A New Species of Long-Necked Turtle (Testudines: Chelidae) from the Arnhem Land Plateau, Northern Territory, Australia

SCOTT THOMSON, ROD KENNETT, AND ARTHUR GEORGES

Published by Chelonian Research Foundation in association with IUCN/SSC Tortoise and Freshwater Turtle Specialist Group, IUCN/SSC Marine Turtle Specialist Group, Chelonian Research Institute, Conservation International, Chelonia Institute, Wildlife Conservation Society, and IUCN (The World Conservation Union) – Species Survival Commission
A New Species of Long-Necked Turtle (Testudines: Chelidae) from the Arnhem Land Plateau, Northern Territory, Australia

SCOTT THOMSON1, ROD KENNETT2, and ARTHUR GEORGES3

1Applied Ecology Research Group and CRC for Freshwater Ecology, University of Canberra, ACT 2601, Australia [Fax: 61-2-6201-5305];
2Centre for Indigenous Natural and Cultural Resource Management and Faculty of Science, Northern Territory University, Darwin, NT 0809, Australia

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 burragangdji, sp. nov.; turtle; taxonomy; 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 Elersia macracus (Cann and Legler, 1994), known to science for 20 years only as specimens of unknown origin in the pet trade, the white-eyed river diver Rheodytes leukops (Legler and Cann, 1980), the ‘living fossil’ Elersia lavarackorum from the Nicholson drainage of Queensland (Thomson et al., 1997), the Bellinger River turtle Elersia geographic (Cann, 1998a), the northern yellow-faced turtle Elersia tanyxantha (Cann, 1998b), and the yellow-headed snapping turtle Elersia immirvi (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 Burragangdji. They distinguish it from Aloungiyi (Chelodina rugosa), a common and closely-related species of the coastal floodplains (Lucas and Russel-Smith, 1953). The Jawoyn people of the Katherine region (including Nitmiluk National Park and the southern sections of Kakadu National Park) refer to it as Wurrungay (Sandy Barway, 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 burrungandji 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 (13°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 (13°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, 1841
Chelodina burrungandji, sp. nov.
Arnhem Land Long-Necked Turtle
(Figs. 1-3, 5-6)

Type Specimens. — Holotype: NTM 16101 (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;...
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 plastras, broader heads, and a more attenuated mode of strike-and-gape feeding (excluding Chelodina oblonga from this comparison). Chelodina burrungandji 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 distinguished (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. burrungandji can also be distinguished by the lack of the pronounced head striping and post-typanic 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. burrungandji of an expanded contiguous neural series of between three and five neurals (Thomson and Georg, 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 pterygoïds 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. burrungandji 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 burrungandji held in museums. Refer to Appendix A for explanation of measurements.

<table>
<thead>
<tr>
<th>Museum No.</th>
<th>Sex</th>
<th>CL</th>
<th>CW4</th>
<th>CW8</th>
<th>PL</th>
<th>PLF</th>
<th>PLR</th>
<th>HL</th>
<th>HWT</th>
<th>HH</th>
</tr>
</thead>
<tbody>
<tr>
<td>UC 2088 F</td>
<td>242.0</td>
<td>150.9</td>
<td>159.0</td>
<td>188.0</td>
<td>72.8</td>
<td>77.5</td>
<td>61.9</td>
<td>43.6</td>
<td>7.6</td>
<td></td>
</tr>
<tr>
<td>UC 2089 M</td>
<td>206.3</td>
<td>126.8</td>
<td>138.3</td>
<td>160.4</td>
<td>65.1</td>
<td>68.5</td>
<td>60.5</td>
<td>59.7</td>
<td>7.1</td>
<td></td>
</tr>
<tr>
<td>UC 2090 F</td>
<td>240.3</td>
<td>148.8</td>
<td>159.2</td>
<td>185.2</td>
<td>79.4</td>
<td>83.4</td>
<td>66.9</td>
<td>48.7</td>
<td>8.8</td>
<td></td>
</tr>
<tr>
<td>UC 2101 F</td>
<td>266.3</td>
<td>169.1</td>
<td>171.7</td>
<td>195.4</td>
<td>83.4</td>
<td>85.4</td>
<td>75.6</td>
<td>55.3</td>
<td>9.1</td>
<td></td>
</tr>
<tr>
<td>NTM 15235 M</td>
<td>220.0</td>
<td>131.1</td>
<td>136.6</td>
<td>166.7</td>
<td>69.5</td>
<td>72.8</td>
<td>68.1</td>
<td>44.0</td>
<td>7.7</td>
<td></td>
</tr>
<tr>
<td>NTM 15008 F</td>
<td>281.2</td>
<td>175.8</td>
<td>182.3</td>
<td>197.3</td>
<td>85.2</td>
<td>93.8</td>
<td>81.6</td>
<td>56.8</td>
<td>7.7</td>
<td></td>
</tr>
<tr>
<td>NTM 16099 M</td>
<td>213.3</td>
<td>137.8</td>
<td>145.7</td>
<td>168.2</td>
<td>71.3</td>
<td>82.0</td>
<td>65.8</td>
<td>46.1</td>
<td>8.3</td>
<td></td>
</tr>
<tr>
<td>NTM 16010 F</td>
<td>220.7</td>
<td>138.1</td>
<td>140.7</td>
<td>176.2</td>
<td>72.4</td>
<td>73.9</td>
<td>67.8</td>
<td>47.0</td>
<td>7.8</td>
<td></td>
</tr>
<tr>
<td>NTM 16011 M</td>
<td>189.8</td>
<td>116.2</td>
<td>127.1</td>
<td>143.6</td>
<td>60.7</td>
<td>65.3</td>
<td>58.2</td>
<td>36.7</td>
<td>6.7</td>
<td></td>
</tr>
<tr>
<td>NTM 16012 M</td>
<td>166.4</td>
<td>98.6</td>
<td>105.2</td>
<td>133.9</td>
<td>53.6</td>
<td>56.2</td>
<td>60.7</td>
<td>37.6</td>
<td>7.1</td>
<td></td>
</tr>
<tr>
<td>NTM 16333 M</td>
<td>199.2</td>
<td>126.4</td>
<td>135.7</td>
<td>148.3</td>
<td>65.4</td>
<td>70.5</td>
<td>57.9</td>
<td>38.9</td>
<td>8.7</td>
<td></td>
</tr>
<tr>
<td>NTM 22581 F</td>
<td>266.8</td>
<td>170.0</td>
<td>185.4</td>
<td>203.8</td>
<td>90.4</td>
<td>93.8</td>
<td>74.9</td>
<td>52.3</td>
<td>8.7</td>
<td></td>
</tr>
<tr>
<td>NTM 22582 F</td>
<td>246.3</td>
<td>161.3</td>
<td>158.3</td>
<td>186.6</td>
<td>78.1</td>
<td>82.7</td>
<td>72.6</td>
<td>54.0</td>
<td>9.3</td>
<td></td>
</tr>
<tr>
<td>NTM 22583 J</td>
<td>115.4</td>
<td>75.4</td>
<td>81.7</td>
<td>89.3</td>
<td>36.9</td>
<td>42.2</td>
<td>38.3</td>
<td>24.1</td>
<td>5.2</td>
<td></td>
</tr>
</tbody>
</table>
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. burrrrgandjii 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. burrrrgandjii 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) 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. burrrrgandjii 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. burrrrgandjii 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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sex</th>
<th>CL</th>
<th>CW4</th>
<th>CW8</th>
<th>PL</th>
<th>PLF</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. burrrrgandjii</td>
<td>Females 7</td>
<td>249.13 (220.8-266.8)</td>
<td>0.64 (0.61-0.67)</td>
<td>0.66 (0.64-0.70)</td>
<td>0.76 (0.73-0.80)</td>
<td>0.32 (0.30-0.34)</td>
</tr>
<tr>
<td></td>
<td>Males 6</td>
<td>199.37 (166.4-220.9)</td>
<td>0.62 (0.59-0.65)</td>
<td>0.66 (0.62-0.68)</td>
<td>0.77 (0.74-0.81)</td>
<td>0.32 (0.31-0.37)</td>
</tr>
<tr>
<td>C. sp. (Kimberley)</td>
<td>Females 14</td>
<td>232.21 (146.4-293.1)</td>
<td>0.65 (0.55-0.69)</td>
<td>0.68 (0.63-0.73)</td>
<td>0.77 (0.73-0.79)</td>
<td>0.32 (0.31-0.36)</td>
</tr>
<tr>
<td></td>
<td>Males 5</td>
<td>195.38 (174.9-233.5)</td>
<td>0.64 (0.64-0.67)</td>
<td>0.70 (0.67-0.74)</td>
<td>0.79 (0.75-0.87)</td>
<td>0.33 (0.32-0.34)</td>
</tr>
<tr>
<td>C. rugosa</td>
<td>Females 47</td>
<td>243.51 (180.9-303.3)</td>
<td>0.63 (0.58-0.75)</td>
<td>0.69 (0.61-0.84)</td>
<td>0.77 (0.73-0.81)</td>
<td>0.34 (0.29-0.38)</td>
</tr>
<tr>
<td></td>
<td>Males 24</td>
<td>210.58 (145.7-257.4)</td>
<td>0.64 (0.56-0.75)</td>
<td>0.72 (0.63-0.83)</td>
<td>0.83 (0.73-0.83)</td>
<td>0.37 (0.31-0.37)</td>
</tr>
</tbody>
</table>
The most influential variable in the discrimination of females was HH (partial $r^2 = 0.55$; $F = 28.9, p < 0.0001$) followed by HW (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 size were the most influential in providing overall discrimination between the three taxa. This is consistent with the fact that *C. burrungandji* 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 $r^2 = 0.36$, $F = 5.8, p < 0.01$), 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. burrungandji* and the Kimberley form (Fig. 7b). In contrast to the analysis for the females, discrimination was not particularly good. Two of the 14 females were misclassified, one each to *C. burrungandji* and the Kimberley form. Two of the 9 Kimberley males were misclassified as *C. burrungandji* and two of the 4 male *C. burrungandji* were misclassified as the Kimberley form. Hence, while the discrimination between *C. rugosa* and the other taxa is reasonably good, the distinction between *C. burrungandji* 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 burrungandji* 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. Wunungmurra, pers. comm.).

**Etymology.** The specific epithet *burrungandji* derives from the proper noun *Burrungandji* used by the Gagadja people of the western Arnhem Land region (Gundjeihmi language) to distinguish the turtle from all other turtles in the region (Lucas and Russell-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. burrungandji* is the undescribed *Chelodina* sp. (Kimberley). Their nearest relative is *C. rugosa* (holotype: AM R6256 from Cape York, Queensland, Australia).

---

**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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sex</th>
<th>H/C</th>
<th>HL/CL</th>
<th>HWJ</th>
<th>HW</th>
<th>ON</th>
<th>HH</th>
<th>TPL</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>C. burrungandji</em></td>
<td>Females</td>
<td>7</td>
<td>0.29</td>
<td>(0.26-0.31)</td>
<td>0.71</td>
<td>(0.66-0.74)</td>
<td>0.58</td>
<td>(0.54-0.62)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Males</td>
<td>6</td>
<td>0.31</td>
<td>(0.29-0.37)</td>
<td>0.64</td>
<td>(0.52-0.67)</td>
<td>0.53</td>
<td>(0.50-0.57)</td>
</tr>
<tr>
<td><em>C. sp. (Kimberley)</em></td>
<td>Females</td>
<td>14</td>
<td>0.28</td>
<td>(0.25-0.31)</td>
<td>0.72</td>
<td>(0.66-0.78)</td>
<td>0.61</td>
<td>(0.55-0.67)</td>
</tr>
<tr>
<td></td>
<td>Males</td>
<td>5</td>
<td>0.28</td>
<td>(0.26-0.28)</td>
<td>0.71</td>
<td>(0.67-0.75)</td>
<td>0.61</td>
<td>(0.55-0.67)</td>
</tr>
<tr>
<td><em>C. rugosa</em></td>
<td>Females</td>
<td>47</td>
<td>0.28</td>
<td>(0.23-0.34)</td>
<td>0.66</td>
<td>(0.55-0.75)</td>
<td>0.53</td>
<td>(0.45-0.60)</td>
</tr>
<tr>
<td></td>
<td>Males</td>
<td>24</td>
<td>0.27</td>
<td>(0.23-0.34)</td>
<td>0.65</td>
<td>(0.50-0.73)</td>
<td>0.51</td>
<td>(0.48-0.59)</td>
</tr>
</tbody>
</table>

**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. 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+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 the...
Figure 5. Dorsal and ventral view of the carapace of (a) *Chelodina burn Surgery* (UC 2101) and (b) *C. sienbrocki* (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 mot-
tling 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: pec>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 unciniform scales of negligible relief, dark olive green to black in color, sometimes with fine black specks. Eyes are chocolate brown with a gold, occa-
sionally orange, ring bordering the pupil. Upper rhamphotheca olive with lighl black flecks. Lower rhamphotheca olive with numerous black/brown splotches. 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 alternat-
ing gray 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 blant 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 in-
guinal 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,
Table 4. Generalized multivariate distances between species within the Chelodina expansa group (Chelodina subgeneric group "E").

<table>
<thead>
<tr>
<th></th>
<th>C. barringtoni</th>
<th>C. sp. (Kimberley)</th>
<th>C. rugosa</th>
<th>C. siebenrocki</th>
<th>C. purkuri</th>
<th>C. expansa</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. barringtoni</td>
<td>—</td>
<td>5.7</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>C. sp. (Kimberley)</td>
<td>25.3</td>
<td>18.0</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>C. rugosa</td>
<td>29.7</td>
<td>23.5</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>C. siebenrocki</td>
<td>50.2</td>
<td>43.5</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>C. expansa</td>
<td>51.7</td>
<td>56.4</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

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. barringtoni (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. barringtoni 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 process 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).

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: \( (2(5, (3(6, (4(7, (8) \). The atlas-axis complex (sensu Hoffstetter and Gasc, 1969) comprises paired neural arches laterally, the first centrum ventrally, and an intercentrum anterio. 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 procoelous apophysis is large and joins in the

Figure 7. Specimens of Chelodina expansa (a), C. barringtoni (b), and C. sp. (Kimberley) (c) 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. barringtoni from the Kimberley form.
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 the rugosa.

Figure 8. Distribution of Chelodina subgenetic species “B” in Australia, generalized watershed distributions of C. rugosa and C. expansa, with specific localities for C. burrenogundji and the undescribed C. sp. (Kimberley). These latter two escarpment forms do not generally occur in microsympathy with the lowland C. rugosa.

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

ECOLOGY

Habitat. — Chelodina burrenogundji occupies permanent water ranging from pools in rocky sandstone gorges and at the base of the escarpment, to open riverine and billabong habitats with fringing riparian vegetation and offers submergent and emergent aquatic vegetation (e.g., Nymphae sp., Nymphae sp.). In the Katherine River, it occurs in microsympathy with Eryxura subglobosa (Eryxura sp. aff. subglobosa of Georges and Adams, 1996) and in similar riverine and emergent aquatic vegetation (e.g., Eryxura subglobosa). More recently, it can be found with Eryxura dentata in plunge pools below the escarpment.

Reproductive Cycles. — The ovaries of six mature females (all examined in October-November) had enlarged vascularized testes and distended, white epididymes, indicating that spermiogenesis and spermiation are 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 regression through February and March. More rarely, it can be found with Eryxura dentata in plunge pools below the escarpment.

Distribution of Chelodina subgenetic species “B” in Australia, generalized watershed distributions of C. rugosa and C. expansa, with specific localities for C. burrenogundji and the undescribed C. sp. (Kimberley). These latter two escarpment forms do not generally occur in microsympathy 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 the rugosa.

Figure 8. Distribution of Chelodina subgenetic species “B” in Australia, generalized watershed distributions of C. rugosa and C. expansa, with specific localities for C. burrenogundji and the undescribed C. sp. (Kimberley). These latter two escarpment forms do not generally occur in microsympathy 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 the rugosa.

Figure 8. Distribution of Chelodina subgenetic species “B” in Australia, generalized watershed distributions of C. rugosa and C. expansa, with specific localities for C. burrenogundji and the undescribed C. sp. (Kimberley). These latter two escarpment forms do not generally occur in microsympathy with the lowland C. rugosa.
were also present. *Chelodina burrungandjii* feeds voraciously on fish that will die in 10–15 fish in a minute. 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 ayard shrimp, Orthoptera, and crab (probably *Holothusiana*).

*Chelodina burrungandjii* also feeds on plant material. Five individuals (25%, 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 material comprised the entire stomach contents. One individual had consumed 6.3 g of plant material including leaves and bark from a freshwater mangrove (*Burrungtorzicr 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 gap cove 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 nascas contents 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* and the Kimberley form on both discrete character states and females can be unambiguously assigned in the canonical discriminant space. Unpublished electrophoretic analyses of *C. burrungandjii* (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 atlatic follicles and large corpora lutea indicates that *C. burrungandjii* had not nested in the Kimberley area in the year 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 in 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 (*Phyllisi Windjariar, pers. comm., Sarah Flor, pers. comm.*). This suggests that *C. burrungandjii* does not estivate underground 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 feeding for turtles with their hands and feet. Unlike the shallow ephemeral flood plains habituated by *C. rugosa*, waterbodies occupied by *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 capacity 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 (*Burrungtorzicr acutangula*) (Sandy Barraway, pers. comm.; Jessie Brown, pers. comm.; Legler, 1982) and is known to forage for marine invertebrates. The vegetable material included unidentified fruits and pieces of bark, leaves, and roots of *Pandanus* spp. Carevory is the rule among *Chelodina*, so the partial herbivorous tendencies of *C. burrungandjii* are unusual. It may represent an adaptation to deplete 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 Jarawyn 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 Dootly, Jeanne 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).

LITERATURE CITED


