

A New Species of *Chelodina* (Testudines: Pleurodira: Chelidae) from Northern Australia

WILLIAM P. MCCORD^{1,2} AND SCOTT A. THOMSON³

¹East Fishkill Animal Hospital, 455 Route 82, Hopewell Junction, New York 12533, USA; E-mail: chelodina@aol.com

³Applied Ecology Research Group and CRC for Freshwater Ecology, University of Canberra, Canberra, Australia Capital Territory 2601, Australia; E-mail: thomson@aerg.canberra.edu.au

ABSTRACT.—A new species of long-necked turtle from the *Chelodina longicollis* group is described from northern Australia; the species *Chelodina novaeguineae* is restricted to southern New Guinea. The new species differs from its New Guinea counterpart in being a larger species with a broader shell and wider plastron, the skull having paired premaxillae and a narrower parietal ridge, having a single frontal bone, posteriorly partially dividing the parietals, in the form and relationship to the pterygoids of the vomer, and a narrower crista paroccipitalis.

The taxonomy of Australian Chelid turtles has only recently received the attention it deserves. Within the genus *Eseya*, eight new species have been identified, of which four are now described (Georges and Adams, 1992, 1996; Thomson et al., 1997b; Cann, 1997a,b). In addition, one new species of *Emydura* has been described and a large group of invalid taxa identified (Georges and Adams, 1996; Cann, 1997c). At the generic level, inconsistencies between the accepted taxonomy and recent phylogenies have been demonstrated, such as the paraphyly of the genus *Eseya* (Georges and Adams, 1992, 1996).

Long-necked turtles of the genus *Chelodina* occur in Australia, Papua New Guinea, and Indonesia (Irian Jaya and Roti Island) with no specimens, fossil or otherwise, found outside these regions (Rhodin, 1994a; Georges and Thomson, 2002). The genus has been poorly studied taxonomically with recent work focusing in New Guinea (Philippen and Grossman 1990, Rhodin 1994a,b) rather than Australia. The genus is generally recognized to consist of two distinctive groups known as *Chelodina* subgeneric group "A" (*Chelodina longicollis* group) and *Chelodina* subgeneric group "B" (*Chelodina expansa* group; Goode, 1967; Burbidge et al., 1974; Rhodin, 1994a,b; Georges et al., 1998; Thomson, 2000). The *C. longicollis* group currently contains the species: *C. longicollis*, *Chelodina mccordi*, *Chelodina novaeguineae*, *Chelodina oblonga*, *Chelodina pritchardi*, *Chelodina reimanni*, and *Chelodina steindachneri*. The *Chelodina expansa* group contains *Chelodina burrungandjii*, *Chelodina expansa*, *Chelodina kuchlingi*, *Chelodina parkeri*, *Chelodina rugosa*, and *Chelodina siebenrocki* (Rhodin, 1994a,b; Seddon et al., 1997; Cann 1998; Thomson et al., 2000; Georges et al., 2002). *Chelodina*

rankini (Wells and Wellington, 1985), from northeastern Queensland may also be added to the *C. longicollis* group; however, the original description of *Chelodina rankini* contains no diagnosis, does not refer to a published diagnosis that claims to distinguish the species, and refers only to plates published by others. This is not a valid means of obtaining a diagnosis, and none of the other literature cited "purports to give characters differentiating the taxon." We, therefore, consider the name *C. rankini* as a nomen nudum under Article 13a (i) and (ii) of the International Code of Zoological Nomenclature (see also Iverson et al. 2001). It is, therefore, an unavailable name and will not be used in this paper. The position of *C. oblonga* (see *Chelodina colliei*, Thomson, 2000) in this arrangement is controversial. It has been placed in subgeneric group "C" by itself (Burbidge et al., 1974) and into the *C. expansa* subgeneric group "B" (Goode, 1967) in the past. Recent evidence from allozyme electrophoresis (Georges and Adams, 1992; Georges et al., 2002) and mtDNA sequence data (Seddon et al., 1997) places it as the sister of the *C. longicollis* group, a position supported by recent morphological analysis (Thomson et al., 1997a; Thomson, 2000; Georges and Thomson, 2002).

The full range and distribution of the species referred to as *C. novaeguineae* have only been recently assessed. It is clearly a member of the *C. longicollis* group based on electrophoresis (Georges and Adams, 1992) and morphology (Rhodin 1994a,b). Turtles of this group (except *C. oblonga*) can be identified by the presence of a broad plastron, shorter neck to carapace length ratio and rounded head (sensu Goode, 1967). They can be further identified by the lack of remnant spurs of the parietal arches, no elongation of the basisphenoid and no elongation of the occipital condyle (Thomson et al., 1997a).

² Corresponding Author.

Rhodin (1994a) was the first to regard the New Guinean and Australian forms of *C. novaeguineae* to be different noting that the Australian form (in 3 specimens examined) consistently has paired premaxillary foramina, whereas the New Guinea form usually has a single fused premaxilla and lacked premaxillary foramina. Unfortunately, Rhodin felt he did not have sufficient specimens to form a taxonomic conclusion.

Recent reports of widespread populations of *C. novaeguineae* across northern Australia (Goode, 1967; Cann 1972, 1978; King and Horner, 1987; Covacevich et al. 1982; Kennett et al., 1992) has led to collection and study of these remote populations. We now recognize Australian specimens of what was previously known as *C. novaeguineae* to be a distinct species, for which we hereby provide a formal description.

TAXONOMY

Cann's Longneck Turtle
Chelodina canni sp. nov.

Order Testudines Linnaeus, 1758

Suborder Pleurodira Cope, 1864

Family Chelidae Gray, 1831

Subfamily Chelodininae Georges et al., 1998

Type Data.—Holotype: NTM 24515; an adult female (all measurements in millimeters; carapace length, CL = 215.3; carapace width, CW8 = 167.2), preserved in alcohol; collected with the help of local aboriginal people at Malogie Waterhole, near Scarlet Hill on Kalala Station (16°08'S, 133°36'E), Northern Territory, Australia by Arthur Georges in April of 1992 (for a description of the type locality, see Kennett et al., 1992; Plate 1). Allotype: NTM 24516; a male (CL = 150.1; CW = 116.8; see also Plate 1), preserved in alcohol. Paratype: NTM 24517; a female (CL = 208.0; CW = 165.7), preserved in alcohol; collection data as for holotype. See Table 1 for comparisons between type specimens and other species, and Appendix 1 for a complete list of specimens examined.

Distribution.—*Chelodina canni* is known from the Roper River drainage (including Maria Island in the Gulf of Carpentaria) in northeastern Northern Territory, eastward through the drainages of the Gulf of Carpentaria in northwest Queensland. In Cape York, it is found in drainages from Cairns in the north, down to Rockhampton in the south where a narrow hybrid zone with *C. longicollis* is found (Fig. 1). Hybrids are all recognized by allozymes and by morphology. There are four allozyme markers that separate *C. canni* and *C. longicollis*. Hybrids are all heterozygous for these alleles. Thus, despite this hybridization, electrophoretic analysis clearly demonstrates that *C. canni* and *C. longicollis* are distinct species (Georges et al., 2002). The

same 45 turtles tested for allozymes were then looked at to find morphological features that were useful in identifying the hybrids. All hybrids have a deformity of the intergular scute and the underlying bone. They also possess a blend of *C. canni* and *C. longicollis* characters.

Diagnosis.—A large species of *Chelodina* belonging to the *C. longicollis* group and the *C. novaeguineae* species complex (see Table 2). Adults can be diagnosed by the wide, rounded carapace with a moderately deep midvertebral trough (Plate 1); a median carapacial keel either absent or minimal, being most observable in the eastern populations; a wide plastron with dark seams on an otherwise uniformly yellow plastron; first and second marginal scutes equal or nearly equal in dorsal surface area; wide head with a red to pink suffusion on the head, neck, and limbs; and bluntly pointed neck tubercles. Hatchlings have an extensive orange-red ventral head, neck, and plastral pattern extending well onto the dorsal aspect of the marginal scutes (Plate 2).

The large, wide, rounded and deep carapace (especially adult females), separates *C. canni* immediately from *C. steindachneri*, *C. reimanni*, *C. novaeguineae*, most *C. longicollis*, and most *C. pritchardi*. The wide, robust head of *C. canni* readily separates it from all *C. longicollis*, *C. pritchardi*, *C. steindachneri*, and most *C. novaeguineae* and *C. mccordi*. *Chelodina mccordi* has a narrower head and plastron than *C. canni*. In *C. mccordi*, the total dorsal surface area of the second marginal (M2) scute is always larger than that of its first marginal scute (Rhodin, 1994b); however, in *C. canni*, M1 and M2 are not noticeably different in total dorsal surface area. In *C. mccordi* both the anterior and posterior plastral lobes always diminish in width distally from the axillary notch and inguinal notch. This contrasts with most adult *C. canni* where only the posterior plastral lobe diminishes in width distally from the inguinal notch but the anterior plastral lobe of the plastron increases in width moving forward from the axillary notch, before rounding off to form the anterior border of the plastron (Plate 1). The plastral (midline seam) formula of *C. canni* has an interanal seam longer than the interabdominal, whereas in adult *C. mccordi* (in contrast to Rhodin, 1994b) the interabdominal seam is longer than the interanal.

Etymology.—This species is named in honor of John Cann of Sydney, Australia, for his lifetime of work with the freshwater turtles of Australia.

Related Taxa.—The nearest living relative, and thus the sister taxa of this species, based on phylogenetic analysis of allozyme data (Georges et al., 2002), is *C. novaeguineae* (Boulenger, 1888, Lectotype: BMNH 1946.1.22.36; Paralectotype: MSNG C.E. 8407 both from Katow = Mawatta,

TABLE 1. Comparative measurements of *Chelodina canni*, *Chelodina novaeguineae*, and *Chelodina reimanni*. Types for each species are bold. (See Appendix 2 for descriptions of measurements used).

ID No.	Species	Sex	HL	HWT	PW	HT	VT	CL	CW8	PL	PWF ^x
QM 10265	<i>canni</i>	F	44.7	33.7	7.7	13.3	12.7	220.2	150.3	174.6	100.0
QM 13326	<i>canni</i>	JF	34.6	25.9	6.5	10.9	12.0	147.6	110.0	120.1	69.4
QM 13506	<i>canni</i>	M	39.9	29.2	4.8	11.8	12.1	158.1	119.4	126.9	67.1
QM 20627	<i>canni</i>	JM	30.0	21.9	5.2	8.5	8.7	121.5	93.0	99.2	57.1
QM 20628	<i>canni</i>	JF	31.7	22.9	5.0	9.4	10.0	135.4	102.6	107.0	61.9
QM 20630	<i>canni</i>	JM	32.3	23.5	5.2	10.1	9.8	137.9	104.9	111.7	63.9
QM 20633	<i>canni</i>	JF	29.6	22.9	5.8	9.1	9.4	126.9	99.6	103.9	59.5
NTM 22651	<i>canni</i>	F	51.3	40.6	8.3	15.2	15.4	247.5	194.1	197.1	109.3
NTM 24515	<i>canni</i>	F	46.4	34.7	7.9	14.2	13.2	215.3	167.2	174.2	98.3
NTM 24516	<i>canni</i>	M	35.2	24.9	6.9	11.3	11.1	150.1	116.8	118.9	72.1
NTM 24517	<i>canni</i>	F	46.8	35.2	7.7	13.9	13.7	208.0	165.7	168.0	98.4
NTM 31790	<i>canni</i>	F	48.0	32.6	5.7	12.7	13.6	211.4	163.3	171.0	100.7
QM 36751	<i>canni</i>	F	55.3	40.1	7.2	15.3	15.5	247.4	189.5	203.9	121.2
QM 37819	<i>canni</i>	F	49.8	37.0	6.5	14.4	14.9	237.8	175.6	191.1	108.0
QM 45005	<i>canni</i>	F	48.3	33.2	7.6	13.8	13.8	235.5	180.2	185.8	112.0
QM 46457	<i>canni</i>	F	39.8	29.7	9.6	10.4	10.7	187.3	138.3	155.1	88.4
QM 50997	<i>canni</i>	F	41.5	32.4	6.2	13.1	13.4	214.1	172.6	170.7	100.8
QM 50998	<i>canni</i>	F	42.4	31.3	5.5	12.8	14.0	211.1	161.5	170.9	99.6
UF 43911	<i>novaeguineae</i>	.	35.8	23.8	6.4	10.6	10.2	143.5	109.1	112.3	59.1
UF 65520	<i>novaeguineae</i>	.	34.0	24.2	7.6	9.6	9.2	152.1	110.7	112.3	52.8
AMNH 117939	<i>novaeguineae</i>	M	35.8	23.9	4.4	7.9	8.5	145.3	109.9	117.8	53.3
MCZ 134390	<i>novaeguineae</i>	.	38.2	24.4	5.9	8.6	9.9	151.1	113.0	117.0	64.8
MCZ 134391	<i>novaeguineae</i>	.	36.5	23.4	5.5	8.7	8.5	151.8	116.8	120.6	65.5
MCZ 134392	<i>novaeguineae</i>	.	39.1	26.0	6.4	9.3	10.2	155.1	111.7	119.7	61.4
MCZ 134393	<i>novaeguineae</i>	.	39.3	25.7	5.3	8.7	9.0	162.6	118.4	123.0	65.3
MCZ 134394	<i>novaeguineae</i>	.	26.6	17.8	3.9	6.4	6.1	97.9	75.4	79.6	38.3
MCZ 134395	<i>novaeguineae</i>	.	37.2	24.0	5.5	8.6	9.1	150.6	115.9	119.2	60.7
MCA 134396	<i>novaeguineae</i>	.	38.6	25.2	9.4	8.1	8.8	128.7	88.4	99.7	41.2
MCZ 134712	<i>novaeguineae</i>	M	40.2	24.9	4.5	9.3	9.0	160.1	116.5	125.7	65.6
NHM 1946.1.22.36	<i>novaeguineae</i>	F	31.8	22.9	5.4	9.2	9.4	136.9	106.9	108.5	57.3
RMNH 27897	<i>reimanni</i>	M	33.6	24.4	5.9	8.5	9.1	124.6	87.8	95.6	50.3
RMNH 27912	<i>reimanni</i>	F	39.5	28.8	5.8	10.8	11.0	155.3	114.0	117.5	61.8
RMNH 27913	<i>reimanni</i>	F	30.8	24.1	4.6	9.0	9.6	118.0	84.2	94.4	47.2
RMNH 27914	<i>reimanni</i>	M	35.7	24.9	4.8	8.6	8.6	139.3	96.5	103.8	51.1
RMNH 27915	<i>reimanni</i>	F	34.0	25.6	5.7	9.9	10.5	139.8	99.0	105.8	54.5
RMNH 27942	<i>reimanni</i>	J	25.1	20.2	4.3	7.1	8.1	97.9	72.7	75.2	40.4
RMNH 27950	<i>reimanni</i>	F	46.7	33.1	6.0	12.2	12.9	178.0	130.2	140.4	72.9
MTKD 29178	<i>reimanni</i>	F	45.9	33.8	5.4	12.5	15.1	180.5	135.4	139.9	70.3
MTKD 29241	<i>reimanni</i>	M	37.4	27.2	5.1	9.3	10.6	135.3	93.4	103.0	53.3
MTKD 29243	<i>reimanni</i>	F	47.4	32.9	7.1	10.3	10.7	176.2	127.3	135.0	73.6
MTKD live A	<i>reimanni</i>	F	47.4	38.6	8.2	12.0	14.5	188.8	134.2	147.5	76.4
MTKD type 1	<i>reimanni</i>	F	53.9	40.7	8.4	12.2	15.5	216.5	154.6	167.7	89.0
MTKD type 2	<i>reimanni</i>	F	38.4	28.0	5.7	10.9	10.6	159.8	109.0	122.3	59.0

Binituri River, Papua New Guinea. Lat. 09°05'S, Long. 143°00'E).

DESCRIPTION

External Morphology

See all photos labeled "*Chelodina novaeguineae*" with Australian locality data in Cann (1998:61–68).

Carapace.—Carapace length (CL) to at least 169 mm in males (mean adult CL, 161) and at least 240 mm in females (mean adult CL, 221). Carapace broadly oval, but widest at M7 (max-

imum carapace width/maximum CL = 0.76–0.82; mean = 0.79; N = 8; for this and subsequent ratios, compare figs. 6 and 7 in Rhodin, 1994b). Carapace of juvenile distinctly rounded (Plate 2). Carapace surface, except on marginals, highly rugose, with a relatively smooth posterior margin and without obvious growth annuli. Hindmost marginals (M12, supracaudals), only slightly raised over tail. Juveniles with individual tiny rugosities organized into a radiating pattern on carapace scutes. Seam between M1 and M2, instead of being perpendicular to car-

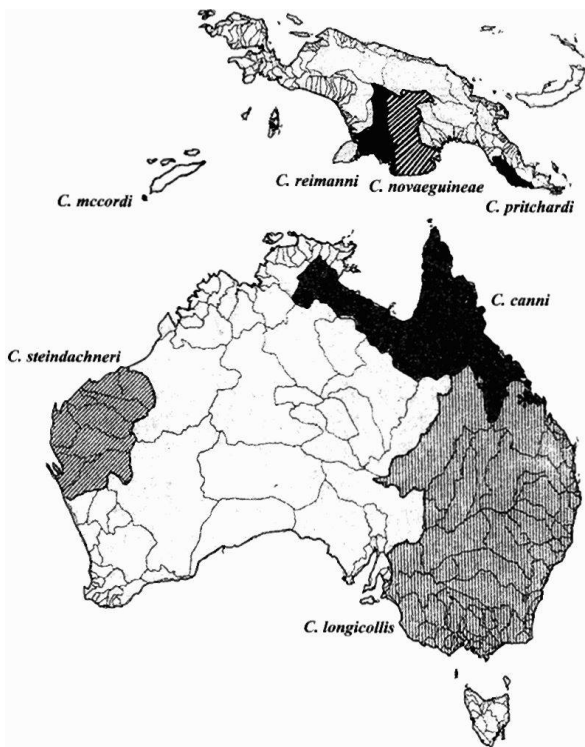


FIG. 1. Distributions of the species of the *Chelodina longicollis* group in Australia, New Guinea, and south-eastern Indonesia. Point locations are given for the new species *Chelodina canni*, and the large asterisk (*) demonstrates the hybrid zone between *C. canni* and *C. longicollis*. Majority of locality data is based on museum voucher specimens; however, some areas have been shaded on the basis of personal communication and field reports.

apace margin, curves anteriorly, producing a relatively short medial (i.e., in contact with the first vertebral and the first costal scutes) seam on the first marginal (53–90% of medial width of M2; mean = 71%; $N = 8$); however, M1 and M2 equal or nearly equal in total dorsal surface area. M4, 5, and 6 much shorter than other marginals; M7–10 distinctly flared. Lateral margins of M4–M7 slightly upturned, forming a very narrow trough along the rim of the shell. Nuchal scute large, rectangular, slightly wider anteriorly than posteriorly, and longer than wide. Vertebrae (V) in order of decreasing width are $1 \sim 5 > 2 \sim 3 > 4$. Regions of costal-vertebral contact distinctly elevated longitudinally, and these two smooth ridges separated by a moderately deep midvertebral trough in which there is no evidence of a median keel in western populations; however, a minimal median keel is present in the easterly populations. Carapace brown to almost black (especially dark in juveniles), with the outer margin of the shell rimmed in yellow.

Plastron.—Plastron slightly upturned anteriorly. Plastron wide in comparison to the other wide-plastroned species of the *C. longicollis*

group (width at axillary notch averaging 50% of CL; range 47–52%; $N = 8$). Front plastral lobe wider than hind plastral lobe, widening in most adults as it goes distally from the axillary notch, before rounding anteriorly (a character subject to ontogenetic changes). Plastral hindlobe narrows distally from the inguinal notch, with distinct anal notch. Bridge moderately long, and lacking axillary and inguinal scutes. Large intergular present, much wider anteriorly than posteriorly, and not reaching the margin of the plastron. Average plastral midline seam length formula (Plate 1): intergular (midline length) $>$ anal $>$ abdominal $>$ femoral $>$ pectoral $>$ gular. Plastron uniformly yellow (Plate 1), with seams darkly marked with brown, and with the scutes variably stained reddish-brown. Ventral surfaces of marginals faded yellow and flecked to mostly covered with reddish-brown staining. Hatchling plastron with bright red-orange markings ventrally, extending over the margin of the carapace on the dorsal aspects of the marginal scutes (similar and more pronounced than *C. mccordi* (Plate 2)). Juvenile plastron generally very dark gray-black to black (Plate 3).

Head and Soft Parts.—Head wide in comparison to other members of the *C. longicollis* group (head width at tympanum/CL = 0.15–0.18; mean = 0.17; $N = 8$), with small irregular scales covering the postorbital regions, but with a smooth skull roof area. Rostrum blunt, not protruding or beaklike. Neck covered with prominent, bluntly pointed tubercles with wide bases. Soft parts gray to brown dorsally, light yellow to cream ventrally, but with the head, neck, and limbs variably suffused with red or pink. Head and neck of hatchlings and juveniles marked with orange to red to dark cherry coloring. Iris usually dark brown, with the inner pupillary margin very light in color.

Male with tail thicker at base and extending noticeably beyond carapace rim in comparison to that of females; adult males smaller (approximately 72%) in body size than adult females.

Osteology

Skull.—The skull of *C. canni* ($N = 9$) is robust anteriorly with a broad rhamphotheca, highly emarginated both from below and behind, to the extent that the parietal arch has disappeared as is typical of the *Chelodina* (Fig. 2). Only a single frontal bone is present which posteriorly partially divides the parietals, a feature unique to this species. The dorsal ridge of the parietals immediately narrows to a ridge, similar to that of *C. reimanni* ($N = 6$) but different from *C. novaeguineae* ($N = 8$). The anterior edge of the skull is rounded when viewed from above, which differs from that of *C. novaeguineae*, which is narrowed and angular. A major difference between

TABLE 2. Characters distinguishing species of *Chelodina* subgeneric group "A" (modified from Rhodin, 1994b). Means for character ratios are presented \pm one standard deviation. "Composite ratio" is defined as: (carapace width \times head width)/(plastron width \times carapace length).

	<i>C. canni</i>	<i>C. longicollis</i>	<i>C. maccordi</i>	<i>C. newaguirre</i>	<i>C. pitichardi</i>	<i>C. reinanni</i>	<i>C. steinhachneri</i>
Sample size	8	37	17	51	43	5	5
Maximum female carapace length (mm)	240	220	215	220	230	210	182
Carapace widest point*	M7	M8	M7	M7-8	M7	M8	M7
Carapace width	Wide	Intermediate	Wide	Narrow	Wide	Narrow	Wide
Carapace width/carapace length	0.79 \pm 0.02	0.78 \pm 0.04	0.79 \pm 0.01	0.72 \pm 0.03	0.79 \pm 0.02	0.69 \pm 0.02	0.86 \pm 0.02
Adults with median carapacial trough	Slight to moderate	Slight	No or slight	No	No	No	Slight to moderate
Head width	Wide	Narrow	Intermediate	Wide	Narrow	Wide	Intermediate
Head width/carapace length	0.17 \pm 0.02	0.15 \pm 0.01	0.16 \pm 0.01	0.17 \pm 0.01	0.15 \pm 0.01	0.20 \pm 0.01	0.17 \pm 0.02
Plastron width	Wide	Wide	Intermediate	Intermediate	Wide	Narrow	Wide
Plastral forelobe width/median plastron length	0.63 \pm 0.02	0.62 \pm 0.03	0.58 \pm 0.01	0.58 \pm 0.02	0.16 \pm 0.01	0.54 \pm 0.03	0.61 \pm 0.01
Adult plastron pattern	Variably very dark	Bold, expanded	Variably dark	Fine, dark	Fine, dark	Variably dark	Fine, dark
First vs second marginal dorsal surface area**	Subequal	M1 larger	M1 smaller	Subequal	M1 larger	Subequal	M1 smaller or equal
Medial width M1/medial width M2***	0.71 \pm 0.13	1.03 \pm 0.13	0.47 \pm 0.09	0.80 \pm 0.11	1.09 \pm 0.13	0.90 \pm 0.11	0.77 \pm 0.01
Composite ratio (Rhodin, 1994b)	High	Low	High	Intermed. (+)	Intermed. (-)	High	Intermed.
Neck tubercles of adult	Pointed, wide base	Pointed, narrow base	Pointed, narrow base	Pointed, narrow base	Pointed, narrow base	Pointed, narrow base	Rounded, narrow base
Red/pink on adults	Yes	No	No	No	No	No	Yes
Hatchling plastron with orange/red	Generously	Moderately	Generously	Minimal	Minimal	Minimal	Moderately
Hatchling head/neck with orange/red	Generously	Minimal	Generously	Minimal	Minimal	Minimal	Minimal
Hatchling marginals orange/red dorsally	Yes	No	No	No	No	No	No

* Generally, carapace appears more rounded and posterior marginal flaring appears less distinctive if widest point is on M7; carapace appears more oval and posterior marginal flaring appears more pronounced if widest point is on M8; *C. canni* appears more rounded and distinctly flared.

** Anterior curvature of seam between M1 and M2 in some species may give the impression that M1 is smaller than its actual surface area may be.

*** Medial width is the seam formed by juncture of marginal scute with the vertebral costal scutes.

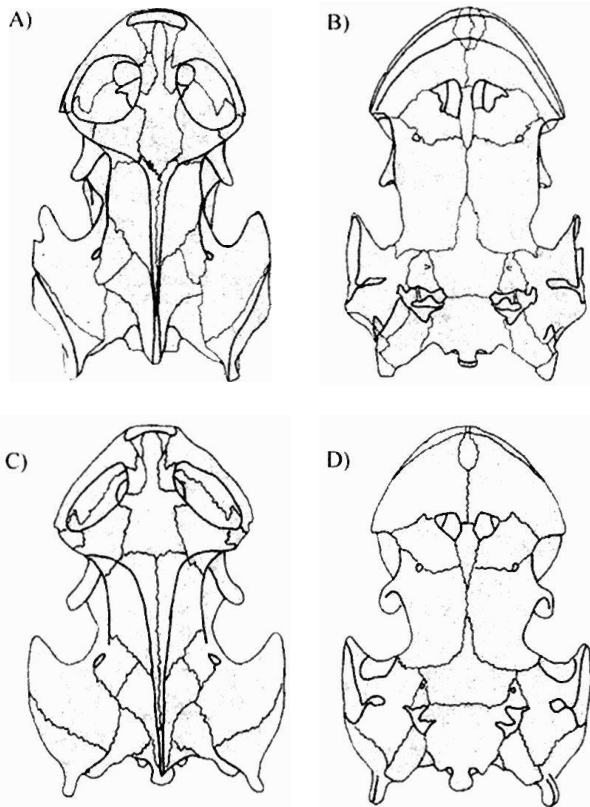


FIG. 2. Dorsal and ventral views of the skulls of *Chelodina canni* (a–b), UC0374 and *Chelodina novaeguineae* (c–d), AGJR-T504 (from Rhodin, 1994a).

C. canni and other members of the *C. novaeguineae* complex (*C. novaeguineae*, *C. reimanni*, *C. mccordi*) is the presence of paired premaxilla in *C. canni*, a feature previously noted by Rhodin (1994a).

There is contact between the vomer and the pterygoids, and the vomer is narrowed posteriorly, partially dividing the anterior half of the pterygoids, whereas in *C. novaeguineae*, the vomer is widened and angular posteriorly, which widely separates the anterior of the pterygoids. The canalis caracoticus internus is completely open with only the anterior foramen present (foramen canalis caracoti internus). This condition contrasts to that of *C. novaeguineae* where the canalis caracoticus internus is partially closed, forming a channel within the prootic. Like all other members of the *C. longicollis* group (although variably present in rudimentary form in *C. longicollis*), *C. canni* has no foramen retropterygoideum (chelicid foramen; McDowell, 1983; Bour and Pauler, 1987; Rhodin, 1994a).

The crista supraoccipitalis is small in this spe-

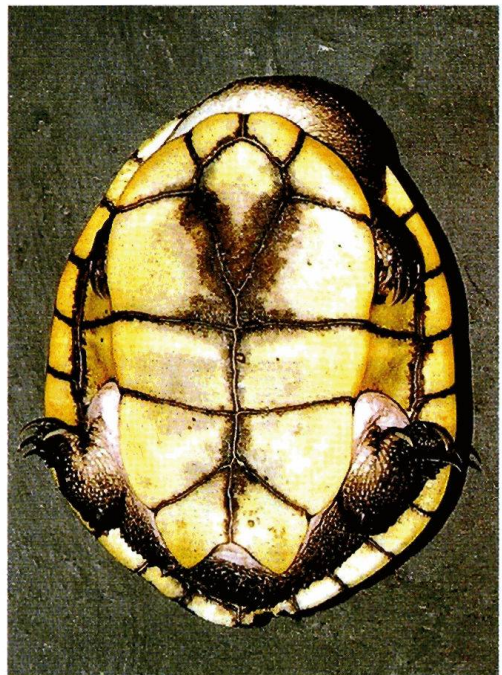
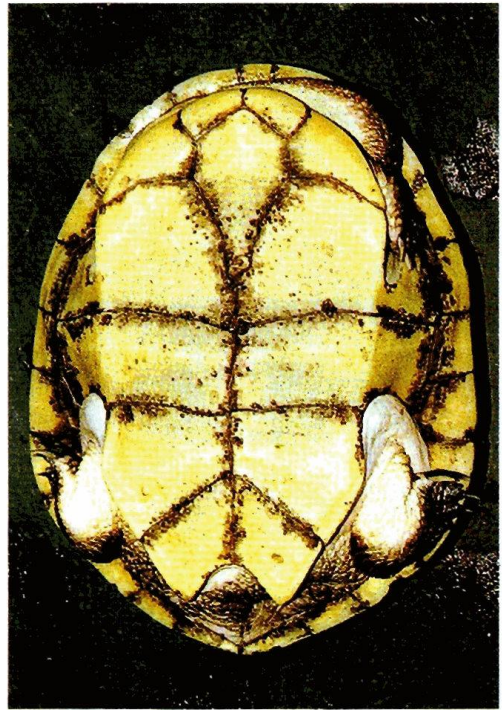
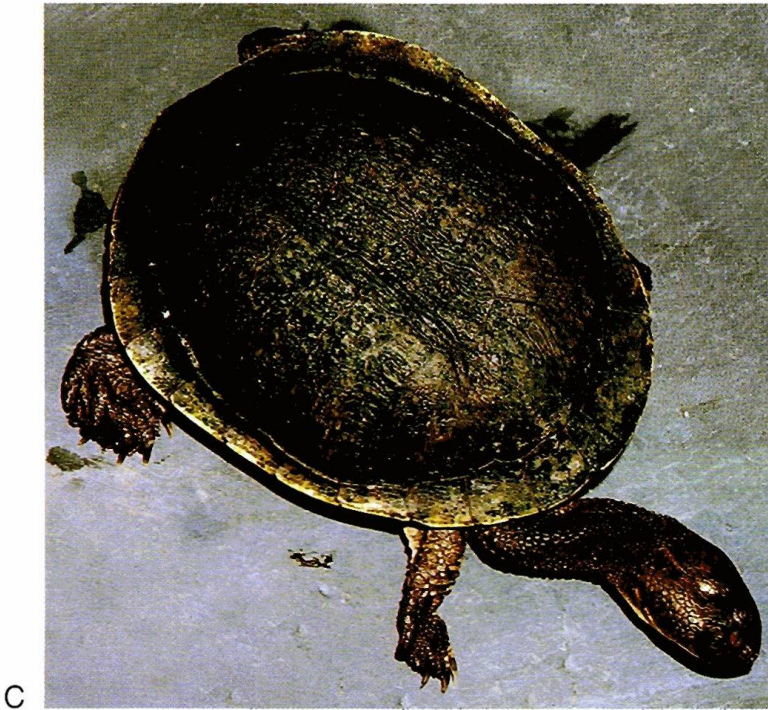
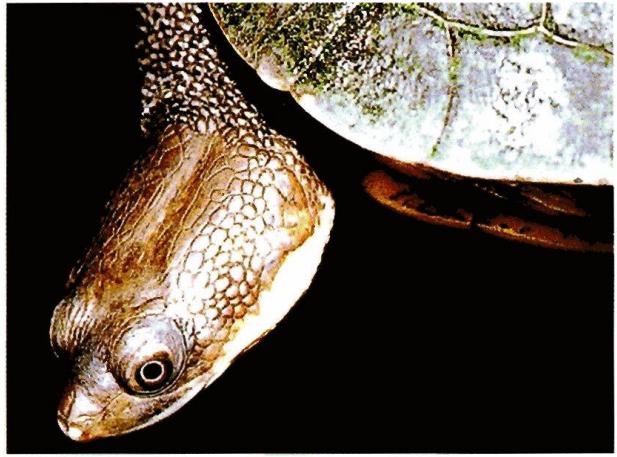
cies and is markedly narrower than the ridge of the parietals; however it is wider in *C. novaeguineae*. The cristae paroccipitalis are large and relatively narrow in *C. canni* and extend horizontally from the base of the occipital condyle; this unit is smaller but wider in *C. novaeguineae* and not as visible.

Shell.—The shell of *Chelodina canni* is typical of members of the *C. longicollis* group in that the pleural bones are all thin and narrow, with only minor antero-posterior widening of the first pleural (Fig. 3). The typical chelicid complement of eight pairs of pleurals, 11 pairs of marginals, a suprapygal, pygal, and nuchal bone are present. Neural bones are not exposed and do not form a contiguous series, the typical Australasian chelicid condition (Rhodin and Mittermeier, 1977; Thomson and Georges, 1996). The nuchal bone in *C. novaeguineae* is narrower posteriorly and more deeply divides the anterior edges of the first pleural pair than that seen in *C. canni*. However, this condition would appear to be affected by the carapace width to length ratio in a range of chelids.

Long-necked turtles of the *C. novaeguineae* complex (here defined to include *C. novaeguineae*, *C. canni*, *C. reimanni*, and *C. mccordi*), within the *C. longicollis* group, all share the feature of an enlarged anterior bridge strut (Thomson et al., 1997b; Thomson and Mackness, 1999; Thomson, 2000). *Chelodina novaeguineae* has the suture for the anterior bridge strut flush against the ventral surface of the carapace; however, *C. canni* has this suture raised up from the carapace on a ridge formed from the first pleural. This feature is shared with *C. reimanni* and *C. mccordi*. There is a medial constriction in the anterior bridge strut suture in *C. novaeguineae* that is present but not as obvious in *C. canni*. The anterior bridge strut is much reduced in the other members of the *C. longicollis* group.

The pelvis of the *C. longicollis* group species sutures to the seventh and eighth pleurals and to the suprapygal bone. In *C. novaeguineae* ($N = 8$) the medial edge of this suture is parallel to the vertebral column and hence the rib of thoracic vertebra 9 is equal in length to that of vertebra 10. In *C. canni* ($N = 9$), however, the medial edge of the suture is closest to the vertebrae adjacent to thoracic 10; hence, the rib of thoracic 9 is approximately twice as long as that of thoracic 10.

The plastron of this species, apart from being wider (especially anteriorly) than most others





A



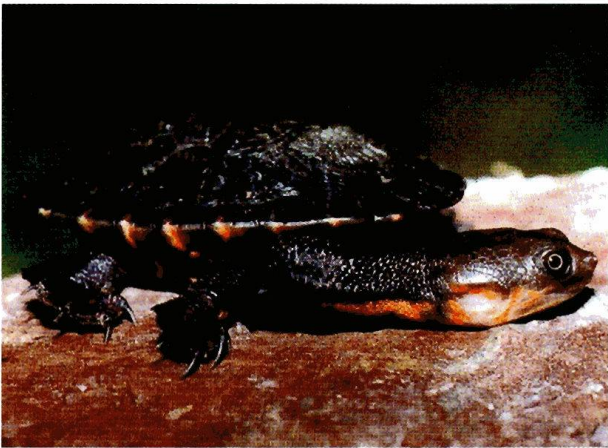
B



C



D



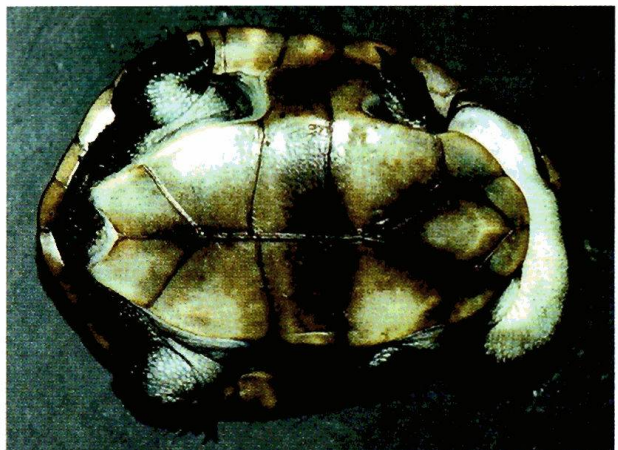
E



F



G



H

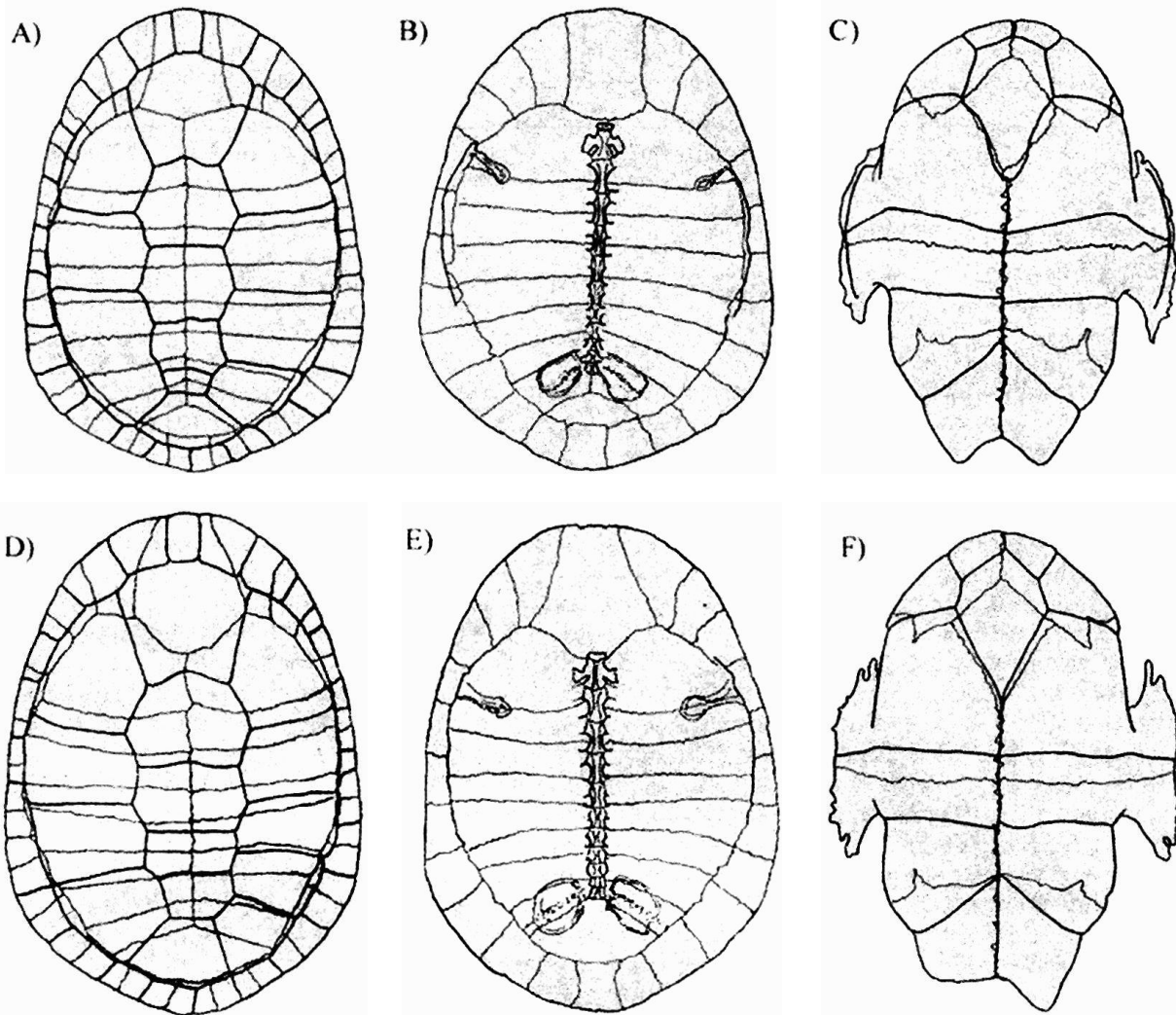


FIG. 3. Dorsal and ventral views of the carapace and ventral view of the plastron of *Chelodina canni* (a-c), UC0374 (a subadult male) and *Chelodina novaeguineae* (d-f), UC2022. Note: Specimen UC0374 does not yet show distal widening of the anterior plastral lobe because of its being a young male.

(except *C. longicollis*), is little different in its osteology from other *C. longicollis* group species.

MULTIVARIATE COMPARISONS

Canonical discriminant analysis (SAS Institute, Inc., Cary, NC, 1988) was used to determine the distinctiveness of *C. canni* and its two closest relatives, *C. novaeguineae* and *C. reimanni* (Rhodin, 1994b; Georges et al., 2002). All raw data were converted to ratios to remove ontogenetic variation from the dataset. Raw data were then excluded from subsequent analysis. Head measurements were expressed as a simple ratio of head length (HL); head length and all shell measurements were expressed as a simple ratio of carapace length (CL). A number of com-

posite ratios were also defined as combinations of three or more raw measurements, but none were retained by the subsequent analysis. Descriptions of all measurements used in this study are in Appendix 2.

An initial analysis was performed between all members of the *C. longicollis* group; however, only the analysis between the three closest species is presented in graphic form. The generalized multivariate distances between all taxa in the *C. longicollis* group, obtained from a discriminant analysis with all raw measurement ratios included, are presented in Table 3 as an indication of their general morphological similarity. Note that the distinction between *C. canni* and *C. novaeguineae* is substantial (34.12 units), and

PLATE 2. Comparison of carapace and plastron of hatchlings and juveniles of *Chelodina canni* from the Northern Territory (A, B, E, and F), and *Chelodina mccordi*, (C, D, G, and H).

TABLE 3. Generalized squared distance (canonical discriminant analysis) to six known species within the *Chelodina longicollis* group, excluding *Chelodina oblonga* (see text for explanation).

Species	<i>canni</i>	<i>longicollis</i>	<i>mccordi</i>	<i>novae-guineae</i>	<i>pritchardi</i>	<i>reimanni</i>
<i>longicollis</i>	55.92	0				
<i>mccordi</i>	40.44	105.28	0			
<i>novae-guineae</i>	34.12	84.81	43.34	0		
<i>pritchardi</i>	40.12	76.08	25.23	39.58	0	
<i>reimanni</i>	45.55	123.29	52.78	19.95	63.62	0
<i>steindachmeri</i>	90.40	148.27	44.24	92.35	75.87	121.77

greater than the distance between *Chelodina reimanni* and *C. novae-guineae* (19.95 units), in support of our recognition of *C. canni* and *C. novae-guineae* 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 the best discrimination. This yielded the subset of head measurements HL, PW, HWT, HWJ, HT, VT and the shell measurements CW4, CW8, V1, V2, PWF and PWR. Clearly, both head shape and shell shape are well represented in the final formula that provided the best discrimination (Fig. 4). A total of 63.2% of the among-groups variation was explained by the first canonical variate. This variate provided the bulk of the discrimination between *C. reimanni* and *C. canni*, also contributing to the discrimination between these two and *C. novae-guineae*. The second canonical variant provided further discrimination between *C. novae-guineae* and the other two forms (Fig. 4). An indication of the strength of discrimination is given by cross-validation (SAS Institute, Inc., Cary, NC, 1988), although it does rely on assumptions of normality, unlikely to be strictly upheld because not all animals were the

same overall size and because growth is allometric. Nevertheless, only four of the 85 animals in the analysis were misclassified. One *C. novae-guineae* was misclassified as *C. reimanni*, and vice versa, one *C. canni* was misclassified as *C. reimanni* and one as *C. novae-guineae*.

The most influential variable in the discrimination was PWF (Partial $R^2 = 0.70$; $F = 95.1$, $P < 0.0001$) followed by PW/HWT (Partial $R^2 = 0.45$, $F = 32.2$, $P < 0.0001$) and IO/OD (Partial $R^2 = 0.35$, $F = 21.0$, $P < 0.0001$); thus, differences in plastron shape were the most influential in providing overall discrimination among the three taxa. This is consistent with the fact that *C. canni* and *C. novae-guineae* are readily distinguished by differences in plastron shape and head shape. There was no clear partition of the raw variables in terms of their association with one or the other canonical variates so we could not carry our interpretation further.

NATURAL HISTORY NOTES

Kennett et al. (1992) described the eggs, hatchlings, habitat, and basic natural history of *C. canni*. A topotypic female in the senior author's collection produced one egg in September 1993, which subsequently hatched after 88 days incubation time. In addition, one of the nontopotypic females produced ten eggs after oxytocin injection in August 1994. The eggs were white and oval, with hard shells. Four of the ten eggs showed no signs of life, and after one month were discarded. Six of them hatched after 95–98 days at approximately 28–29°C in sterile, moist vermiculite. The six live eggs averaged 33.2 × 21.9 mm (ranges, 32.8–33.8, and 21.6–22.2 mm), and the hatchlings averaged 33.6 mm carapace length (range, 31.0–35.2 mm). Two died soon after hatching for unknown reasons. The remaining hatchlings (now subadults) from both sites are identical in every character. Our eggs and hatchlings are only slightly larger than those described by Kennett et al. (1992)

The range of *C. canni* overlaps that of *C. rugosa*, *Eseya dentata*, *Eseya latisternum*, *Emydura subglobo*, and *Emydura tanybaraga*, but it has been collected syntopically with only *C. rugosa* (Covacevich et al., 1990). The Gangalidda people at

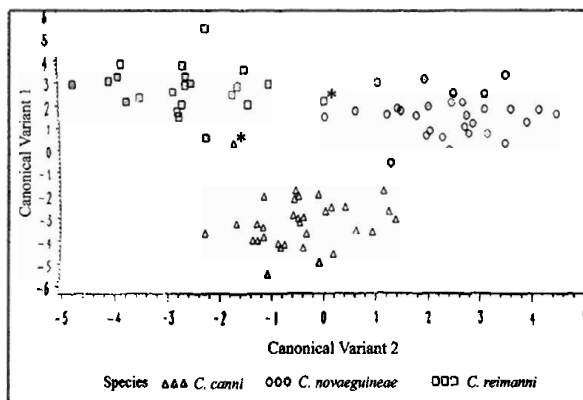


FIG. 4. Plot of canonical variant 1 vs canonical variant 2 of the discriminate analysis of *Chelodina canni*, (Δ), *Chelodina novae-guineae*, (O) and *Chelodina reimanni*, (\square). The two outlying specimens (marked with an asterisk) in the graph are QM 13506 (*C. canni*) from Queensland, Australia and PCHP 4571 (*C. reimanni*) from Irian Jaya.

Old Doomadgee call *C. canni* "bungarra mali", the stinking turtle (Covacevich et al., 1990). The local Aboriginal people at Jinduckin near Mataranka call *C. canni* "nganymalin," meaning smelly armpit turtle (Kennett et al., 1992), owing to the distinctive pungent odor produced by the turtle when handled. This defense mechanism is common for this group of turtles as demonstrated again by the Gogodala people of Balimo, Papua New Guinea, calling a local form of *C. novaeguineae* "ipudinapi" meaning "little smelly turtle" (R. Danaya, pers. comm.).

DISCUSSION

The monophyly of the *C. longicollis* group has been demonstrated using serum electrophoresis (Georges and Adams, 1992) and mtDNA studies (Seddon et al., 1997). Using morphology, it has been suggested that *C. steindachneri* is sister to all other members of that group (Rhodin, 1994b). However, the allozyme and sequence studies have demonstrated that *C. oblonga* is the sister of the *C. longicollis* group and not a part of the *C. expansa* group (Seddon et al., 1997). Further studies using morphological evidence (Thomson et al., 1997a; Thomson, 2000) support the findings of Seddon et al., (1997). It has been demonstrated that *C. novaeguineae* is restricted to New Guinea and does not occur in Australia, and hence the Australian population is a distinct species, herein described as *C. canni*. A phylogeny for the *Chelodina* based on allozyme electrophoresis is presented in the forthcoming paper by Georges et al. (2002) and a complete morphological analysis which will incorporate the allozyme data is forthcoming from Thomson, hence, we do not propose to produce one here.

Acknowledgments.—We thank A. Georges of the Applied Ecology Research Group and J. Cann for collecting many of the specimens loaned to us; the Northern Territory and Queensland Departments of Environment for granting permission for such collecting; and the Australian Nature Conservation Agency for granting permission to export live specimens to the senior author. A. Rhodin preserved the types, measured eggs and hatchlings, and shared data from previous research. J. Iverson, of Earlham College, guided the senior author in the early stages of this manuscript; M. Joseph-Ouni of EO Wildlife Conservation and Artistry helped organize the data herein presented and produced the distribution map; P. Horner of the Northern Territory Museum registered the type specimens. P. Couper and J. Covacevich of the Queensland Museum, J. Cann, A. Georges, J. Iverson, R. Kennett and A. Rhodin provided comments on an earlier draft of this manuscript.

LITERATURE CITED

- BOULENGER, G. A. 1888. On the chelydoid chelonians of New Guinea. *Annali del Museo Civico di Storia Naturale di Genova* 6:449–452.
- BOUR, R., AND I. PAULER. 1987. Identity of *Phrynops vanderhaegei* Bour 1973, and related species. *Mésogée*. 47:3–23.
- BURBIDGE, A. A., J. A. W. KIRSCH, AND A. R. MAIN. 1994. Relationships within the Chelidae (Testudines: Pleurodira) of Australia and New Guinea. *Copeia* 1974:392–409.
- CANN, J. 1972. Notes on some tortoises collected in northern Australia. *Victorian Naturalist* 89:165–168.
- . 1978. *Tortoises of Australia*. Angus and Robertson, Sydney, New South Wales, Australia.
- . 1997a. Georges short-necked turtle. *Monitor* (Victorian Herpetological Society, Melbourne) 9: 18–23, 31–32.
- . 1997b. Irwin's Turtle. *Monitor* (Victorian Herpetological Society, Melbourne) 9:36–40, 31–32.
- . 1997c. The Northern Yellow-faced Turtle. *Monitor* (Victorian Herpetological Society, Melbourne) 9:24–29, 31–32, 34–35.
- . 1998. *Australian Freshwater Turtles*. Beaumont Publishing Ptc Ltd., Singapore.
- COVACEVICH, J., G. J. INGRAM, AND G. V. CZECHURA. 1982. Rare frogs and reptiles of Cape York Peninsula, Australia. *Biological Conservation* 22:283–294.
- COVACEVICH, J., P. COUPER, K. McDONALD, AND D. TRIGGER. 1990. Walunarra, Bungarra nali, and the Gangalidda at Old Doomadgee. *Memoirs of the Queensland Museum* 29:322.
- GEORGES, A., AND M. ADAMS. 1992. A phylogeny for Australian chelid turtles based on allozyme electrophoresis. *Australian Journal of Zoology* 40:453–476.
- . 1996. Electrophoretic delineation of species boundaries within the short-necked chelid turtles of Australia. *Zoological Journal of the Linnean Society, London* 118:241–260.
- GEORGES, A., AND S. THOMSON. 2002. Evolution and zoogeography of the Australian freshwater turtles. In J. R. Merrick, M. Archer, G. Hickey, and M. Lee (eds.), *Evolution and Zoogeography of Australasian Vertebrates*. Australian Scientific Publishing Pty. Ltd., Sydney, New South Wales, Australia (In Press).
- GEORGES, A., J. BIRRELL, K. SAINT, W. P. MCCORD, AND S. DONNELLAN. 1998. A phylogeny for side-necked turtles (Chelonia: Pleurodira) based on mitochondrial and nuclear gene sequences. *Biological Journal of the Linnean Society* 67:213–246.
- GEORGES, A., M. ADAMS, AND W. P. MCCORD. 2002. Delineation of species boundaries and a phylogeny for the snake-necked freshwater turtles of Australasia (Testudines: Chelidae: *Chelodina*). *Zoological Journal of the Linnean Society, London* (In Press).
- GOODE, J. 1967. *Freshwater Tortoises of Australia and New Guinea* (in the Family Chelidae). Lansdowne Press, Melbourne, Victoria, Australia.
- IVERSON, J. B., S. A. THOMSON, AND A. GEORGES. 2001. Validity of taxonomic changes for turtles proposed by Wells and Wellington. *Journal of Herpetology* 35:361–368.

- KENNETT, R. M., A. GEORGES, K. THOMAS, AND T. C. GEORGES. 1992. Distribution of the long-necked freshwater turtle *Chelodina novaeguineae* and new information on its ecology. *Memoirs of the Queensland Museum* 32:179–182.
- KING, M., AND P. HORNER. 1987. An additional freshwater turtle species and the confirmation of *Chelodina novaeguineae* in the Northern Territory, Australia. *The Beagle* 4:83–84.
- MCDOWELL, S. B. 1983. The genus *Emydura* (Testudines: Chelidae) in New Guinea with notes on the penial morphology of Pleurodira. In A. G. J. Rhodin and K. Miyata (eds.), *Advances in Herpetology and Evolutionary Biology: Essays in Honor of Ernst Williams*, pp. 169–189. Museum of Comparative Zoology, Harvard University, Cambridge, MA.
- PHILIPPEN, H. D., AND M. GROSSMAN. 1990. Eine neue Schlangenhalschildkröte von Neuguinea: *Chelodina reimanni* sp. n. (Reptilia, Testudines, Pleurodira: Chelidae). *Zoologische Abhandlungen. Staatliches Museum für Tierkunde, Dresden*, 46:95–102.
- RHODIN, A. G. J. 1994a. Chelid turtles of the Australian archipelago: I. A new species of *Chelodina* from southeastern Papua New Guinea. *Breviora* 497:1–36.
- . 1994b. Chelid turtles of the Australian archipelago: II. A new species of *Chelodina* from Roti Island, Indonesia. *Breviora* 498:1–31.
- RHODIN, A. G. J., AND R. A. MITTERMEIER. 1977. Neural bones in chelid turtles from Australia and New Guinea. *Copeia* 1977:370–372.
- SEDDON, J. M., A. GEORGES, P. R. BAVERSTOCK, AND W. P. McCORD. 1997. Phylogenetic relationships of chelid turtles (Pleurodira: Chelidae) based on mitochondrial 12S rRNA gene sequence variation. *Molecular Phylogenetics and Evolution* 7:55–61.
- THOMSON, S. A. 2000. The identification of the holotype of *Chelodina oblonga* (Testudines: Chelidae) with a discussion of taxonomic implications. *Chelonian Conservation and Biology* 3:745–749.
- THOMSON, S. A., AND A. GEORGES. 1996. Neural bones in Australian chelid turtles. *Chelonian Conservation and Biology* 2:82–86.
- THOMSON, S. A., AND B. MACKNESS. 1999. Fossil turtles from the early Pliocene Bluff Downs Local Fauna, with a description of a new species of *Elsaya*. *Transactions of the Royal Society of South Australia* 123:101–105.
- THOMSON, S. A., M. ADAMS, S. SEDDON, AND A. GEORGES. 1997a. The western Australian turtle *Chelodina oblonga* (Testudines: Chelidae) and its phylogenetic placement within the genus *Chelodina* [Abstract:290]. Joint Meeting of the American Society of Ichthyologists and Herpetologists, the Herpetologists League and the Society for the Study of Amphibians and Reptiles, Seattle, Washington, June 26 to July 2 1997.
- THOMSON, S. A., A. WHITE, AND A. GEORGES. 1997b. Re-evaluation of *Emydura lavarackorum*: Identification of a living fossil. *Memoirs of the Queensland Museum* 42:327–336.
- THOMSON, S. A., R. KENNETT, AND A. GEORGES. 2000. A new species of long necked turtle (Testudines: Chelidae) from the Arnhem Land plateau, Northern Territory, Australia. *Chelonian Conservation and Biology* 3:675–685.
- WELLS, R., AND R. WELLINGTON. 1985. A classification of the Amphibia and Reptilia of Australia. *Australian Journal of Herpetology, Supplementary Series* 1:1–61.

Accepted: 5 October 2001.

APPENDIX 1

Specimens of *Chelodina* examined with locality data (listed alphabetically by locality within each species). Abbreviations used: AMS, Australian Museum (Sydney); AMNH, American Museum of Natural History (New York); MCZ, Museum of Comparative Zoology (Boston); MTKD, Staatliches Museum für Tierkunde (Dresden); NHM (ex BMNH), Natural History Museum (London); NTM, Museum and Art Galleries of the Northern Territory (Darwin); PCHP, Peter Pritchard Collection (Oveido); QM, Queensland Museum (Brisbane); RMNH, Nationaal Natuurhistorisch Museum (Leiden); UC, University of Canberra (Canberra); UF, University of Florida Museum (Gainesville); UM, University of Michigan Field Series (Michigan); UPNG, University of Papua New Guinea (Port Moresby); UU, University of Utah (Salt Lake City); WAM, Western Australian Museum; ZMB, Museum für Naturkunde (Berlin) (note: all UC specimens are skeletons).

Chelodina longicollis Group

Chelodina canni QM 4486, 4488, 4491, 13506, 46457, 66654, AMNH 138236, NTM 22651 No data; QM 62543–45 22 km west of Georgetown, 18°17'S, 143°20'E; AMNH 86545–46 Armraynald; QM 35136 Aurukun Reserve, Wathanhiin Outstation, 13°21'S, 141°44'E; UU 14717 Barrett's Lagoon, 6.5 miles west and 2.8 miles north of Cooktown, 15°28'S, 145°15'E; UU 14716 Batten Cr., prob. 13 miles W.S.W. Borroloola, 16°04'S, 136°17'E; QM 57883 Bullocky Dam, Gilbert River overflow; QM 37819, 49917 Cape York Pen, Gilbert River, 17°53'S, 142°34'E; UU 14718 Edwards River, probably west southwest of Musgrave), Cape York, 14°40'S, 142°25'E; AM 129346 Greta Creek, near Bowen, 20°01'S, 148°15'E; QM 58412 Horse Tailer Waterhole, Archer Bend, 13°25'S, 142°02'E; QM 47923 Ingham, 18°39'S, 146°01'E; AM 132785 Kalala Station, Daly Waters region, Roper River Drainage, 16°08'S, 133°36'E; UC0374 Malogie Waterhole, near Scarlet Hill on Kalala Station, 16°08'S, 133°36'E; QM 53635 Kalala Station, near Daly Waters, Stuart Swamp, 16°14'S, 133°27'E; NTM 16325 Kalala Station, 16°11'S, 133°19'E; NTM 31790 Lake Eames, Vanderlin Island, 15°41'S, 135°43'E; MV 4-5 Lockhart River, 12°58.00'S, 143°31.00'E; NHM 1908.2.25.1 Lower Burdekin River, 19°42'S, 147°18'E; QM 45005 Lynd Highway, 19°14'S, 144°02'E; AM 132784, 135351, NTM 16324, 24515–17, MCC 16 Malogie Waterhole, Daly Waters region, Roper River Drainage, 16°08'S, 133°36'E; UU 14715 Mataranka Station,

1.5 miles east of Mataranka P.O., 14°56'S, 133°04'E; QM 36751 Mitchell River; UU 16841 Near Ayr, Queensland, prob. Burdekin Drg., 19°42'S, 147°18'E; MV 6 near Cape Direction, 12°51.00'S, 143°33.00'E; UC 324–25, 374 near Elliott, 17°20'S, 133°15'E; QM 53064 Old Doomadgee area, 16°57'S, 138°49'E; QM 50736–37, 50739 Old Doomadgee, 5 km southwest of, Lonelys Lagoon, 16°58'S, 138°05'E; QM 50731–32, 50997–98 Old Doomadgee, 5 km southwest of, unnamed temporary lagoon, 16°58'S, 138°05'E; QM 48940 Old Doomadgee, Old Jetty, 16°57'S, 138°49'E; QM 5269 Palm Island, 18°04'S, 146°33'E; NTM 17074 Police Waterhole, near Boorooloola, 16°03'S, 136°21'E; QM 10265 Proserpine, 20°24'S, 148°35'E; QM 31505–08 Silver Plains Station, east of Coen, Unnamed Lagoon, 13°59'S, 143°33'E; AMNH 86543–44, 86547 Staaten River; QM 37566 Stewart River, 23 km north north west Mount Croll, 14°07'S, 143°16'E; QM 26344, 50730 Townsville Town Common, 19°16'S, 146°E 49; QM 15560, 15900 Townsville, Black River, 19°13'S, 146°38'E; QM 13326 Townsville, Thornley Peak, 19°16'S, 146°49'E; QM 20627–28, 20630–31, 20633, 20635 Wakooka Outstation, lagoon 6.4 km west, 14°35'S, 144°03'E; QM 56408–12, 56447–57 Waverley Station, St. Lawrence Road, off Bruce Hwy, 22°23'S, 149°03'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 mccordi* MCZ 76730–32, PCHP 3261, 3399, 4031–43, UC 2005, 2008–09, 2011–13, 2015–19 Roti Island, 11°00'S, 123°00'E; *Chelodina novaeguineae* AMNH 117939, MCZ 120353, 127404, 134390–91, 134709–10, 134712, MV 14409, 38540 Abam, Oriomo River, 08°56'S, 143°10'E; UC 2014, 2022, 2025–26, 2030 Balimo, 08°5'S, 142°50'E; UPNG 6447–48 Bosset, 07°15'S, 141°05'E; MCZ 142500 Daru Roads, 09°04'S, 143°21'E; MCZ 53758–61 Fly/Strickland River, 07°22'S, 141°35'E; MCZ 153930 Girigagrede, Binaturi River, 09°06'S, 142°59'E; MCZ 138101, 142495, 154340 Katatai, 09°00'S, 143°21'E; CE 8407, NHM 1946.1.22.36 Katow; MCZ 134711, 38643, 40700 Kuru 08°55'S, 143°03'E; AM 40070, AMNH 59874 Lake Daviumbo, 07°07'S, 141°16'E; MCZ 134392, 14408 Lake Murray, 06°47'S, 141°26'E; AMNH 57589–91, MCZ 137516, MV 38539 Mabaduan, 06°35'S, 140°55'E; MCZ 153046–48, 153906, 153923, 153926 Masingle, Binaturi River; AGJR 246, UF 43911, 65520 no data; ZMB 36215 no data; MV 14519 Pahoturi River, 09°05'S, 142°40'E; MCC 1–15, 17 McCord Collection, from Balimo, PNG 08°5'S, 142°50'E; AMNH 104010 Peawa, Oriomo River, 08°55'S, 143°10'E; MCZ 134393 Pogo, Pahoturi River; AMNH 58410 Tarara; MCZ 134394–96 Togo, Pahoturi River, 09°15'S, 142°40'E; MCZ 127405 Ume, Binaturi River, 09°05'S, 143°07'E; *Chelodina oblonga* QM 59272–73, 59283 Perth, 31°56'S, 115°50'E), UC 0161–63 Perth, 31°56'S, 115°50'E; *Chelodina pritchardi* MCZ 175813 Hula, Kemp Welch River, 10°06'S, 147°43'E; UC 2038–42, 2044 Kemp Welch River, 09°55'S, 147°40'E; AMNH 135735, 139735 near Hula, Kemp Welch River, 10°06'S, 147°43'E; *Chelodina reimanni* RMNH 27940, 27942, 27950 Boeti near Merauke; MTKD 29178, 29241, 29243, "live A," "type 1," "type 2" PCHP 3222, 4398, 4563–64, 4566–67, 4570–71 RMNH 27897, 27912–15, UC 2021, 2023–24, 2027–29 Merauke, 8°50'S 140°30'E; ZMB 56236 no data. *Chelodina steindachneri* AM33117, MCZ33501, UC248, 266, 271, 281, 284, 290 no data; AM 100425–33 middle branch of Gascoyne River at the Great Northern Highway, 25°12'S, 119°20'E; UU 16781 Western Australia; UU14721 Whela Creek, Poonthoon Pool, 14 miles west and 13 miles north of Mileu, 26°11'S, 117°07'E *Chelodina expansa* group *Chelodina burrungandjii* UC 2088–90, 2101 Gunyarr pools, adjacent to Katherine River Gorge, 14°18'S, 133°31'E; NTM 13525 Mann River, upper reaches, 13°01'S, 133°58'E; NTM 16008–12 Koolpin Gorge, 13°28'S, 132°38'E; NTM 16333 Sleisbeck, Katherine River, 13°47'S, 132°49'E; UU 17730–31 Avis Lagoon, Liverpool R., Arnhem Land, 12°45'S, 133°49'E; 17732 Double B., East Alligator River, Arnhem Land, 13°09'S, 133°22'E; 17733–34 Liverpool River, Arnhem Land, 12°37'S, 133°55'E; 17735 Mann River, Arnhem land, 15°01'S, 133°58'E; 17736 Jimjim Waterhole, 4 km south and 3 km east, Coinda, 12°57'S, 132°33'E; 17737 South Alligator Drive 9.5 km north and 25 km east, Coinda, 12°49'S, 132°33'E; 18833 Katherine River, Arnhem Land, 13°22'S, 133°08'E; 18834–39 Magela Creek 17.5 km north Kub-O-Wer Hill, 12°50'S, 133°03'E; 18840–41 East Alligator River Arnhem Land, 13°12'S, 133°19'E; 18842–52 Jim Jim Creek Arnhem Land, 13°19'S, 133°01'E; 18853–58 Wilton River 14.5 km southeast Shadforth Hills, 13°14'S, 134°12'E; 18859 Mann River, Arnhem Land, 13°15'S, 133°35'S; NTM 22581–83 Sleisbeck, Katherine River, 13°53'S, 132°47'E; *Chelodina expansa* UC 2099 Albury 36°05'S, 146°55'E; UC 2074, 2190–94 Mungabareena Reserve, Albury 36°06'S, 147°00'E; UC 223 Murray/Darling; QM J59284, UC, 254, 259, 269, 278, 283, 287, 396 no data, pet trade; *Chelodina kuchlingi* WAM R29411 Kalumburu Western Australia, 14°18'S, 126°28'E; *Chelodina parkeri* AM 21159 Aketa, Aramia River, 08°01'S, 142°45'E; AM 21434 Aramia River, near Balimo, 8°01'S, 142°57'E; AM 127898 Awaba, 08°00'S, 142°35'E; UPNG 6893, 6895 Balamale; MCZ 134402,

149722, UF 43812-14 Balimo, 08°03'S, 142°56'E; AM 21353 Balimo, Aramia River 08°01'S, 142°57'E; UF 43912 Balimo, Makapa Village, Aramia River 08°01'S, 142°57'E; UF 43913 Balimo, Tai Village, 08°01'S, 142°57'E; MV 54433 Balumuk; UPNG 6428 Bosset, 07°15'S, 141°05'E; MCZ 149723 Daru, 09°04'S, 143°21'E; UC 215, 220, 327, 2006-07 Fly River District, 07°0'S, 141°30'E; AM 117000, MCZ 129897, 134400-01, 134464-65, 153041 Lake Murray, 06°47'S, 141°26'E; AM 74693 Lake Murray, or Aramia River, 07°00'S, 141°26'E; AM 21423-25 Mawa, Lake Murray, 6°49'S, 141°22'E; AMNH 133083 Port Moresby, captive, 09°28'S, 147°09'E; *Chelodina rugosa* AM 37506-07 12 miles northeast Bamaga, Cape York, 10°51'S, 142°28'E; AM 101319 2.7 km northeast Vrilya Point, Cape York Peninsula, 11°13'S, 142°08'E; AM 37500-05 29 miles north of Coen, Cape York, 13°32'S, 143°02'E; QM 33368 Aurukun, Bigatuk Lake, 13°22'S, 141°44'E; MV 49932 Awaba, 08°00'S, 142°35'E; QM 35146 Big Lake, Aurukun Reserve, 13°21'S, 141°43'E; QM 17514 Big Stinking Lagoon, Calvert River, Robinson River, 16°22'S, 137°39'E; UU 14405-06 Boyd Lagoon, 6.2 miles west and 4 miles south of Merluna, 13°07'S, 142°21'E; QM 40078-79 Brisbane, Cannon Hill, 27°28'S, 153°05'E; QM 57649 Burton Lagoon, King Junction, 15°53'S, 143°31'E.; AM 6256, UU 14418 Cape York, 11°48'S, 142°21'E; UU 14389-90 Crocodile Hill, Parry Creek, 9 miles south and 10 miles east of Wyndham, 15°38'S, 128°18'E; UU 14407-08 Croll Creek, 19.3 miles north and 7.8 miles west of Coen, 13°40'S, 143°02'E; UC 0302, 0320-23, 0326-27 Douglas River, 13°40'S, 131°10'E; AM 44923 Edwards River, 14°40'S, 142°25'E; AM 28464 Eumundi, 26°29'S, 152°57'E; UC 2102 Gulf Country; QM 58426 Horse Lagoon, near Gilbert River; UU 14403-04 Horseshoe Lagoon, 4.2 miles north and 10.8 miles east of Old Laura, 15°12'S, 144°27'E.; QM 17633-34 Horseshoe Lagoon, approximately 80 km west Cooktown. GR237067 Cooktown, 1:250000, 15°17'S, 144°37'E.; QM 45850 Lake Emma, west of Cooktown on Old Laura Road, 15°17'S, 144°39'E; AM 143559 Manning Gorge, Mount Barnett Station, 16°39'S, 125°55'E; QM 53324 Marina Plains, Cape York Peninsula, 14°33'S, 143°52'E; QM 37622 Massey Creek mouth, 5 km west 13°54'S, 143°33'E; AMNH 82532 Mitchell River Mission, Cape York, 10°06'S, 147°43'E; MV 8439 Mornington Island, 16°30'S, 139°30'E; QM 59264, NWC 528, 529, UC 256 no data; QM 47912-14 Old Doomadgee, 16°57'S, 138°49'E; QM 53063 Old Doomadgee area, 16°57'S, 138°49'E; QM 50738 Old Doomadgee, 3 km southwest of, Wananooi Lagoon 16°57'S, 138°51'E; QM 50995-96 Old Doomadgee, 5 km southwest of, unnamed lagoon, 16°58'S, 138°05'E; QM 53065-67 Perched Lake near MacMillan River, Shellburne Holding; UU 14409-17 Pond, Coen Airport, 12.5 miles north and 5 miles west of Coen, 13°45'S, 143°05'E; AM 48364 Saibai Island, Torres Strait, 09°23'S, 142°40'E; QM 20636 Saltwater Lagoon, 5 km northeast Wakooka Outstation, 14°31'S, 144°34'E; QM 3852 Vanderlin Island, Pellew Group, 15°42'S, 136°59'E; QM 20629, 20632, 20634, Wakooka Outstation, lagoon 6.4 km west, 14°35'S, 144°03'E; QM 20637-39 Wakooka, lagoon 17.6 km south, on Wakooka-Starcke Road, 14°37'S, 144°41'E.; AM 138463 Willum Swamp, Weipa Peninsula, 12°40'S, 141°00'E; *Chelodina siebenrocki* MCZ 134466 Boze, Binituri River, 09°05'S, 143°00'E; UC 212, 2010, 2020 Fly River District, 07°00'S, 141°30'E; AMNH 111645-46, MCZ 135397-98, 139541-42, 140866-67 142496-97, 153042 Katatai, 09°00'S, 143°21'E; RMNH 27935 Kelappa Lima, Merauke River; RMNH 27920 Koembi, west of Merauke; MCZ 153920 Kunini, Binituri River; MCZ 153044 Masingle, Binituri River; RMNH 27891, 27894-95, 27898-99, 27902-06, 27908-11, 27918-19, 27937-38, 27945-47 Merauke 08°28'S, 140°20'E; MCZ 141288 Mawatta, Pahoturi River 09°12'S, 142°52'E; ZMB 18837, 36219, 36221-22, 49660 no data; MCZ 134403-04, 134467-68 Togo, Pahoturi River, 09°15'S, 142°40'E; MCZ 153045 Ume, Binituri River, 09°05'S, 143°07'E.; *Chelodina* sp. aff. *rugosa* Kimberley. UU 17738-55 Campbell Creek 4 km southwest of Ellenbrae Homestead, 15°59'S, 127°02'E; 17756 Hann River, 10.5 km southeast Gibb River Station, 16°28'S, 126°21'E; 17757 Barnett River Gorge, 27 km northeast of Mt. Barnett Homestead, 16°32'S, 127°08'E; 17758-60 Carson River, 3.2 km west northwest of Carson River Homestead, 14°29'S, 126°44'E; 17761 Carson River, 17 km south and 1.5 km east of Kalumburu, 14°27'S, 126°44'E; 17762-65 Drysdale River, 4 km northeast of Drysdale River Homestead, 15°31'S, 126°24'E; 17766-69 Mitchell R., 2.5 km west southwest of Mitchell River Homestead, 15°08'S, 125°46'E; 17770-75 Isdell River 34.5 km west and 4.5 km north of Mt. House Homestead, 17°01'S, 125°26'E; 18157 Manning Cr. 2.5 km wwest Mt. Barnett Station, 16°39'S, 125°55'E; 18158 Adcock River, Mt. House, 17°03'S, 125°42'E; 18515-17 Kalumburu, 14°17'S, 126°39'E; 18818-30 Drysdale River, Drysdale River Homestead, 15°31'S, 126°24'E; 18831-32 Campbell Creek 4 km southwest of Ellenbrae Homestead, 15°59'S, 127°02'E; AM 123805 Mitchell Plateau, upstream from Little Merten's Falls, 14°49'S, 125°43'E; 133443-44 Merten's Creek, tributary of Mitchell River, Mitchell Plateau, 14°49'S, 125°43'E; 133445 Vic. of Surveyors Pool, tributary of Mitchell River, Mitchell Plateau, 14°40'S, 125°44'E; 136058-65 Bell's Creek approximately, 3.5 km upstream from Bell's Gorge, Isdell River, 17°01'S,

AUSTRALIAN TURTLE SYSTEMATICS

125°12'E; 136148–52 Vic. of Surveyors Pool, tributary of Mitchell River, Mitchell Plateau, 14°40'S, 125°44'E; 136171 Merten's Creek, tributary of Mitchell River, Mitchell Plateau, 14°49'S, 125°43'E; 137999 Bell's Creek approximately, 3.5 km upstream from Bell's Gorge, Isdell River, 17°01'S, 125°12'E; 140403 Manning Gorge, Mount Barnett Station, 16°39'S, 125°55'E; 142496 Bells Gorge, 17°01'S, 125°12'E; 143558 Manning Gorge, Mount Barnett Station, 16°39'S, 125°55'E.

APPENDIX 2.

Descriptions of Measurement Used

HL: Head length: straight line from anterior edge of the premaxilla 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 (see Fig. 4): width of skull at juncture of the parietals and postorbitals. IO: Interorbital width: width of frontal bone between the orbits. OD: Orbital diameter: maximum horizontal internal diameter of the orbit. ON: Orbital nasal distance: minimum distance from the orbit to the exter-

nal naris. HH: Head height: vertical height of skull from the palate to the frontal. HT: Horizontal diameter of the otic chamber: measured from the condyle mandibularis to the top of the otic chamber. TPL: Tympanum to parietal length (see Fig. 4): length of the remainder of the parietal arch from the tympanum on the quadrate to the end of the arch.

Shell Measurement

CL: Carapace length: midline from the cervical to the suprapygal. CW: Maximum carapace width with CW4: Carapace width four: straight width at the junction of the fourth and fifth marginal scutes. CW8: Carapace width eight: straight width of carapace 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: maximum midline length of the plastron. PWF: Width of anterior lobe of plastron: measured in straight line at the junction of the humerals and pectorals. PWR: Width of posterior lobe of plastron: measured in straight line at the junction of the abdonimals and femorals.