fish and shrimp, but unlike other *Chelodina* which are all obligate carnivores, this species appears to feed on both plant and animal material. The turtle is well known to Aboriginal people of the region who collect it for food, and they report that it consumes leaves and fruits of aquatic and riparian vegetation and reproduces in the dry season.

KEY WORDS. – Reptilia; Testudines; Chelidae; *Chelodina burrungandjii*, sp. nov.; turtle; taxonomy; ecology; diet; reproduction; habitat; indigenous knowledge; conservation; Australia

Conservation of Australia's freshwater turtle fauna is hampered by poor taxonomy at the species level. Many distinct forms, known to scientists for many decades, have remained undescribed. Formal recognition and data on distribution and abundance are often essential prerequisites for marshalling government support for conservation (Georges, 1993). These undescribed forms have been largely ignored in the action and recovery plans that govern the threatened species initiatives in Australia. However, there has been recent progress. The Mary River turtle *Elusor macrurus* (Cann and Legler, 1994), known to science for 20 years previously only as specimens of unknown origin in the pet trade, the white-eyed river diver *Rheodytes leukops* (Legler and Cann, 1980), the 'living fossil' *Elseya lavarackorum* from the Nicholson drainage of Queensland (Thomson et al., 1997), the Bellingen River turtle *Elseya georgesii* (Cann, 1998a), the northern yellow-faced turtle *Emydura tanybaraga* (Cann, 1998b), and the yellow-headed snapping turtle *Elseya irwini* (Cann, 1998c) are all recent additions to the Australian turtle fauna, and testimony to the advancing state of our knowledge of this group. Electrophoretic surveys (Georges and Adams, 1992, 1996) indicate that there are many more distinct forms awaiting formal description, lending support to earlier indications based on morphology (Cann, 1978; Legler 1981).

In particular, a new form of turtle from the Arnhem Land Plateau first came to the attention of science when collected during surveys of the Arnhem Land region by

Grahame Webb in the early 1970s. Aboriginal people in the region are familiar with the turtle and have hunted it for food and ceremonial purposes for generations. The Gagadju people of Kakadu National Park recognize it as a distinct form in their language, referring to it as *Burrungandji*. They distinguish it from *Almangiyi* (*Chelodina rugosa*), a common and closely-related species of the coastal floodplains (Lucas and Russel-Smith, 1993). The Jawoyn people of the Katherine region (including Nitmiluk National Park and the southern sections of Kakadu National Park) refer to it as *Wurruyung* (Sandy Barraway, *pers. comm.*), but this name is also used to refer to *C. rugosa*.

Legler (1982) too, in an unpublished report, recognized the form as a new species, and its status as a distinct taxon was later confirmed by electrophoretic comparisons (Georges and Adams, 1992; Georges et al., in prep.), but it has remained unnamed. In this paper, we describe this new species of long-necked turtle of the genus *Chelodina* (Fig. 1), and provide some information on its natural history and ecology.

MATERIALS AND METHODS

Turtles representing all known species of *Chelodina* from Australia and New Guinea were obtained from museums and private collections. Additional specimens were collected directly from the field, examined and measured,

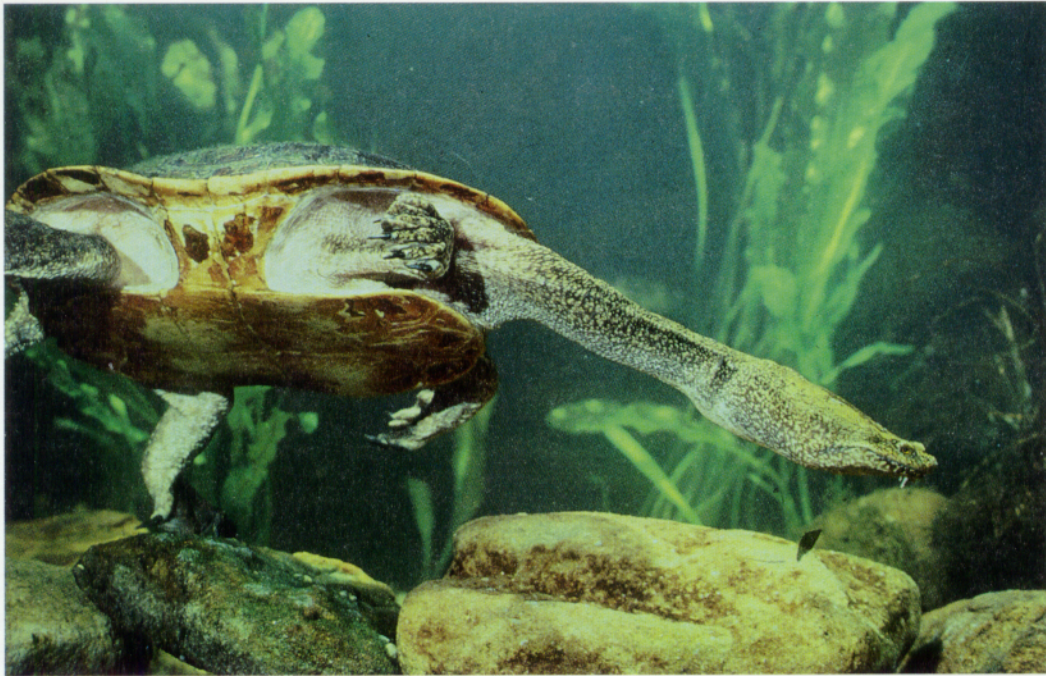


Figure 1. *Chelodina burrungandjii* from Koolpin Gorge, Arnhem Land, Northern Territory, Australia. Photo by John Cann.

and either retained for skeletal preparations or marked and released at their point of capture. Data on coloration are therefore based on examination of both live animals in the field and museum specimens. The measurements routinely taken are described in Appendix A. Skeletal preparations were made using methods outlined in Thomson et al. (1997). Skeletal terminology and description follows that of Gaffney (1979) for skulls and Zangerl (1969) for shells. Appendix B lists all museum specimens examined.

All means are presented with their standard errors, not standard deviations, unless otherwise specified. Discriminant analysis (SAS Institute, 1988) was used to determine how well external measurements of head and shell could distinguish among the *Chelodina* species, and the new species described here and its closest relatives in particular.

For the ecological studies specimens were collected by diving with mask and fins and trapping in baited traps at the Gunyarr pools adjacent to the Katherine River Gorge in Nitmiluk National Park (133°31'10"E, 14°18'30"S) on 23–24 August 1996 and 24–25 October 1996, and in a section of the upper Katherine River (133°05'E, 13°46'S) on 4–6 November 1996. A total of 22 specimens (12 females, 7 males, 2 juveniles, 1 sex not recorded) were captured at Gunyarr pools and 10 specimens (5 females, 4 males, 1 juvenile) in the upper Katherine River. Of these, 11 females and 8 males were examined via laparoscope to determine sex, reproductive status, and body condition. Males with enlarged vascularized testes and epididymes that were white, coiled, and distended with sperm (Kennett, 1994) were judged as mature. All such mature specimens had longer thicker tails than females of the same size (c.f. *C. rugosa*, Kennett, 1994, 1996). Females with thickened, muscular oviducts, or ovaries with enlarged vitellogenic follicles or corpora lutea, were judged as mature.

Stomach samples were collected from 30 turtles (16 females, 11 males, 2 juveniles, 1 sex not recorded) by stomach flushing within 2 hours (usually sooner) of capture. A steady flow of water supplied by a submersible electric pump was passed into the stomach through a flexible plastic tube with the turtle held in a horizontal position (after Georges et al., 1986). The turtle was then inverted and water flowed out of the esophagus and mouth carrying the stomach contents with it. Stomach contents were preserved in 70% alcohol and later examined under a stereoscopic microscope.

SYSTEMATICS

Order: Testudines Linnaeus, 1758

Suborder: Pleurodira Cope, 1864

Family: Chelidae Gray, 1831

Chelodina burrungandjii, sp. nov.

Arnhem Land Long-Necked Turtle
(Figs. 1–3, 5–6)

Type Specimens. — Holotype: NTM 16010 (UC Blood Ref: 0316), adult female collected by Rod Kennett in Koolpin Gorge, South Alligator River (13°28'S, 132°38'E) on 6 September 1989 (Fig. 2a). Allotype: NTM 16011 (UC Blood Ref: 0317), adult male with same data as the holotype (Fig. 2b). See Table 1 for comparative measurements.

Referred Specimens. — NTM 13525, 16008-12, 16333, 22581-83; UC 2088-90, 2101; UU 17730-37, 18833-59.

Diagnosis. — A medium to large snake-necked chelid turtle of the genus *Chelodina* most closely resembling its sister taxon from the Kimberley, referred to hereinafter as *Chelodina* sp. (Kimberley). It belongs in the subgeneric group "B" or the *Chelodina expansa* group (Goode, 1967;

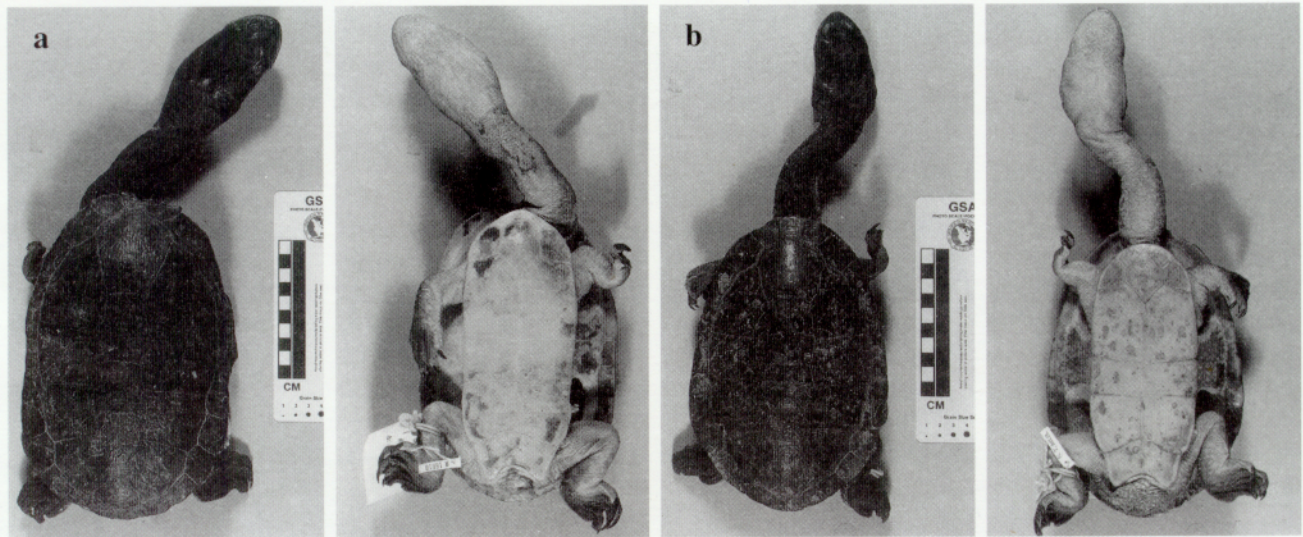


Figure 2. *Chelodina burrungandjii* type specimens: (a) the female holotype (NTM 16010, CL = 220 mm); (b) the male allotype (NTM 16011, CL = 189 mm). Both specimens are spirit-preserved.

Burbidge et al., 1974; Rhodin and Mittermeier, 1976) which includes described forms *Chelodina expansa*, *Chelodina rugosa*, *Chelodina siebenrocki*, and *Chelodina parkeri*. This subgeneric group is distinguished from the group “A” species (the *Chelodina longicollis* group) by their relatively longer, thicker necks, reduced plastra, broader heads, and a more attenuated mode of strike-and-gape feeding (excluding *Chelodina oblonga* from this comparison). *Chelodina burrungandjii* can be distinguished from other members of the *C. expansa* group by the presence of a relatively shortened, broad, flat head. *Chelodina expansa* also has a flattened head but it is not short and broad and even similarly sized individuals are readily identified (Figs. 3–4). The oblong carapace and plastron in adults readily distinguishes this species from all other members of this group except the Kimberley form (Table 2) and the upward turning of the lateral marginals distinguishes this species from *C. rugosa*, *C. siebenrocki*, and *C. parkeri* (Figs. 5–6). The speckled neck coloration is not found among other Australian members of this group, though it is apparent but not as strongly defined in the Kimberley form. It is not as pronounced as that seen in *C. parkeri* from which *C. burrungandjii* can also be distinguished by the lack of the pronounced head striping

and post-tympanic white patch, key characters for *C. parkeri* (Rhodin and Mittermeier, 1976; Pritchard, 1979). Unique among the members of the *C. expansa* group is the consistent presence in *C. burrungandjii* of an expanded contiguous neural series of between three and five neurals (Thomson and Georges, 1996) (Fig. 5a). This feature readily distinguishes it from the Kimberley form which has the usual *C. expansa* group condition of no exposed neurals. Apart from the broad flat skull (Table 3), this species also possesses a narrow crista paroccipitalis and pterygoids with enlarged ventro-lateral processes that extend to the condylus mandibularis.

Multivariate Comparisons. — Canonical discriminant analysis (SAS Institute, 1988) was used to determine the distinctiveness of *C. burrungandjii* and its two closest relatives (based on analysis of electrophoretic data of Georges and Adams, in prep), *C. rugosa* and *Chelodina* sp. (Kimberley). Males and females were analyzed separately. Head measurements were expressed as a ratio of head length (HL); head length and all shell measurements were expressed as a ratio of carapace length (CL). A number of composite variables were defined as combinations of the raw measurements, but none were retained by the subsequent analyses.

Table 1. Measurements of specimens of *Chelodina burrungandjii* held in museums. Refer to Appendix A for explanation of measurements.

Museum	No.	Sex	CL	CW4	CW8	PL	PLF	PLR	HL	HWT	HH
UC	2088	F	242.0	150.9	159.0	188.0	72.8	77.5	63.9	43.6	7.6
UC	2089	M	206.3	126.8	138.3	160.4	65.1	68.5	60.5	39.7	7.3
UC	2090	F	240.3	148.8	159.2	185.2	78.4	83.4	66.9	48.7	8.8
UC	2101	F	266.3	169.1	171.7	195.4	83.4	85.4	75.6	55.5	9.1
NTM	13525	M	220.9	131.1	136.6	166.7	69.5	72.8	68.1	44.0	—
NTM	16008	F	261.2	175.6	182.3	197.3	85.2	93.8	81.6	56.8	7.7
NTM	16009	M	213.3	137.8	145.7	168.2	71.3	82.0	65.8	46.1	8.3
NTM	16010	F	220.7	138.1	140.7	176.2	72.4	73.9	67.8	47.0	7.8
NTM	16011	M	189.8	116.2	127.1	143.6	60.7	65.3	58.2	36.7	6.7
NTM	16012	M	166.4	98.6	105.2	133.9	53.6	56.2	60.7	37.6	7.0
NTM	16333	M	199.2	126.4	135.7	148.3	65.4	70.5	57.9	38.9	—
NTM	22581	F	266.8	179.0	185.4	203.8	90.4	93.8	74.9	52.3	8.3
NTM	22582	F	246.3	161.3	158.3	186.6	78.1	82.7	72.6	54.0	9.3
NTM	22583	J	115.4	75.4	81.7	89.3	36.9	42.2	38.3	24.1	5.2

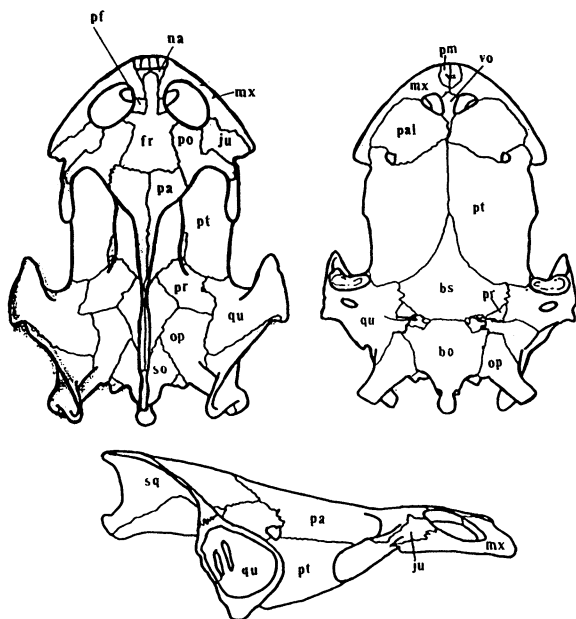


Figure 3. Dorsal, ventral, and lateral views of the skull of *Chelodina burrungandjii* (UC 2101). Abbreviations: bo, basioccipital; bs, basisphenoid; fr, frontal; ju, jugal; mx, maxilla; na, nasal; op, opisthotic; pa, parietal; pal, palatine; pf, prefrontal; pm, premaxilla; po, postorbital; pr, prootic; pt, pterygoid; qu, quadrate; so, supraoccipital; sq, squamosal; vo, vomer.

Generalized multivariate distances between all taxa in the *C. expansa* group, obtained from a discriminant analysis with all raw measurement ratios included, are presented in Table 4 as an indication of their general morphological similarity. Note that the distinction between *C. rugosa* and *C. burrungandjii* is substantial (25.3 units), and greater than the distance between *C. rugosa* and *C. parkeri* (16.1 units), in support of our recognition of *C. rugosa* and *C. burrungandjii* as separate species.

Stepwise selection (significance level for entry = 0.05; for removal = 0.10) was used to obtain a subset of the original variables that provided best discrimination. For females, this yielded a subset of head measurements (HL, HH, HWT,

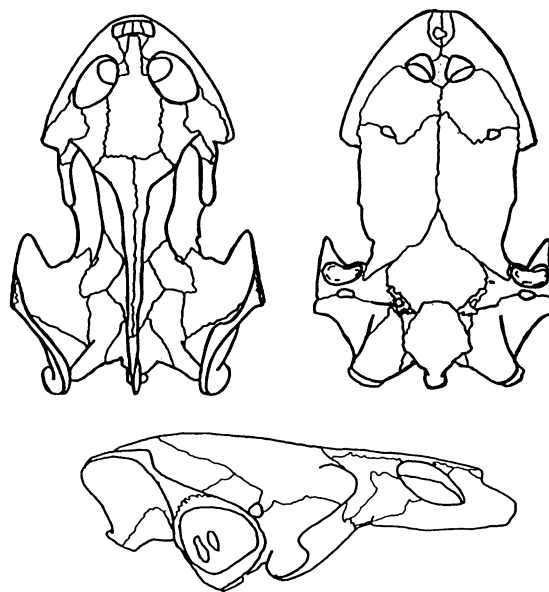


Figure 4. Dorsal, ventral, and lateral views of the skull of *Chelodina rugosa* (UC 0320).

HWJ) and shell measurements (CW4, CW8, and PLR). Clearly, both head shape and shell shape are well represented in the final formula that provided best discrimination. Discrimination was good (Fig. 7). A total of 92.8% of the among-groups variation was explained by the first canonical variate. This variate provides the bulk of the discrimination between *C. rugosa* and the other two forms, but contributes little to the discrimination between *C. burrungandjii* and the Kimberley taxon (Fig. 7). An indication of the strength of discrimination is given by cross-validation (SAS Institute, 1988), though it does rely on assumptions of normality, unlikely to be strictly upheld because not all animals were the same overall size and growth is allometric. Nevertheless, only two of the 50 animals in the analysis were misclassified. One *C. burrungandjii* was misclassified as the Kimberley taxon, and vice versa. The distinction between *C. rugosa* and the other two forms was 100%.

Table 2. Carapace length (in mm) and selected carapace ratios — mean, (range), and [SE] — for three species of *Chelodina*. All ratio measurements divided by CL. See Appendix A for explanation of measurements.

Species	Sex	n	CL	CW4	CW8	PL	PLF
<i>C. burrungandjii</i>	Females	7	249.13 (220.8-266.8) [6.35]	0.64 (0.61-0.67) [0.0085]	0.66 (0.64-0.70) [0.0093]	0.76 (0.73-0.80) [0.0076]	0.32 (0.30-0.34) [0.0046]
	Males	6	199.37 (166.4-220.9) [7.93]	0.62 (0.59-0.65) [0.0087]	0.66 (0.62-0.68) [0.011]	0.77 (0.74-0.81) [0.0094]	0.32 (0.31-0.33) [0.0031]
<i>C. sp. (Kimberley)</i>	Females	14	232.21 (148.4-293.1) [11.74]	0.65 (0.55-0.69) [0.0089]	0.68 (0.63-0.73) [0.0074]	0.77 (0.73-0.79) [0.0041]	0.32 (0.31-0.36) [0.0043]
	Males	5	195.18 (174.9-233.5) [10.16]	0.66 (0.64-0.67) [0.0053]	0.70 (0.67-0.74) [0.011]	0.76 (0.75-0.78) [0.0048]	0.33 (0.32-0.34) [0.0028]
<i>C. rugosa</i>	Females	47	243.51 (189.9-303.9) [3.98]	0.63 (0.58-0.75) [0.0055]	0.69 (0.61-0.84) [0.0068]	0.77 (0.73-0.81) [0.0030]	0.34 (0.29-0.38) [0.0024]
	Males	24	210.58 (145.7-257.4) [5.37]	0.64 (0.56-0.75) [0.0077]	0.72 (0.63-0.83) [0.0084]	0.77 (0.73-0.83) [0.0051]	0.35 (0.31-0.37) [0.0031]

The most influential variable in the discrimination of females was HH (partial $r^2 = 0.55$; $F = 28.9$, $p < 0.0001$) followed by HWT (partial $r^2 = 0.43$, $F = 17.6$, $p < 0.0001$) and HL (partial $r^2 = 0.34$, $F = 11.2$, $p < 0.0001$), so differences in head shape were the most influential in providing overall discrimination between the three taxa. This is consistent with the fact that *C. burrungandjii* and the Kimberley form were first recognized as different species by differences in head shape. There was no clear partition of the raw variables in terms of their association with one or the other canonical variates, a situation not improved by varimax rotation, so we could not carry our interpretation further.

For males, the subset of variables that provided best discrimination were HWJ (partial $r^2 = 0.53$, $F = 12.2$, $p < 0.0005$), HH (partial $r^2 = 0.49$, $F = 11.0$, $p < 0.0005$), VT (partial $r^2 = 0.36$, $F = 5.8$, $p < 0.01$), and HL (partial $r^2 = 0.28$, $F = 4.0$, $p < 0.05$). A total of 92.5% of the among-groups variation was explained by the first canonical variate, which again provides the bulk of the discrimination between *C. rugosa* and the other two forms, but contributes little to the discrimination between *C. burrungandjii* and the Kimberley form (Fig. 7b). In contrast to the analysis for the females, discrimination was not particularly good. Two of the 14 *C. rugosa* were misclassified, one each to *C. burrungandjii* and the Kimberley form. Two of the 9 Kimberley males were misclassified as *C. burrungandjii* and two of the 4 male *C. burrungandjii* were misclassified as the Kimberley form. Hence, while the discrimination between *C. rugosa* and the other taxa is reasonably good, the distinction between *C. burrungandjii* and the Kimberley form breaks down for males. The distinction between these two may become more pronounced as they grow, and males grow to smaller sizes than females.

Distribution. — *Chelodina burrungandjii* is restricted to the Arnhem Land Plateau (Fig. 8), a large sandstone plateau in the Northern Territory. It is found rarely in the plunge pools at the base of the Arnhem escarpment. Specimens have been collected from the upper reaches of the

Mann, Liverpool, South Alligator, East Alligator, Katherine (Daly River drainage), and the Wilton rivers (Roper River drainage). The rivers of northeastern Arnhem Land, that is, east of the Goyder River, contain *C. rugosa* and Aboriginal people from the region do not appear to know of another long-necked species (*B. Wununngmurra*, *pers. comm.*).

Etymology. — The specific epithet *burrungandjii* derives from the proper noun *Burrungandji* used by the Gagadju people of the western Arnhem Land region (Gundjeihmi language) to distinguish the turtle from all other turtles in the region (Lucas and Russel-Smith, 1993). We chose this name to recognize the long association between Aboriginal people and the turtle and their prior and detailed knowledge of the freshwater turtle fauna of Australia.

Related Taxa. — The nearest living relative of *C. burrungandjii* is the undescribed *Chelodina* sp. (Kimberley). Their nearest relative is *C. rugosa* (holotype: AM R6256 from Cape York, Queensland, Australia).

DESCRIPTION

External Morphology

Carapace. — The carapace (Fig. 5) is oblong and flared over the hind legs in the region of M7–9. There is a second lesser expansion of the shell at M5, although this is subject to ontogenetic variation. The widest point of the carapace is usually at M8, and there is slight upturning of the marginals between M4 and M6. The scutes are smooth but there is a fine reticulated pattern over the entire carapace, and this is present in the underlying bone also. M2, M3, and M4 are the widest of the marginal scutes. A wide cervical scute is present. The first vertebral scute is significantly wider than the rest, a typical *Chelodina* condition. Vertebral formula is $V1 > V2 > V3 > V5 > V4$. In old specimens there is a marked median furrow along the vertebral region. The V1/C1 sulcus contacts the middle of M3; C1/C2 sulcus contacts

Table 3. Selected skull ratios — mean, (range), and [SE] — for three species of *Chelodina*. All ratio measurements divided by HL except HL divided by CL. See Appendix A for explanation of measurements.

Species	Sex	n	HL/CL	HWT	HWJ	ON	HH	TPL
<i>C. burrungandjii</i>	Females	7	0.29 (0.26-0.31) [0.0064]	0.71 (0.68-0.74) [0.0090]	0.58 (0.54-0.62) [0.0088]	0.06 (0.04-0.08) [0.0058]	0.18 (0.09-0.13) [0.0046]	0.40 (0.36-0.48) [0.014]
	Males	6	0.31 (0.29-0.37) [0.014]	0.64 (0.62-0.67) [0.0093]	0.53 (0.50-0.57) [0.012]	0.07 (0.06-0.08) [0.0038]	0.12 (0.11-0.12) [0.0022]	0.37 (0.32-0.45) [0.021]
<i>C. sp. (Kimberley)</i>	Females	14	0.28 (0.25-0.31) [0.0043]	0.72 (0.66-0.78) [0.0087]	0.61 (0.55-0.67) [0.0093]	0.07 (0.04-0.09) [0.0036]	0.14 (0.11-0.16) [0.0046]	0.37 (0.32-0.42) [0.0078]
	Males	5	0.28 (0.26-0.28) [0.0039]	0.71 (0.63-0.75) [0.022]	0.61 (0.55-0.67) [0.017]	0.08 (0.07-0.09) [0.0036]	0.14 (0.13-0.17) [0.0077]	0.38 (0.37-0.41) [0.0070]
<i>C. rugosa</i>	Females	47	0.28 (0.23-0.34) [0.0036]	0.66 (0.55-0.75) [0.0060]	0.54 (0.45-0.60) [0.0057]	0.08 (0.05-0.12) [0.0020]	0.17 (0.14-0.20) [0.0034]	0.35 (0.28-0.45) [0.0053]
	Males	24	0.27 (0.25-0.31) [0.0035]	0.65 (0.60-0.73) [0.0068]	0.53 (0.48-0.59) [0.0057]	0.08 (0.05-0.11) [0.0033]	0.17 (0.12-0.19) [0.0055]	0.34 (0.21-0.44) [0.0099]

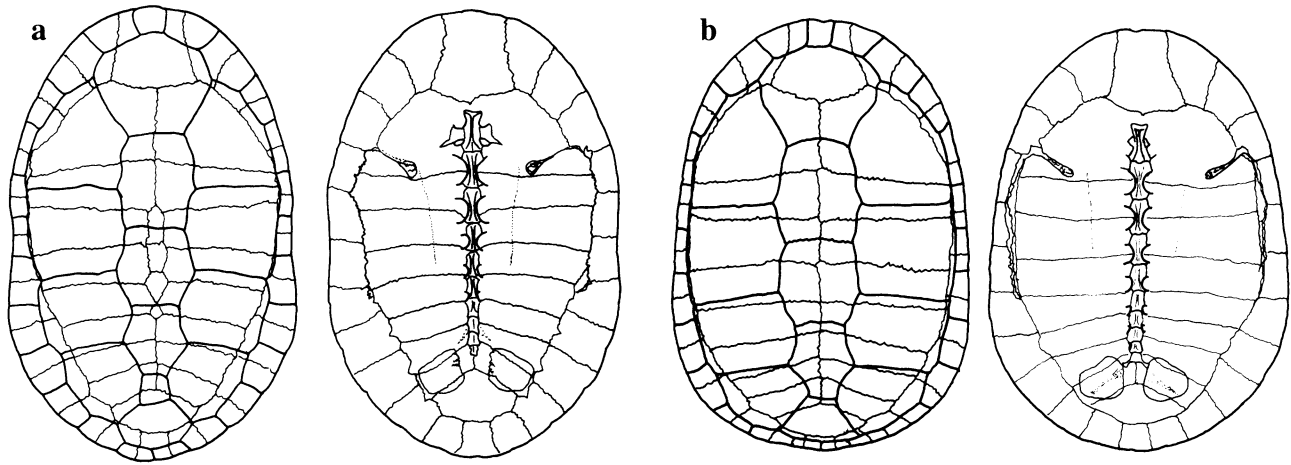


Figure 5. Dorsal and ventral view of the carapace of (a) *Chelodina burrungandjii* (UC 2101) and (b) *C. siebenrocki* (UC 0212).

the posterior of M4; C2/C3 sulcus contacts the anterior of M7; C3/C4 sulcus contacts the anterior of M9 and the C4/V5 sulcus contacts M11. The carapace is dark brown to black, occasionally brown with extensive darker mottling and striations.

Plastron. — The plastron (Fig. 6) is rectangular in general shape, in the sense that lines drawn to join the widest points of the anterior and posterior lobes of the plastron are roughly parallel. The widest point of the anterior lobe occurs toward its posterior extent, whereas that of the posterior lobe occurs in the middle. The scutes of the plastron are smooth, despite a fine reticulate pattern in the underlying bone. Plastral scute formula is: pect>int>fem>abd>hum>an>gul. The plastron and the ventral surfaces of the marginals are cream in color with no darkening of scute margins. They are commonly stained caramel brown to orange in larger, slower-growing individuals.

Head and Soft Parts. — The dorsal to mid-lateral surface of the head is covered with smooth, soft skin broken into numerous irregular uncornified scales of negligible relief, dark olive green to black in color, sometimes with fine black specks. Eyes are chocolate brown with a gold, occasionally orange, ring bordering the pupil. Upper rhamphotheca olive with light black flecks. Lower rhamphotheca olive with numerous black/brown striations. Tympanum is light olive with dark mottling. Barbels are variable in number, typically two are prominent, but up to four run in a line along the inside edge of each lower jaw. Ventral surface of head and throat in adults is covered with loose granular skin. Granules beneath the head often line up to form striations radiating back from the apex of the chin. In most animals, the ventral surface of the head and neck is cream to white; in others, the granulations may be alternating grey and white to form a speckled pattern. The dorsal surface of the neck is dark olive green with a dark mottling, which occasionally coalesces to black and is covered in small low blunt tubercles. Dorsum of limbs and tail similar coloration to dorsum of neck; ventral surface of limbs and tail uniform cream with slight granulation. Crescent shaped scales on limbs colored as per dorsum of limbs, even when

extending onto the lighter latero-ventral surfaces. The inguinal and axillary pockets are cream to white, typically unremarkable; rarely with heavy gray/mauve blotches evenly spaced and extending back from the sides of the neck. In juveniles, the speckled pattern of the ventral surfaces of the head and neck is usually absent; instead, the ventral surface of neck and limbs is cream, as are the inguinal and axillary pockets.

Size and Sexual Dimorphism. — All laparoscoped males up to 185 mm CL were immature whereas all males of 197 mm and greater were mature, hence sexual maturity in males occurs at around 185 to 197 mm CL. All laparoscoped females up to 217 mm CL were immature whereas all females of 229 mm and greater were mature, hence sexual maturity in females occurs around 217 to 229 mm CL. The largest mature female recorded in this study was 271.3 mm CL and the largest mature male 220.2 mm CL. The mean CL of the five largest females was 250.9 ± 2.3 mm and of the five largest males was 211.3 ± 2.8 mm, so the species shows sexual size dimorphism, as in other *Chelodina*. Mature males also have longer, thicker tails than females, a character that develops with onset of sexual maturity, as in other chelid turtles (Georges,

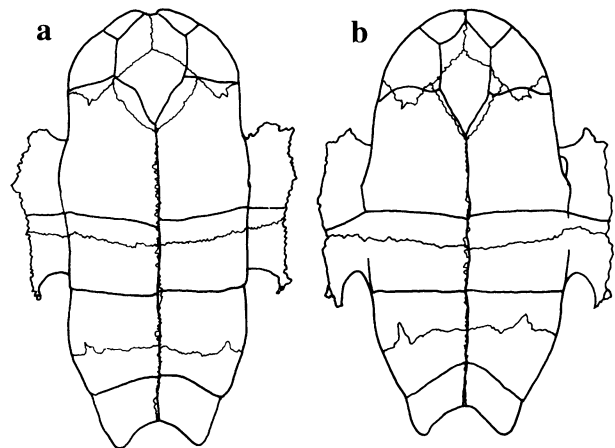


Figure 6. Ventral views of the plastron of (a) *Chelodina burrungandjii* (UC 2101) and (b) *C. siebenrocki* (UC 0212).

Table 4. Generalized multivariate distances between species within the *Chelodina expansa* group (*Chelodina* subgeneric group “B”). They were derived from a canonical discriminant analysis (SAS Institute, 1988) applied to all raw measurement ratios. *Chelodina rugosa* and *C. siebenrocki* are probably synonymous (Georges et al., in prep.), but are kept separate in this table until the additional data in support of this conclusion are published.

	<i>C. burrungandjii</i>	<i>C. sp.</i> (Kimberley)	<i>C. rugosa</i>	<i>C. siebenrocki</i>	<i>C. parkeri</i>	<i>C. expansa</i>
<i>C. burrungandjii</i>	—					
<i>C. sp.</i> (Kimberley)	5.7	—				
<i>C. rugosa</i>	25.3	18.0	—			
<i>C. siebenrocki</i>	29.7	23.5	3.0	—		
<i>C. parkeri</i>	50.2	43.5	16.1	14.8	—	
<i>C. expansa</i>	51.7	54.6	46.2	50.8	52.6	—

1983; Kennett, 1996). This species is smaller than *Chelodina rugosa*, making it the smallest Australian member of the *Chelodina expansa* group.

Osteology

Skull. — The skull of *C. burrungandjii* (Figs. 3–4) is highly flattened and shortened in comparison to other members of the *C. expansa* group (Table 3). The anterior head height of *C. burrungandjii* is approximately half that of the height of the tympanum, whereas in *C. rugosa* these measurements are approximately equal. The skull is deeply emarginated both posteriorly and temporally to the extent that the parietal roof is almost absent. It exists only as an enlarged process dorsal to the squamosal. The processi trochlearis pterygoidei are visible in their entirety from above. The eye sockets are large, set dorso-laterally in the skull and widely separated. Dorsally, the broadening of the frontal bone and the shortening of the maxillae (reducing the forward extent of the front of the skull) have yielded the shorter, wider skull shape. The interorbital length is similar to that of *C. rugosa*, but the diameter of the orbits is relatively smaller. Ventrally the palatines are shorter and broader than in *C. rugosa* and the vomer makes contact with the pterygoids in most specimens but divides the palatines in all specimens to some degree (Fig. 2), a character that also distinguishes this species from *C. expansa* and *Chelodina sp.* (Kimberley).

The basisphenoid is wider in comparison to other *C. expansa* group species and the quadrate is elongated from the medial contact with the basisphenoid to the lateral edge of the base of the tympanum. The quadrate is angled forward and is less robust than that of other species. The region of the squamosal into which the digastricus maxillae muscles insert is large, and extends towards the braincase as is typical of *C. expansa* group species. Likewise, the region of the squamosal dorsal to the tympanic cavity is narrowed to form a ridge, with no flattening or flaring. The crista paroccipitalis is narrow when viewed ventrally, a feature that is diagnostic for this species. The ventral process of the prefrontals is short and contacts the maxilla but is restricted to the dorsal orbit.

Cervical Spine. — The central cervical articulation formula (*sensu* Williams, 1950) is the same as for all chelid turtles and this would appear to be a synapomorphy for the Chelidae: (2(, (3(, (4(, (5(,)6(,)7(, (8). The atlas-axis complex (*sensu* Hoffstetter and Gasc, 1969) comprises paired neural arches laterally, the first centrum ventrally, and an intercentrum anteriorly. These units are completely fused into a single and elongated vertebra, and it is this unit which adds substantially to the neck length of *Chelodina*. The remaining cervicals are similar to each other in structure. The centra each possess a sagittal blade, forming a series that is least developed in the eighth cervical and highest in the second. The transverse processes are large and triangular in dorsal view and occupy the posterior third of the centrum. Each postzygapophosis is large and joins in the

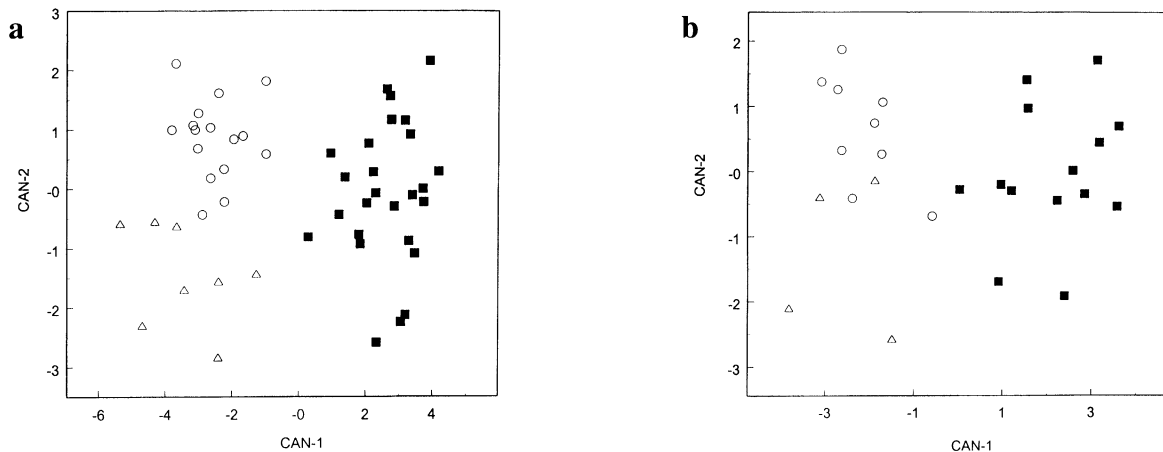


Figure 7. Specimens of *Chelodina rugosa* (■), *C. burrungandjii* (○), and *C. sp.* (Kimberley) (Δ) plotted in canonical variate space: (a) females; (b) males. In both analyses, 92.5% of the among-species variation was explained by CAN-1, which separated *C. rugosa* from the other forms. The remaining 7.5% was explained by CAN-2, which separated *C. burrungandjii* from the Kimberley form.

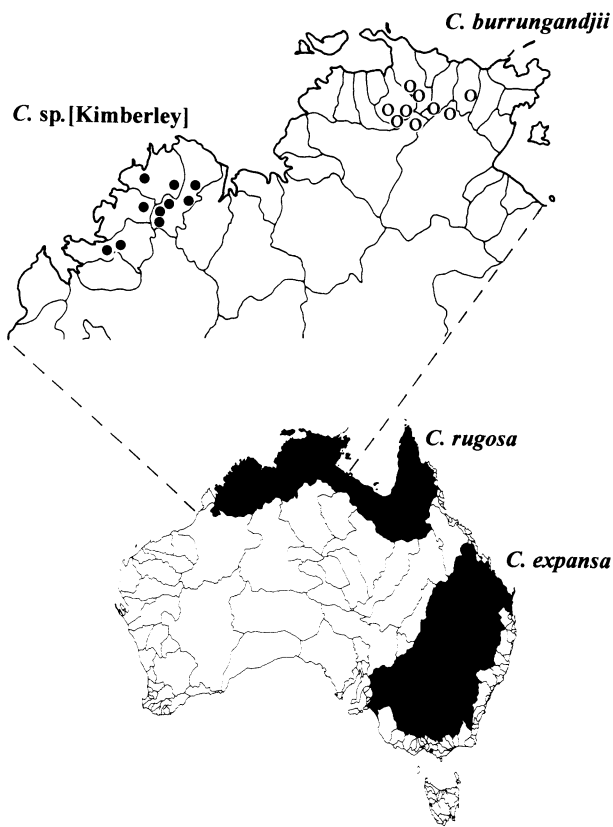


Figure 8. Distribution of *Chelodina* subgeneric group "B" species in Australia: generalized watershed distributions of *C. rugosa* and *C. expansa*, with specific localities for *C. burrungandjii* (○) and the undescribed *C. sp.* (Kimberley) (●); these latter two escarpment forms do not generally occur in microsympatry with the lowland *C. rugosa*.

midline with its partner to give a semilunar shape to the zygapophysis in cervicals three to eight.

Shell. — The carapace (Fig. 5) is made up of the usual complement of bones found in the Chelidae. The nuchal bone is approximately square in shape with elongation of peripherals one to three and pleural pair one present, as is typical in the *C. expansa* group. Dorsally there is usually a series of contiguous neural bones separating pleural pairs three to six. On examination of five shells neurals were always present, the number of exposed neurals ranged from three to five. The anterior bridge struts are enlarged and are at an angle of approximately 15° to the rib/gomphosis of pleural one. A medial expansion of the sutural surface is present with the rest of the suture equal in width to the peripheral-plastral suture. Medially to the expansion of the anterior bridge strut is a large muscle attachment rugosity. This rugosity runs posteriorly to the midpoint of the fourth pleural and is the attachment point for the retrahens capitis collicque muscles. The first four ribs are enlarged and expanded away from the vertebral column to make space for the enlarged longissimus dorsi muscles.

The gomphosis of pleural one inserts between peripherals four and five; pleural two inserts into the posterior third of peripheral five; pleural three into the posterior third of peripheral five; pleural four into the posterior third of pe-

ripheral six; pleural five into the posterior of peripheral seven; pleural six into the posterior of peripheral eight; pleural seven into the middle of peripheral nine; pleural eight into the middle of peripheral ten. Peripheral seven also contains the posterior bridge strut that does not make any contact with the pleurals.

The plastron (Fig. 6) is unusual among *Chelodina* in that the intergular is extremely wide. The most anterior point of the plastron, at the junction of the epiplastra, is not ossified. This causes the complete separation of the gular scutes and the encroachment of the intergular on the plastral margin in many specimens.

ECOLOGY

Habitat. — *Chelodina burrungandjii* occupies permanent water ranging from pools in rocky sandstone gorges and at the base of the escarpment, to more open riverine and billabong habitats with fringing riparian vegetation and often dense submergent and emergent aquatic vegetation (e.g., *Nymphaea* spp., *Nymphoides* spp.). In the Katherine River, it occurs in microsympatry with *Emydura subglobosa* (*Emydura* sp. aff. *subglobosa* of Georges and Adams, 1996) and in the Alligator Rivers region it occurs sympatrically with the common sawshell *Elseya latisternum*. More rarely, it can be found with *Elseya dentata* in plunge pools below the escarpment.

Reproductive Cycles. — The ovaries of six mature females (all examined in October–November) were in early stages of vitellogenesis, typically containing small numbers (2–5) of enlarged vitellogenic follicles (3–9 mm in diameter) and larger numbers of smaller follicles (< 2 mm). Two of these females had small (< 1–2 mm diameter) corpora lutea on their ovaries, most likely remaining from the previous breeding season. The ovaries of two females were in a quiescent phase with no enlarged follicles, but the presence of ovarian scars indicated a history of breeding. The remaining female was in a late stage of regression with several small (< 3 mm) atretic follicles, identified as such by their discoloration (Georges, 1983) and small (< 1 mm diameter) corpora lutea.

Six mature males (all examined in October–November) had enlarged vascularized testes and distended, white epididymes indicating that spermiogenesis and spermiation were underway. This pattern is broadly similar to that of *C. rugosa* in which testes and epididymes become enlarged in October–November and peak in January, followed by spermiation through February and March as testes and epididymes regress. Mating in *C. rugosa* is presumed to commence in January–February and may continue for several months (Kennett, 1994, 1999). More samples are needed to confirm if this pattern is typical of *C. burrungandjii*.

Diet. — *Chelodina burrungandjii* is predominantly carnivorous, feeding mainly on fish and shrimp. Nine turtles (39% excluding 7 with empty stomachs) had fed on fish, and fish accounted for 31% by weight of the pooled stomach contents. Fish species included the northern purple-spotted gudgeon (*Mogurnda mogurnda*) but unidentified species

were also present. *Chelodina burrungandjii* feeds voraciously in captivity and will devour 10–15 fish in a few minutes. Sixteen turtles (70%, excluding 7 with empty stomachs) had fed on *Macrobrachium* shrimp. Shrimp comprised 49% by weight of the total diet. Legler (1982) also reports a predominance of shrimp and fish in the diet and also recorded atyid shrimp, Orthoptera, and crab (probably *Holothusiana*).

Chelodina burrungandjii also feeds on plant material. Five individuals (22%, excluding 7 with empty stomachs) contained vegetation in their stomachs and vegetation comprised 20% by weight of the pooled stomach contents. In all but one case, vegetative matter comprised the entire stomach contents. One individual had consumed 6.3 g of plant material including leaves and bark from a freshwater mangrove (*Barrangtonia acutangula*), double the average weight of stomach contents (3.0 ± 0.52 g, $n = 23$). In one sample, the leaf material was folded and glued together, presumably as shelter for an aquatic invertebrate, and the leaf may have been ingested along with the invertebrate as the intended prey. Two individuals each contained an unidentified seed capsule. Feces from an individual from the Mann River comprised leaves only.

Chelodina burrungandjii probably utilizes both a sit-and-wait ambush strategy in addition to more active pursuit of prey. The broad flattened head likely represents an adaptation to a gape and suck mode of feeding (Pritchard, 1988; Legler and Georges, 1993). Sample sizes were inadequate for analysis but there did not appear to be sex or size bias in diet composition except that larger individuals (usually females) tended to consume larger individual prey items.

DISCUSSION

Chelodina burrungandjii is clearly a distinct species separate from *C. rugosa*, to which it was previously assigned. This is evident from the presence of discrete characters that diagnose the two and from the discriminant analysis based on measurements of the head and shell presented in this paper. It confirms the diagnostic differences identified using allozyme electrophoresis in a pilot study based on a single specimen of *C. burrungandjii* (Georges and Adams, 1992) and in a more substantial survey soon to appear (Georges et al., in prep.). Other workers are currently preparing formal description of the Kimberley form so we do not present such a description here. It is clearly very similar to *C. burrungandjii*, much more so than either are to *C. rugosa* (Table 3). However, specimens can be reliably assigned to either *C. burrungandjii* or the Kimberley form on both discrete character states and females can be unambiguously assigned in the canonical discriminant space. Unpublished electrophoretic analyses of Georges et al. (in prep.) indicates that the two have very recently diverged, lacking even a single fixed allelic difference.

The ecological data and anecdotal information provide additional evidence of a difference between *C. burrungandjii* and *C. rugosa*. The observed absence of large atretic fol-

licles and large corpora lutea indicates that *C. burrungandjii* had not nested in at least the 8–10 weeks prior to examination. It is likely that the follicles would have been even more degenerated if they had nested at the end of the wet season in March–April as does *C. rugosa* (Kennett, 1994, 1999). Degeneration of corpora lutea on the ovaries of *C. rugosa* is largely complete by the end of August and are only rarely observed later than this (Kennett, 1994, 1999). However, we cannot be definitive on the distinction between the nesting seasons of the two species because in some years when conditions permit, *C. rugosa* may continue nesting into the dry season, as late as July–August (Kennett, 1994, 1999). Dry-season nesting of *C. burrungandjii* is consistent with the knowledge of local Aboriginal people who report that they find nests of *C. burrungandjii* during the dry season and that it digs nests in riverside sand banks like a freshwater crocodile (Phyllis Windjarra, pers. comm., Sarah Flora, pers. comm.). This suggests that *C. burrungandjii* does not nest underwater like its congener *C. rugosa* (Kennett et al., 1992), but given the close taxonomic relationship between the two species (Georges and Adams, 1992), the tolerance of *C. burrungandjii* eggs to immersion (Kennett et al., 1993, 1998; Seymour et al., 1997) is worthy of further investigation.

Waterbodies occupied by *C. burrungandjii* undergo dramatic annual fluctuations in depth, water flow, and turbidity under the influence of the monsoonal wet-dry climate of the region. During the dry season, when water levels are lower, groups of Aboriginal people hunt turtles by wading through the water and feeling for turtles with their hands and feet. Unlike the shallow ephemeral flood plain habitats occupied by *C. rugosa*, waterbodies occupied by the *C. burrungandjii* rarely dry completely. According to local Aboriginal people, *C. burrungandjii* does not estivate underground during the dry season as *C. rugosa* does, but whether this arises from lack of capability or lack of necessity is uncertain.

The diet of *C. burrungandjii* is also distinctly different from that of *C. rugosa* (Kennett and Tory, 1996), in that it appears to feed, at least partially, on plant material. Local Aboriginal people also report that *C. burrungandjii* feeds on leaves and flowers of water lilies, seeds of *Pandanus* spp., and leaves of the freshwater mangrove (*Barrangtonia acutangula*) (Sandy Baraway, pers. comm.; Jessie Brown, pers. comm.). Legler (1982) also regarded a high occurrence of vegetable material in stomach samples of *C. burrungandjii* as evidence of partial herbivory. The vegetable material included unidentified fruits and pieces of bark, leaves, and roots of *Pandanus* spp. Carnivory is the rule among *Chelodina*, so the partial herbivorous tendencies of *C. burrungandjii* are unusual. It may represent an adaptation to depauperate sandstone environments and seasonal shortages of fish and shrimp prey.

ACKNOWLEDGMENTS

We thank Ross Sadlier (AM), Patrick Couper (QM), Paul Horner (NTM), John Legler (University of Utah), and Peter Pritchard (Chelonian Research Institute) for loans and

access to museum material. Logistic support for this study was provided by the Parks and Wildlife Commission NT. The assistance of Brent Williams and other park staff at Nitmiluk National Park is especially acknowledged. We thank the Jawoyn people, especially Sandy Barraway, for permission to work on their lands and for providing information on Aboriginal knowledge of the turtles. We thank Meredith Anderson, Glenda Georges, Sean Doody, Jeanne and Marie Young, Jane Kahler, Grant Flanagan, Cameron Yates, Colin Wilson, and Chris Jones for assistance in the field. We thank Brent Williams, Peter Pritchard, Anders Rhodin, and John Legler for helpful comments on the manuscript, Virginia Ebsworth for sorting stomach samples, and Karen Coombes for identifying shrimp. The study was funded in part by the CRC for Freshwater Ecology, Canberra (ASCW-208).

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APPENDIX A
Descriptions of Measurement Used

Skull. — HL: Head length; straight line from base of nose to the back of the crista supraoccipitalis. HWT: Head width tympanum; maximum straight width of skull at tympanum. HWJ: Head width jaw; maximum straight width of skull at posterior of maxilla. PW: Parietal width; width of skull at juncture of the parietals and frontal. IO: Interorbital width; width of frontal bone between the orbits. OD: Orbital diameter; horizontal maximum straight diameter of the orbit. ON: Orbital nasal distance; minimum distance from the orbit to the external naris. HH: Head height; vertical height of skull from the palate to the frontal. HT: Horizontal diameter of the otic chamber: measured from the external ridges of the otic chamber on the quadrate. VT: Vertical diameter of the otic chamber: measured from the condyle mandibularis to the top of the otic chamber. TPL: Tympanum to parietal length; length of the remainder of the parietal arch from the tympanum on the quadrate to the end of the arch.

Shell. — CL: Carapace length; from the cervical to the suprapygial. CW4: Carapace width four; straight width at the junction of the fourth and fifth marginal scutes. CW8: Carapace width eight; straight width at the juncture of the seventh and eighth marginal scutes. V1: Width vertebral one; maximum width of the first vertebral scute. V2: Width vertebral two; maximum width of the second vertebral scute. PL: Plastron length; midline length of the plastron. PLF: Width of anterior lobe of plastron measured in straight line at the junction of the humerals and pectorals. PLR: Width of posterior lobe of plastron measured in straight line at the junction of the abdominals and femorals.

APPENDIX B
Specimens Examined

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. NT = Northern Territory; WA = Western Australia; QLD = Queensland; NSW = New South Wales.

Chelodina burrungandjii: UC 2088-90, 2101 Gynyard pools, adjacent to Katherine R. Gorge, NT (14°18'30"S, 133°31'10"E); NTM 13525 Mann R., upper reaches, NT (13°01'S, 133°58'E); NTM 16008-12 Koolpin Gorge, NT (13°28'S, 132°38'E); NTM 16333, 22581-83 Slesbeck, Katherine R., NT (13°47'S, 132°49'E); UU 17730-31 Avis Lagoon, Liverpool R., Arnhem Land, NT (12°45'S, 133°49'E); UU 17732 Double B., East Alligator R., Arnhem Land, NT (13°09'S, 133°22'E); UU 17733-34 Liverpool R., Arnhem Land, NT (12°37'S, 133°55'E); UU 17735, 18859 Mann R., Arnhem Land, NT (15°01'S, 133°58'E); UU 17736 Jimjim Waterhole, 4 km south and 3 km east Cooinda, NT (12°57'S, 132°33'E); UU 17737 South Alligator R., 9.5 km north and 25 km east Cooinda, NT (12°49'S, 132°33'E); UU 18833 Katherine R., Arnhem Land, NT (13°22'S, 133°08'E); UU 18834-39 Magela Cr., 17.5 km north Kub-O-Wer Hill, NT (12°50'S, 133°03'E); UU 18840-41 East Alligator R., Arnhem Land, NT (13°12'S, 133°19'E); UU 18842-52 Jim Jim Cr., Arnhem Land, NT (13°19'S, 133°01'E);

UU 18853-58 Wilton R., 14.5 km southeast Shadforth Hills, NT (13°14'S, 134°12'E);

Chelodina expansa: QM J59284, UC 0223 unknown;

Chelodina longicollis: QM 59266, UC 0199 Hawkesbury R., NSW (33°45'S, 150°42'E), QM 59267-68, 59281-2 Jervis Bay, NSW (35°08'S, 150°42'E), QM 59274, UC 0134, 0164, 0169 Canberra, NSW (35°17'S, 149°08'E), UC 0166 Oasis Creek, Dubbo, NSW (32°15'S, 148°36'E), UC 0174 Mumber, nr. Rockhampton, QLD (23°23'S, 150°31'E);

Chelodina mccordi: UC 2005, 2008-9, 2011-13, 2015-19 Roti Island, Indonesia (11°00'S, 123°00'E);

Chelodina novaeguineae: UC 0324-5 nr. Elliott, NT (17°30'S, 133°35'E), UC 2014, 2022, 2025-6, 2030 Balimo, Papua New Guinea (8°5'S, 142°50'E);

Chelodina oblonga: QM 59272-73, 59283, UC 0161-63 Perth, WA (31°56'S, 115°50'E);

Chelodina parkeri: UC 0215, 0220, 2006-7 Fly R. District, Papua New Guinea (7°0'S, 141°30'E);

Chelodina pritchardi: UC 2038-42, 2044 Kemp Welch R., Papua New Guinea (9°55'S, 147°40'E);

Chelodina reimanni: UC 2021, 2023-24, 2027-29 Merauke, Irian Jaya, Indonesia (8°50'S, 140°30'E);

Chelodina rugosa: QM 59264 Darwin area, NT; UC 0302, 0320-23, 0326-27 Douglas R., NT (13°40'S, 131°10'E);

Chelodina siebenrocki: UC 0212, 2010, 2020 Fly R. District, Papua New Guinea (7°0'S, 141°30'E);

Chelodina sp. (Kimberley): UU 17738-55, 18831-32 Campbell Creek 4 km southwest of Ellenbrae Homestead, WA (15°59'S, 127°02'E); UU 17756 Hann R., 10 km southeast Gibb R. Station, WA (16°28'S, 126°21'E); UU 17757 Barnett R. Gorge, 27 km northeast of Mt. Barnett Homestead, WA (16°32'S, 127°08'E); UU 17758-60 Carson R., 3.2 km westnorthwest of Carson R. Homestead, WA (14°29'S, 126°44'E); UU 17761 Carson R., 17 km south and 1.5 km east of Kalumburu, WA (14°27'S, 126°44'E); UU 17762-65 Drysdale R., 4 km northeast of Drysdale R. Homestead, WA (15°31'S, 126°24'E); UU 17766-69 Mitchell R., 2.5 km westsouthwest of Mitchell R. Homestead, WA (15°08'S, 125°46'E); UU 17770-75 Isdell R., 34.5 km west and 4.5 km north of Mt. House Homestead, WA (17°01'S, 125°26'E); UU 18157 Manning Cr., 2.5 km west Mt. Barnett Station, WA (16°39'S, 125°55'E); UU 18158 Adcock R., Mt. House, WA (17°03'S, 125°42'E); UU 18515-17 Kalumburu, WA (14°17'S, 126°39'E); UU 18818-30 Drysdale R., Drysdale R. Homestead, WA (15°31'S, 126°24'E); AM 123805 Mitchell Plateau, upstream from Little Merten's Falls, WA (14°49'S, 125°43'E); AM 133443-44, 136171 Merten's Creek, tributary of Mitchell R., Mitchell Plateau, WA (14°49'S, 125°43'E); AM 133445, 136148-52 vic. of Surveyors Pool, tributary of Mitchell R., Mitchell Plateau, WA (14°40'S, 125°44'E); AM 136058-65, 137999 Bell's Creek, approx. 3.5 km upstream from Bell's Gorge, Isdell R., WA (17°01'S, 125°12'E); AM 140403, 143558 Manning Gorge, Mount Barnett Station, WA (16°39'S, 125°55'E); AM 142496 Bell's Gorge, WA (17°01'S, 125°12'E).

Received: 7 March 1999

Reviewed: 29 January 2000

Revised and Accepted: 15 June 2000