Zootaxa 5448 (4): 531–555
https://www.mapress.com/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5448.4.6
http://zoobank.org/urn:lsid:zoobank.org:pub:B82C87CC-501B-4844-ACAB-21BD1377E2A3

History and historical DNA: Identity of *Chelodina intergularis* Fry, 1915 and type localities of *C. intergularis* and *C. rugosa* Ogilby, 1890

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Abstract

Based on the phylogenetic placement of a near-complete mitogenome sequence of the holotype of *Chelodina intergularis* Fry, 1915 generated with hDNA approaches, we present evidence for the synonymy of this nominal species with *Chelodina rugosa* Ogilby, 1890. The type specimens of both taxa are housed in the Australian Museum, Sydney. Scrutinizing historical records, we conclude that the type locality of both taxa is most likely the vicinity of Somerset, at the northern extremity of Cape York Peninsula, Queensland, Australia. We figure and describe both type specimens. Our results support the earlier conclusion that the exceptional arrangement of intergular and gular scutes in the holotype of *C. intergularis* is an individual aberration.

Key words: Chelidae, collection history, hDNA, mitogenome, museomics, nomenclature, side-necked turtles, taxonomy

Introduction

Short-read DNA technology and protocols originally developed for ancient DNA (aDNA) sequencing allow today for novel uses of historical museum material for a multitude of questions and applications (e.g., Raxworthy & Smith 2021; Fong *et al.* 2023). One important application is the clarification of taxonomic controversies by sequencing name-bearing type material (e.g., Kehlmaier *et al.* 2019, 2023). A prominent group with many unresolved nomenclatural challenges is the side-necked turtle family Chelidae Gray, 1825 from South America, Australia, New Guinea, and a few eastern Indonesian islands (Georges & Thomson 2010; TTWG 2021). Using historical DNA (hDNA) sequencing, Kehlmaier *et al.* (2019) generated near-complete mitochondrial genomes (mitogenomes) from type material that resolved a number of nomenclatural questions for Australasian taxa (see also Kuchling 2020; Kehlmaier *et al*. 2024). Unfortunately, several crucial type specimens were not available for that study, among them the holotype of *Chelodina intergularis* Fry, 1915.

Long-necked turtles of the genus *Chelodina* Fitzinger, 1826 have a wide distribution across New Guinea and Australia and also occur on the Indonesian islands Timor and Roti. The genus contains 17 currently recognized species in three morphologically divergent clades ranked as subgenera (TTWG 2021). The first species described

Accepted by A. Bauer: 9 Apr. 2024; published: 14 May 2024

and the type species (Fitzinger 1826) of the genus and subgenus *Chelodina* is "*Emys longicollis*" (= *Testudo longicollis* Shaw, 1794) with an imprecise type locality of "New Holland" [=Australia]. The second *Chelodina* species described was the morphologically distinctive *Chelodina oblonga* Gray, 1841 with type locality "Western Australia," representing the monotypic subgenus *Macrochelodina* named by Wells & Wellington (1985). After *C. oblonga* several other taxa were described (TTWG 2021), of which only those with relevance for the present study are mentioned here. Ogilby (1890) named *Chelodina rugosa* from Cape York (Queensland), followed by Werner's (1901) description of *Chelodina siebenrocki* from the former German colony in New Guinea ("Deutsch-Neu-Guinea"), two taxa representing the third subgenus, *Chelydera*, erected by Thomson & Georges (in Shea *et al.* 2020). However, Siebenrock (1909, 1915) synonymised *C. rugosa* and *C. siebenrocki* with *C. oblonga*, which was then considered to occur in Northern Australia, New Guinea, and southwestern Australia. In the following decades, and until today, species placed in the subgenus *Chelydera* experienced continued taxonomic unrest.

Fry (1915) described *Chelodina intergularis*, with the questionable type locality of "Australia." The description of *C. intergularis* was based on the unusual scutation of the plastral forelobe of its holotype, a shell in the Australian Museum, Sydney. While in *Chelodina* the intergular scute generally does not reach the anterior plastral rim because the flanking gular scutes meet medially, this is not the case in the type of *C. intergularis*. In this specimen, the intergular divides the gular scutes so that the tapered intergular tip is part of the rim. Mertens & Wermuth (1955) and Wermuth & Mertens (1961) accepted *C. intergularis* as a valid Australian species (stating that its exact distribution is unknown), resurrected the New Guinean species *C. siebenrocki* from the synonymy of *C. oblonga* and restricted the name *C. oblonga* to the populations in northern and south-western Australia. In contrast to Mertens & Wermuth (1955) and Wermuth & Mertens (1961), Goode (1967) used the name *C. siebenrocki* for populations from northern Australia and New Guinea and restricted *C. oblonga* to the southwestern Australian taxon. Goode (1967: 44) pointed out "It seems probable that the two shells in the Australian Museum, Sydney, described respectively as *C. rugosa* Ogilby 1890 (from Cape York) and *C. intergularis* Fry 1915 (from 'Australia') are specimens of *C. siebenrocki*. The extent of the intergular, which is marginal on *C. intergularis* is probably just an abnormality of a form more commonly known on less significant shields." Thus, Goode (1967) was unsure about the synonymy of these three nominal species. Burbidge *et al.* (1974) restricted later the name *C. siebenrocki* to turtles from New Guinea and used *C. rugosa* for northern Australian individuals and *C. oblonga* for the south-western Australian taxon. Based on allozyme profiles at 45 presumptive loci, Georges *et al*. (2002) synonymized later *C. siebenrocki* with *C. rugosa*.

Notably, Burbidge *et al.* (1974) examined one specimen of *C. rugosa* from Darwin, Northern Territory, and another possibly conspecific individual from Kalumburu in the Kimberley region of Western Australia, for their immunoelectrophoretic investigation and found "a strong affinity" between them, despite morphological differences. While the turtle from the Kimberley later became the holotype of *Chelodina kuchlingi* Cann, 1997, the original description did not mention its previously reported immunological relationship to *C. rugosa* from the Northern Territory. *Chelodina kuchlingi* was long regarded as a junior synonym of what is now *C. rugosa* sensu lato (Georges & Thomson 2010; TTWG 2010, 2011, 2012; Ellis & Georges 2015; for the usage of the name *C. rugosa* see TTWG 2021 and below), but *C. kuchlingi* was resurrected by the Turtle Taxonomy Working Group (TTWG 2014, 2017). Kehlmaier *et al*. (2019) supported the validity of *C. kuchlingi* based on its deeply divergent mitogenome, placing its holotype basal to two studied specimens of *C. rugosa* and the holotype of *C. siebenrocki*. However, the geographic provenance ("Kalumburu") of the holotype of *C. kuchlingi* has later been questioned and emended (Kuchling 2020; see also Table 1).

After *C. kuchlingi*, three further species of the subgenus *Chelydera* were described: *Chelodina burrungandjii* Thomson *et al.*, 2000 from the Arnhem Land Sandstone Plateau of the Northern Territory, *C. walloyarrina* (McCord & Joseph-Ouni, 2007) from the Kimberley Sandstone Plateau in Western Australia, and *C. kurrichalpongo* (Joseph-Ouni *et al.*, 2019) from the Northern Territory. Even though these three taxa are accepted and listed by the Turtle Taxonomy Working Group (TTWG 2021), the taxonomic validity of the latter two species as well as the nomenclatural availability of their names are disputed by some. Neither *C. walloyarrina* nor *C. kurrichalpongo* are recognized by the "Official List of Species of Australian Reptiles and Amphibians" of the Australian Society of Herpetologists as of 30 November 2023 (http://www.australiansocietyofherpetologists.org/ash-official-list-of-australian-species) because the original descriptions appeared in publications not subjected to scientific peer review. Moreover, in the case of *C. walloyarrina*, Georges *et al*. (2002) found no fixed allelic differences compared to *C. burrungandjii*, i.e., between populations from Arnhem Land, Northern Territory, and Kimberley, Western Australia, suggesting taxonomic identity. Therefore, for the purposes of this paper, we treat *C. walloyarrina* as synonymous

with *C. burrungandjii* and follow the lead of the Australian Society of Herpetologists and subsume under *C. rugosa* sensu lato populations from southern New Guinea and Queensland, Australia (*C. rugosa* sensu stricto, i.e., in the sense of TTWG 2021 including *C. siebenrocki*), as well as those from the Northern Territory, Australia, described as *C. kurrichalpongo*.

TABLE 1. Specimens, tissues and sequences used for phylogenetic reconstructions. Collection acronyms: AM = Australian Museum, Sydney; AMNH = American Museum of Natural History, New York; ANWC = Australian National Wildlife Collection (CSIRO), Canberra; BMNH = The Natural History Museum, London; MCZ = Museum of Comparative Zoology, Harvard University, Cambridge; MTD = Museum für Tierkunde, Senckenberg Naturhistorische Sammlungen, Dresden; NLWL = College of Life Sciences, Anhui Normal University, Wuhu; SAM = South Australian Museum, Adelaide; WAM = Western Australian Museum, Perth; ZMB = Museum für Naturkunde, Berlin. Tissue vouchers are held at the Wildlife Tissue Collection, University of Canberra, Canberra.

Taxon, type status	Provenance	Museum specimen	Tissue voucher	Accession number	Reference for sequence data
Chelodina burrungandjii	Australia: Western Australia: King Edward River, Surveyors Pool (S14° 40' 15.6" E125° 44' 6")	-	UC_0671	KY776447	Kehlmaier *et al*. (2019)
Chelodina canni	Australia: Northern Territory: Roper River, Sunday Creek (S16° 7' 4.8" E133° 34' 19.2")	-	UC_0657	KY776448	Kehlmaier *et al*. (2019)
Chelodina expansa	Australia: Queensland: Fitzroy River, Moura (S24° 36' 10.8" E149° 54' 46.8")	-	AA032872	KY705230	Kehlmaier *et al*. (2019)
Chelodina expansa	Australia: New South Wales: Murray River, Mungabareena (S36° 5' 34.8" E146° 56' 52.8")	-	UC_0175	KY776450	Kehlmaier *et al*. (2019)
Chelodina gunaleni, holotype	Indonesia: Central Papua Province (Irian Jaya): Uta River Basin, Mimika District	AMNH R160133	-	LR215671	Kehlmaier *et al*. (2019)
Chelodina intergularis, holotype	"Australia?"	AM R6255	-	OY859728	This study
Chelodina kuchlingi, holotype	Australia: Western Australia: Kalumburu (S14° 18' E126° 28'), but according to Kuchling (2020) Parry Creek, lower Ord River floodplain, Western Australia	WAM R29411	-	LR215672	Kehlmaier *et al*. (2019)
Chelodina longicollis, holotype	"New Holland"	BMNH 1947.3.5.86	-	LR215688	Kehlmaier *et al*. (2019)
Chelodina longicollis	Australia: Australian Capital Territory (S35° 11' 24" E149° 6' 36")	-	AA045603	KJ713173	Zhang & Georges (2014)
Chelodina mccordi, paratype	Indonesia: East Nusa Tenggara Province: southwestern Roti Island: Danau Naloek, near Busalangga (S10° 48' E123° 00')	MCZ 176731	-	LR215673	Kehlmaier *et al*. (2019)
Chelodina mccordi	Indonesia: Roti Island	-	UC_0493	KY705231	Kehlmaier *et al*. (2019)
Chelodina mccordi roteensis, holotype	Indonesia: East Nusa Tenggara Province: eastern Roti Island: Lake Enduy	AMNH R160132	-	LR215674	Kehlmaier *et al*. (2019)

...Continued on the next page

TABLE 1. (Continued)

Taxon, type status	Provenance	Museum specimen	Tissue voucher	Accession number	Reference for sequence data
Chelodina mccordi timorlestensis, holotype	Indonesia: Timor-Leste: Lautém District: Plain of Lake Ira Lalaro, east of Lospalos (ca. S8° 28' E127° 07')	WAM 165888	-	LR215675	Kehlmaier *et al*. (2019)
Chelodina novaeguineae, lectotype	S. E. New Guinea: Katow	BMNH 1946.1.22.36	-	LR215676	Kehlmaier *et al*. (2019)
Chelodina novaeguineae	Papua New Guinea: lower Fly River, Sepuka Village	-	AA042290	KY776446	GenBank
Chelodina oblonga, holotype	Western Australia	BMNH 1947.3.5.89	-	LR215677	Kehlmaier *et al*. (2019)
Chelodina oblonga	Australia: Western Australia: Swan River, Perth (S31° 57' E115° 51')	-	UC_0227	KY776449	Kehlmaier *et al*. (2019)
Chelodina parkeri	Papua New Guinea: Fly River, Suki-Aramba Swamp (S8° 14' 42" E141° 46' 1.2")	-	AA042607	KY705232	Kehlmaier *et al*. (2019)
Chelodina pritchardi	Papua New Guinea: Laloki River (S9° 1' 51.6" E146° 52' 8.4")	SAM R67213	AA021711	KY705233	Kehlmaier *et al*. (2019)
Chelodina reimanni, holotype	Indonesia: West Papua (West Irian): Merauke River	MTD 29178	-	LR215678	Kehlmaier *et al*. (2019)
Chelodina reimanni, paratype	Indonesia: West Papua (West Irian): Merauke River	MTD 42828	-	LR215679	Kehlmaier *et al*. (2019)
Chelodina rugosa	Australia: Northern Territory: Finnis River, Knuckies Lagoon (S12° 25' 33.6" E130° 56' 16.8")	-	UC_0313	KY776451	Kehlmaier *et al*. (2019)
Chelodina rugosa	Papua New Guinea: Morehead River, Tonda Creek	-	AA42811	KY705234	GenBank
Chelodina rugosa	Unknown, probably New Guinea, Indonesia (Chinese pet trade)	NLWL080003	-	HQ172157	Wang *et al*. (2012)
Chelodina siebenrocki, holotype	"Deutsch Neu-Guinea"*	ZMB 16491	-	LR215680	Kehlmaier *et al*. (2019)
Chelodina steindachneri	Australia: Western Australia: Millbillillie Station (S26° 37' 15.6" E120° 19' 48")	ANWC R5058	UC_0238	KY776452	Kehlmaier *et al*. (2019)
Chelodina timorensis, holotype	Indonesia: eastern East Timor: Lautem District (regency), Tutuala Subdistrict: Lake Ira Lalaro	AMNH R160135	-	LR215681	Kehlmaier *et al*. (2019)
Elseya flaviventralis	Australia: Northern Territory: South Alligator River, Pine Creek Crossing (S13° 29' 56.4" E132° 28' 15.6")	-	UC_0255	KY776454	Kehlmaier *et al*. (2019)

* The provenance of the holotype of *C. siebenrocki* is unclear. Its supposed type locality is "Deutsch-Neu-Guinea" (Werner 1901). However, the former German colony in northeastern New Guinea was approximately 450 km beyond the known distribution range in southern New Guinea (compare the map for *C. rugosa* in TTWG 2021 and the political borders shown in the map "Neuguinea und der Bismarckarchipel" in Scobel 1899: 184).

Given the description of *C. intergularis* based on a dry shell of possibly aberrant morphology (Goode 1967) and without good locality data, it remains untested whether *C. intergularis* is a senior synonym of *C. burrungandjii* (including populations referred to by some as *C. walloyarrina*), *C. kuchlingi* or *C. kurrichalpongo*—or alternatively a junior synonym of *C. rugosa*. In this vein, Kehlmaier *et al.* (2019) speculated that the name *C. intergularis* could refer to the distinctive Northern Territory lineage of *C. rugosa* sensu lato to which the name *C. kurrichalpongo* was applied (Joseph-Ouni *et al.* 2019), while Thomson *et al*. (2000) noted that the intergular scute reaches the plastral margin in many *C. burrungandjii*. This trait is also present in the holotype of *C. kuchlingi* (Cann 1997; Cann & Sadlier 2017). None of these species were explicitly compared to and distinguished from *C. intergularis* when they were described.

Here we present a near-complete mitogenome for the holotype of *C. intergularis* obtained with hDNA approaches and compare it to the previously published relevant mitogenomes from Kehlmaier *et al.* (2019) and GenBank. In addition, to assess the identity of *C. intergularis*, we use historical sources to obtain information on the geographic provenance of the holotypes of *C. intergularis* and *C. rugosa* and describe and compare the types with other species of the subgenus *Chelydera*. The holotype of *C. rugosa* was not sampled for genetics to avoid compromising the specimen because the identity of *C. rugosa* sensu stricto is clear.

Material and Methods

Wet lab. The holotype of *Chelodina intergularis* (Fig. 1; Australian Museum, Sydney, AM R6255; dry shell) was sampled in a dedicated cleanroom facility at the Evolutionary Biology Laboratory at the Australian National University, Canberra, by Alicia Grealy (CSIRO, Canberra). Further processing took place in another cleanroom at Senckenberg Dresden, which is physically isolated from the local main laboratory to avoid contamination by foreign DNA (see Fulton & Shapiro 2019). DNA was extracted from 43.3 mg of dry bone powder using the protocol of Dabney *et al.* (2013), with a final elution of twice 12.5 µl TET buffer and an incubation at room-temperature for 5 min. A negative control was processed along with the sample and screened for contamination. DNA concentration and quality were assessed using a Qubit 3.0 Fluorometer (Thermo Fisher Scientific) and a 4200 TapeStation system (Agilent). Twenty-seven nanogram (27 ng) of extracted DNA were converted into a double-indexed single-stranded Illumina sequencing library following Gansauge & Meyer (2019). To increase the amount of endogenous library molecules, two-rounds of in-solution hybridization capture were performed in a dedicated capture-only workspace in the main laboratory using DNA baits generated from modern PCR products (Maricic *et al.* 2010; Horn 2012). A specimen of *Emydura australis* (WAM TR1429) was used for the preparation of the individual bait libraries. Long-range PCR reactions for the mitochondrial baits were performed in 50 µl volumes, containing 1 µl of high-molecular DNA extract and 1 unit of TaKaRa LA Taq DNA Polymerase, Hot-Start Version (Clontech Laboratories Inc.), using the reaction mixture recommended by the manufacturer. PCR conditions comprised an initial denaturation at 93°C for 3 min, followed by 35 cycles of 93°C for 15 sec, 60 or 63°C for 30 sec, 68°C for 10 min and a final elongation step at 68°C for 20 min. For primer sequences, annealing temperatures, and fragment lengths see Table S1. PCR products were visualized on a 1% agarose gel. The combined long-range PCR products covered most of the mitochondrial genome from tRNA-Phe (situated before 12S) to the 5′-half of the control region, missing out approximately 350 bp. Sequencing was conducted inhouse using an Illumina MiSeq platform, generating 5,015,698 75 bp paired-end raw reads.

Bioinformatics. Adapter trimming with Skewer 0.2.2 (Jiang *et al.* 2014), read merging (minimum length 35 bp), quality filtering (minimum Q-score 20), and duplicate removal with BBmap-suite 37.24 (https://sourceforge.net/projects/bbmap/) (Bushnell *et al.* 2017) reduced the readpool to 2,451,179 quality-filtered reads (48.9% of raw reads). The remaining reads were screened for contamination using FastQScreen 0.11.4 (Wingett & Andrews 2018) and a set of predefined mitochondrial sequences (Table S2), including the mitogenome of *Chelodina rugosa* (GenBank accession number HQ172157). The assembly of the mitogenome was achieved applying MITObim (Hahn *et al.* 2013) and a two-step baiting and iterative mapping approach with an allowed mismatch value of 2, and GenBank sequence HQ172157 (*C. rugosa*) as a starting seed. The resulting contig was visualized and checked for assembly artefacts in Tablet 1.21.02.08 (Milne *et al.* 2013). Artefacts were manually removed from the assembled contig and all positions with coverage below threefold masked as ambiguous (N) using the maskfasta subcommand of BEDTools 2.29.2 (Quinlan & Hall 2010). Sequence length distribution of mapped reads was calculated with a customized awk

command and Microsoft Excel. The temporal authenticity of the mapped reads was tested with mapDamage 2.0 (Jónsson *et al.* 2013), which accounts for nucleotide misincorporations due to DNA degradation. The contig was aligned to the complete mitogenome of *C. oblonga* (KY776449) and annotated accordingly (Table S3).

FIGURE 1. Holotype of *Chelodina intergularis*, Australian Museum, Sydney (AM R6255). Photos: G. Shea.

Alignment and phylogenetic reconstructions. The newly generated near-complete mitogenome of the *Chelodina intergularis* type was aligned with 27 mitogenomes from DDJB/ENA/GenBank. The alignment included all mitogenomes for *Chelodina* available by 31 December 2023; *Elseya flaviventralis* (KY776454) served as outgroup (Table 1). The alignment was adjusted manually and cropped to its final length. Each protein-coding gene was screened for the presence of internal stop codons using MEGA X (Kumar *et al.* 2018). Problematic sequence features were deleted prior to phylogenetic analyses: (1) Stop codons of coding genes, as these do not code for any amino acid; (2) gene overlap between coding regions and between tRNAs, as these short regions cannot be attributed to a single locus and may underlie a distinct evolutionary model; (3) alignment positions that cause frame shifts in coding regions; and (4) non-coding spacer DNA. In total, 270 positions were removed, so that the final alignment comprised 15,890 bp. It can be downloaded from figshare using the link https://doi.org/10.6084/m9.figshare.25133879.

Phylogeny was inferred using this dataset and the Maximum Likelihood and Bayesian approaches implemented in RAxML 8.0.0 (Stamatakis 2014) and MrBayes 3.2.6 (Ronquist *et al.* 2012); best evolutionary models and partitioning schemes were determined using PartitionFinder2 (Lanfear *et al*. 2017); see also Tables S3–S5. For Maximum Likelihood, the GTR+G substitution model was used for 10 independent searches with different starting conditions and the rapid bootstrap option, following the recommendation of Stamatakis (2016: 59–60) to avoid the GTR+I+G model. Finally, 1000 nonparametric thorough bootstrap replicates were calculated, and the values were plotted against the best tree. For Bayesian inference, four parallel runs (each with eight chains) were conducted with two million generations (burn-in of 0.25, print frequency of 1000, and sample frequency of 500). Calculation parameters were examined using Tracer 1.7.1 (Rambaut *et al*. 2018). Uncorrected p distances were obtained in MEGA X (Kumar *et al.* 2018) with the pairwise deletion option turned on.

Historical data and morphology of the type specimens. To determine the collection history of the holotype of

Chelodina intergularis and narrow down its type locality, the collection records and supporting historical information were scrutinized. In doing so, we also examined historical evidence for the type locality of *C. rugosa*, another species represented by its holotype in the collection of the Australian Museum. The two holotypes were examined, measured and photographed. Measurements were taken to a precision of 0.1 mm with a 300 mm Vernier calliper (Mitutoyo), and the Vernier scale read under a dissecting microscope to ensure accuracy. Traits of these specimens were compared to those of relevant members of the subgenus *Chelydera*.

Results and Discussion

Mitogenome and phylogeny. The near-complete mitogenome sequence of the holotype of *Chelodina intergularis* is 16,149 bp long and includes 3,137 ambiguous positions (19.4%). It was assembled from 15,361 unique reads (0.63% of the quality filtered readpool), with an average read length of 76 bp (35–143 bp), and a 74-fold average coverage per site. The sequence is deposited under accession number OY859728 in the European Nucleotide Archive.

Both phylogenetic analyses yielded identical tree topologies (Fig. 2), matching those for *Chelodina* published in Kehlmaier *et al.* (2019) and reflecting the propensity of the genus for mitochondrial introgression and mitochondrial capture (Hodges 2015; Kehlmaier *et al*. 2019). This explains why the mitochondrial phylogeny of *Chelodina* differs considerably from the species tree (Hodges 2015) and conflicts with the subgenera. Nevertheless, identical or similar mitogenome sequences are highly informative for unravelling the geographic source and the identity of the respective individuals.

The mitogenomes identified as *C. rugosa* are paraphyletic with respect to the mitogenome of the holotype of *C. siebenrocki*. These sequences correspond to two deeply divergent clades. One is represented by a single mitogenome of a *C. rugosa* sensu lato from the Finnis River, Northern Territory (KY776451, "*C. kurrichalpongo*"), while the other clade contains the mitogenome of the holotype of *C. siebenrocki*, which is sister to a weakly divergent clade comprised of the mitogenomes of a *C. rugosa* of unknown provenance (HQ172157, Chinese pet trade, presumably New Guinea), the holotype of *C. intergularis*, and another *C. rugosa* (KY705234) from Papua New Guinea (Tonda Creek, Morehead River). Basal to this clade is the mitogenome sequence of the holotype of *C. kuchlingi*. The uncorrected p distances for these samples range from 0.20–6.37% (Table 2). The holotype of *C. intergularis* differs from the three *C. rugosa* by 0.20–5.00%. These results, and in particular the near-identity of the mitogenome sequence of *C. intergularis* and the *C. rugosa* sample (KY705234) from Papua New Guinea (uncorrected p distance 0.20%), suggest that *C. intergularis* represents a morphologically abnormal *C. rugosa*, as proposed by Goode (1967). However, the divergence value of 5.00% compared to the Northern Territory *C. rugosa* (KY776451) implies that the name *C. intergularis* does not refer to this population, in contrast to the considerations of Kehlmaier *et al*. (2019). An identity with *C. kuchlingi* or the deeply divergent *C. burrungandjii* can also be ruled out (uncorrected p distances of 5.60% and 8.49%, respectively).

Historical data. The holotype of *Chelodina intergularis* Fry, 1915 was registered in the Australian Museum on 5 September 1913, with the provenance "Australia?" and the note that it was from the "Old Collection."

TABLE 2. Uncorrected p distances (percentages) for near-complete mitogenomes (15,890 bp) of the *Chelodina rugosa* complex, *C. burrungandjii*, and *C. kuchlingi* based on the alignment used for Figure 2.

		1	2	3	4	5	6	7
1	*Chelodina siebenrocki* holotype LR215680	-						
2	*Chelodina rugosa* HQ172157	1.49	-					
3	*Chelodina intergularis* holotype	1.29	0.46	-				
4	*Chelodina rugosa* KY705234	1.50	0.51	0.20	-			
5	*Chelodina rugosa* KY776451	5.45	5.62	5.00	5.62	-		
6	*Chelodina kuchlingi* holotype LR215672	6.21	6.37	5.60	6.34	3.84	-	
7	*Chelodina burrungandjii* KY776447	8.87	9.08	8.49	9.06	8.98	5.93	-

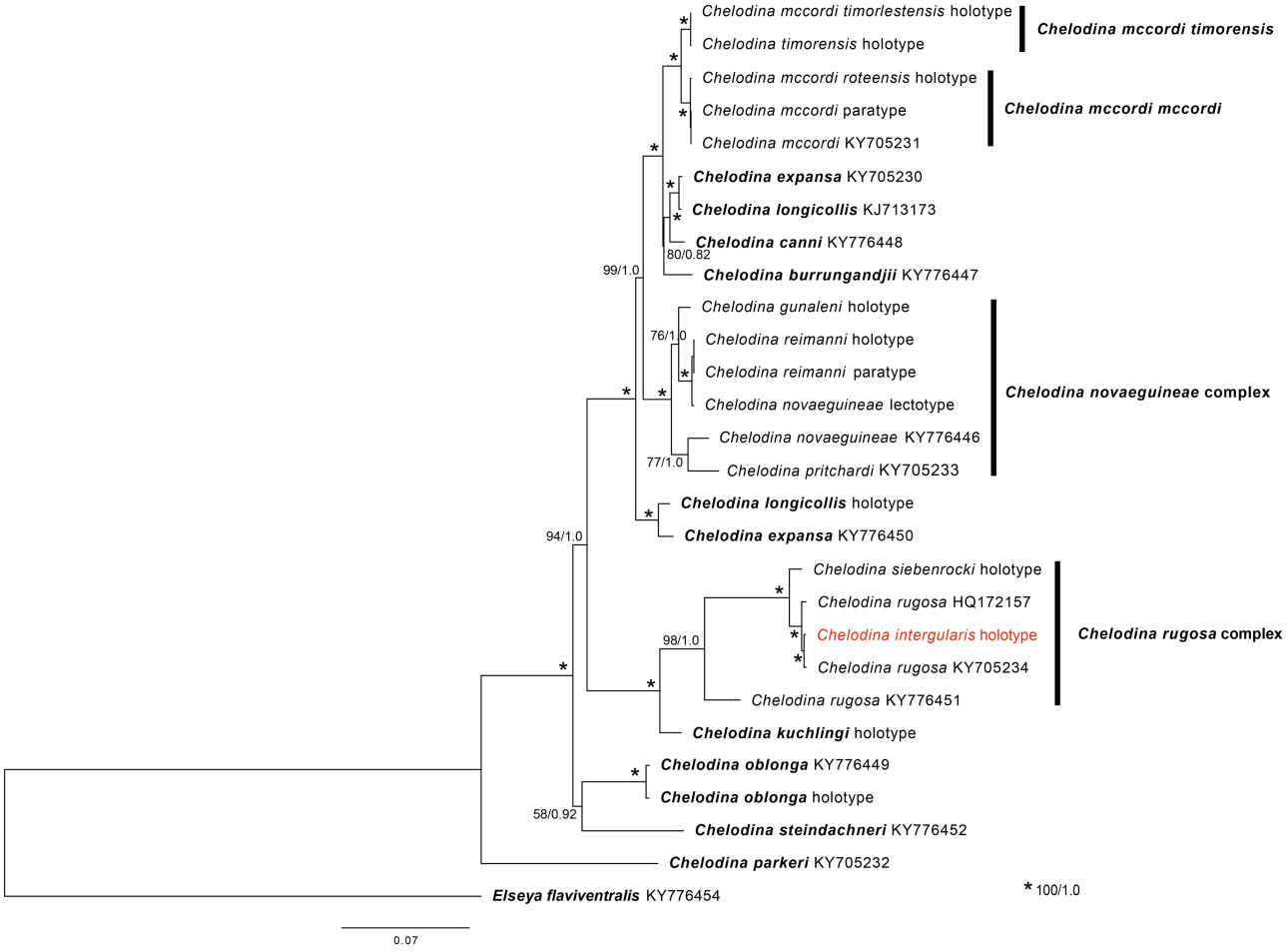

FIGURE 2. Maximum Likelihood tree using near-complete mitogenomes of *Chelodina* species, rooted with *Elseya flaviventralis*. Numbers at nodes are bootstrap values and posterior probabilities from a Bayesian tree of the same topology. Asterisks indicate maximum support under both approaches. Species names do not imply validity or nomenclatural availability; accepted names of terminals on the right in bold. Sequences from type specimens are flagged; that of the *C. intergularis* type is highlighted in red. Codes following species names are GenBank/ENA accession numbers. For specimen/voucher tissue information, see Table 1. The mitogenomic phylogeny conflicts with subgenera and reflects a complex pattern of transspecific introgression and mitochondrial capture (Hodges 2015; Kehlmaier *et al*. 2019).

Although the Australian Museum was first established in 1829 (Strahan 1979), no system of registration was realized until January 1875, when the "A register," covering all donations to the collection, commenced. At first, this was just a listing of specimens received, without registration numbers allocated to them, but numbering started part-way through the "A register" with numbered lead tags tied to the specimens to allow correspondence between the register entries and the specimens. The "A register" ceased about October 1883, and was followed by the "B register," commencing about September 1883 (there was some overlap between the two in the first month), which continued to December 1886. After that time, separate departmental registers were used, with the herpetological collections receiving numbers starting with "R" (Shea & Sadlier 1999). During the period of operation of the "A register," Edward Gillet Worcestor Palmer was employed to inventory the backlog of material in the earlier collections, and these were entered into what became known as the "Palmer register," which operated between about 1877–1888. Specimens were catalogued by taxonomic group, and bear numbers without a prefix. However, the "Palmer register" does not contain all then uncatalogued specimens. Additional unregistered or untagged material was located later, even though some of these specimens may have been registered before, but lost their tags; such unregistered material was identified in later registers as "Old Collection" specimens. This was also the case with the holotype of *C. intergularis*, which received in the "R register" the number R6255.

Despite the lack of a formal registration system prior to 1875, it is possible to gain some knowledge of the

receipt of donations in this era from two sources. The Annual Reports of the Australian Museum included lists of donations for each year, beginning in 1858, and monthly lists of donations to the Museum were also published in the local press, particularly in the Sydney Morning Herald, commencing in November 1853. These provided the names of the donors, but often not localities, and the monthly lists were not complete. However, together these sources provide an indication of what was received, and in some cases it is possible to cross-reference the listed specimens with their register entries, either contemporary in the case of the "A" and "B registers," or subsequently in the case of the "Old Collection" entries in the "R register."

A complication is due to the fact that the monthly donation lists and the donation lists in the Annual Reports only enumerate donations, generally from members of the public. The activities of paid museum collectors, and of collections purchased, are not routinely reported, particularly in the early years. However, it is often possible to gain some information on these from separate lists in the Annual Reports.

Unfortunately, the entry for the holotype of *C. intergularis* lacks any nominated collector, and hence we must operate by a system of compiling a list of early donated specimens of chelid turtles, together with potential museum collectors and their travels, and then remove from the list those specimens that cannot have been a dry shell of an adult turtle, or cannot have been collected from northern Australia within the range of *C. rugosa*. Luckily, the far north of the continent was not regularly visited prior to the establishment of the registration system, and there are annotations with many of the specimens from the 1870s and 1880s that indicate the turtles donated were young or alive that preclude those specimens from consideration.

Among the pre-registration (pre-1875) collections, the donation lists report 35 chelid or possible chelid specimens (Appendix 1). Many of these are identified as "tortoises," reflecting the Australian use of the vernacular term tortoise for freshwater chelonians until recently. None of these are subsequently identifiable in the "Palmer register" as all *Chelodina* specimens in that register lack localities and collectors. It is possible to exclude most of these as a source for the holotype of *C. intergularis* because they were donated by children or women who were unlikely to have collected in northern Australia, or were small turtles, donated alive, or the nominated or inferred source for the specimens was south of the range of *C. rugosa*.

However, there remain ten donors of specimens from this era that require further attention. We are unable to locate any trace of the Mr John Hanlon who donated a turtle in March 1858. The Captain Dunning who donated a turtle in January 1860 was the master of the barque *Frowning Beauty*, which arrived in Sydney from Newcastle on 8 January 1860 (Anonymous 1860d), and the turtle is therefore likely to be from the Hunter Valley or nearby. Charles Moore, who donated a turtle in May 1862, was the director of the Botanic Gardens and Moore Park Zoological Gardens in Sydney (King 1974), and the turtle is likely to have been one that died at the Gardens, making it unlikely to be represented by a fully cleaned shell lacking any other skeletal components. The Mr A. Butt, who donated a turtle in November 1862, was donor of several other specimens to the museum during that era, including live specimens, and was recorded to be resident at 81 Devonshire St, Sydney (Anonymous 1862c). The Mr Adams, who donated a turtle in January 1863, is not otherwise identified. However, he is possibly the same as the R. Adams, who donated a hornbill (*Buceros* sp.)—a non-Australian bird species, in October 1864 (Anonymous 1864a). That Adams seems to have been Robert Adams, a customs house agent based at the Circular Quay docks, and residing at Balmain in Sydney. Messrs. Henry R. Hurford and Co., source of a turtle in February 1863, are known to have operated a pianoforte warehouse in Castlereagh St, Sydney (Anonymous 1863d). Mr R. Ronald Esq., who donated a turtle in December 1864, appears to have been Rowan Ronald, the manager of the Australian Paper Company, operating out of his home at 13 Queen's Place (now Dalley St, Sydney), but which had a factory near Liverpool in western Sydney (Anonymous 1865c). His numerous advertisements on behalf of the company were routinely titled R. Ronald. Charles Manton, the source of a turtle in February 1865, is likely to be Charles Henry Manton, a wine merchant of Victoria Street, Sydney (soon afterwards insolvent) (Anonymous 1866d). We can locate two John Goulds in the Sydney region and surrounds, and it is not clear which one donated the turtle in November 1868, the John Gould resident at Raglan St Manly, or the John M. Gould, a Maitland attorney (Sands 1868).

We can find no evidence that any of these people travelled to far northern Australia, where they could have collected the holotype of *C. intergularis*.

In contrast, there is good evidence for such travel by Dr Rattray, who donated a *Chelodina* in January 1866. Dr Alexander Rattray (born 1831 in Dundee, Scotland, deceased 25 March 1906, England), who received his medical degree at the University of Edinburgh with the thesis "On some of the more important diseases of the cervix uteri" (Anonymous 1867a), was surgeon aboard H.M.S. *Salamander*. That ship was sent to Australia in January 1864,

and was assigned to supply provisions, communications and protection for the new station at Somerset, at the tip of Cape York, which was first established in August 1864 (Rattray 1868a), the first official settlement on Cape York. Rattray was aboard the *Salamander* throughout its several voyages to Somerset between 1864 and 1867, after which time the ship returned to England. The movements of the *Salamander* between 1864 and January 1866 are documented in Appendix 2. During this time, she visited Somerset on four occasions, sometimes for several weeks. On the first trip, in August 1864, Captain Carnegie of the *Salamander* led a party across the peninsula, and along the Kennedy River to the furthest navigable point (Anonymous 1864b). As an extension of his duties as a physician and surgeon, Rattray had an interest in the effect of tropical climate on human health, along with geological interests, and three papers were later penned by him on his observations on Cape York (Rattray 1868a, 1868b, 1869). The first of these comments on the local fauna, but does not mention chelid turtles. While no locality is provided for the *Chelodina* he collected, he had arrived in Sydney from several weeks at Somerset via single day stops at Rockingham Bay (Cardwell) and Port Denison (Bowen), and four days in Brisbane, with little opportunity to collect at those intermediate points, and had previously donated specimens from Cape York to the Australian Museum in March and December 1865 (Anonymous 1865d, 1866e). Hence, we consider Rattray's *Chelodina* one possible source for the holotype of *Chelodina intergularis*.

Between 1875 and 1900, there were an additional 13 donations of chelid turtles to the Australian Museum collection, as recorded in the "A," "B" and "R registers," and in the monthly donation lists and annual reports (Appendix 3). Eleven of these can be immediately excluded for the same grounds as for those in the pre-registration era, and the other two (donations from E.S. Hill in 1877 and J. M'Lean [McLean] in 1887) are from people based in, or likely to be based in, Sydney. Edward Smith Hill was a Trustee of the Australian Museum, resident in Woollahra (Anonymous 1880c). We can locate several J. McLeans resident in Sydney in 1887: James McLean, a stonemason in Albion St (likely the same James McLean stonemason at Riley St), Sydney; James McLean, carpenter of Riley St, Sydney; James McLean, a dealer of Alton St, Woollahra; four other James McLeans of unstated professions (residences at Ann St, Sydney, Goodlet St, Sydney, Sutherland St, Paddington, and May St, St Peters, respectively; John McLean, a master mariner of Essex St and Princess St, Sydney; John McLean, a cab proprietor of Kingston Rd, Camperdown; two other John McLeans of unstated professions, at Albert St and Bay St, Sydney, respectively, and a Joseph McLean, clerk of Merlin St, St Leonards (Sands 1887), and we are unsure which of these donated the turtle. Only one record (the two juvenile turtles, genus unspecified, from Torres Strait, donated by a Mr Gray) was from anywhere within the range of *C. rugosa*, and that record may have been based on sea turtles. None of the other donors are known to have visited northern Australia. While a few of the later entries are under the name *C. oblonga*, a species which does not occur in Sydney, we consider that these entries merely reflect changes in opinion of the curator at the time as to the identity of the local long-necked species.

Beyond donations to the collection, it is important to consider collections by museum staff. Prime among these is John Adolphus Thorpe, who also collected the holotype of *C. rugosa*. Thorpe was born 10 June 1838 in Clapham, Surrey, the son of Henry Adolphus Thorpe, bootmaker and bird stuffer, and his first wife Elizabeth (England, Select Births and Christenings, 1538–1975; 1851 England Census, accessed via www.ancestry.com.au) and he arrived in Sydney on 22 August 1856, aged 18, aboard the *Herald*, described as a gardener (New South Wales State Records, Assisted Immigrant Passenger Lists, 1828–1896, accessed via www.ancestry.com.au). Thorpe was employed as taxidermist at the Australian Museum between 3 June 1869–1907 (Anonymous 1881b; Strahan 1979), but shortly before commencing at the Australian Museum, he had spent 17 months at Somerset on Cape York along with the naturalist and collector James Frederick Cockerell (1847–1897), arriving via the ship *Salamander* (North 1901–1904: 43, 1906–1909: 378; Monteith 1987). The *Salamander* visited Somerset on two occasions in 1867, leaving Brisbane on 8 February (Anonymous 1867b), and again leaving Brisbane on 18 July (Anonymous 1867c). The latter was the last occasion the *Salamander* visited Somerset before continuing to England. Searching manifests of ship arrivals back in Sydney (via the website Mariners and Ships in Australian Waters [www.marinersandships.com.au] which, despite the title, only covers arrivals in Sydney), there was a John Thorpe arriving back in Sydney aboard the ship *City of Brisbane* from Brisbane on 21 December 1868, a passenger in steerage (naturalists were generally operating on a tight budget and tended to travel in steerage rather than in cabins). This would have given him a 17-month period from July 1867. So, he presumably arrived at Somerset on the final July 1867 voyage of the *Salamander*, and his return to Sydney was just six months prior to commencing employment at the Australian Museum. The holotype of *C. rugosa* is noted as being collected in 1869 (Ogilby 1890), although this is the year after Thorpe left Cape York and we assume that this is the year of donation rather than collection. By mid-1869, Thorpe

was a museum employee, which likely explains why the donation is not recorded in the monthly or annual donations lists for 1869. The first listing of donated Thorpe specimens appears much later, in January 1875, followed later that year by birds from Cape York in October 1875 (Anonymous 1875a, 1875b), and he frequently appears as a donor of specimens subsequently. The change in this interval is that Krefft was curator until 1874, a position taken over by Ramsay in 1875 after Krefft's dismissal, and hence policy on recognising donations by museum staff likely changed at this time. Thorpe collected extensively for the Australian Museum, with numerous annotations of birds collected in the four volumes of North's *Nests and Eggs of Australian Birds* (North 1901–1904, 1906–1909, 1911–1912, 1913–1914), but appears to have visited north Queensland only during 1867–1868, and there are no other entries in any archival sources of chelid turtles donated by him. Thorpe died at his home, "Shirley," in Glenmore Rd, Paddington, Sydney, on 6 August 1907 (Anonymous 1907).

Given that Thorpe spent 17 months in the vicinity of Somerset, and is known to have collected one *Chelodina* there, and that specimen is also a dried shell, we think it is quite possible that he picked up a second *Chelodina* shell. Against this view is that Ogilby (1890) was only aware of the one *Chelodina* shell from Thorpe when he described *C. rugosa*. The condition of the two shells is rather different (see descriptions below), but there are some similarities in preparation, notably removal of part or all of the thoracic vertebral centra and some rib heads that could argue for the same preparator for both specimens.

The second museum employee known to have collected within the range of *C. rugosa* in the era of the Australian Museum's "Old Collections" is Alexander Morton. Morton was born 11 September 1854 in New Orleans, and emigrated to Queensland with his father, then worked as a ship captain before spending time in England and continental Europe, then studying natural science (Mercer 1986). In 1877, Morton was appointed Curator's Assistant at the Australian Museum, and was sent to accompany the explorer and naturalist Andrew Goldie to New Guinea. In 1878, Morton was sent by the Museum to collect in the Northern Territory (NT). He arrived in Palmerston (Darwin) aboard the *William M'Kinnon* on 4 October 1878 (Anonymous 1878a, 1878b), and departed aboard the *William M'Kinnon* again five months later on 10 March 1879 (Anonymous 1879d). Initially based around Darwin and Yam Creek, he spent the latter part of his time in the NT on the Coburg Peninsula. He returned from Port Essington about 8 March, just before leaving the NT (Anonymous 1879e). While newspaper reports in Darwin during his time there note that he lost much of his bird collection and many other specimens due to a dynamite explosion aboard the *Apis* steam launch on 28 November (Anonymous 1878c, 1878d), the published list of his specimens (Anonymous 1880d) is still extensive.

The Morton NT reptiles are registered A4843–4908, in March 1879. There are five chelonians among them. One is just registered as "turtle" from Port Darwin (A4877½ [i.e., written in between A4877 and A4878]). The other four are all identified as sea turtles from Torres Strait, hatched in September 1878 (A4905–4907, *Caretta* [now *Eretmochelys*] *imbricata* juveniles; A4908, *Chelonia* sp. [later annotation "*Natator depressa*?"]). These specimens are also listed in the 1879 Annual Report (Anonymous 1880c), with a similar separation between the first specimen and the remaining ones. While A4877½, which is registered separately from the two sea turtles, might be a chelid, it is unlikely to be the dry shell of *Chelodina intergularis* as the *C. intergularis* sequence data places it with *C. rugosa* from Papua New Guinea (KY705234) rather than Northern Territory *C. rugosa* (KY776451; Fig. 2; Table 1, see also below).

Morton's other significant Australian collecting area for the Australian Museum was the Burdekin and Mary River basins in 1882 (Anonymous 1883b; Cox *et al.* 1883). While he was known to have collected chelid turtles on this expedition, these areas are too far south for *C. rugosa*. In 1884, Morton left the Australian Museum and took up curatorial positions in Tasmania, first at the Royal Society of Tasmania, which would become the Tasmanian Museum and Botanical Gardens, and later the Queen Victoria Museum and Art Gallery at Launceston, before dying on 27 May 1907 at Sandy Bay, Tasmania (Mercer 1986).

In summary, we identify three possible sources of "Old Collection" chelids from within the range of *C. rugosa* that may have collected the holotype of *C. intergularis*: (1) Dr Alexander Rattray of H.M.S. *Salamander*, (2) the naturalist and taxidermist John Adolphus Thorpe, and (3) the museum collector Alexander Morton. Only Rattray and Thorpe are known to have collected chelids in the eastern part of the distribution of *C. rugosa*, the region that the genetic evidence suggests as source of the *intergularis* holotype, and both collected around the nascent Somerset settlement at the tip of Cape York. Hence, we consider that the most likely locality for the holotype of *C. intergularis* is the vicinity of Somerset, at the northern extremity of Cape York, the same as the source of the holotype of *C. rugosa*. This collection site is also in line with our genetic results (Fig. 2; Table 1). The negligible genetic divergence

of the mitogenome of a *C. rugosa* from Papua New Guinea (KY705234) compared to that of the holotype of *C. intergularis* and their phylogenetic placement make perfect sense. The Cape York Peninsula is only separated from Papua New Guinea by the very shallow Torres Strait, and the two landmasses have long been connected, not only during glacial low sea level stands but also in the earlier Holocene (Voris 2000). Thus, the *C. rugosa* populations on either side of the Torres Strait were separated only a few thousand years ago, explaining their genetic similarity. Another turtle taxon, *Emydura subglobosa subglobosa*, has a similar but converse distribution, with substantial populations in southern New Guinea extending to the northern Cape York Peninsula (TTWG 2021).

Weighing in all available evidence, we identify Somerset (northern Cape York Peninsula), Queensland, with the type locality both of *C. rugosa* Ogilby, 1890 and its junior subjective synonym *C. intergularis* Fry, 1915. This is in agreement with the previous suggestion to restrict the type locality of *C. rugosa* to the Cape York Peninsula north of the Jardine River (Cann & Sadlier 2017: 79).

Descriptions of the holotypes

Chelodina intergularis Fry, 1915

Holotype: Australian Museum, Sydney (AM R6255), Figure 1

Measurements. Straight carapacial length (midline) 193.3 mm; maximum carapacial width 136.4 mm; carapacial width at mid-bridge level 130.1 mm; maximum plastral length (from level of paired caudal tips to extreme anterior margin) 157.5 mm; midline plastral length 141.1 mm; plastral width at anterior extremity of bridge 72.0 mm; maximum posterior plastral width 68.8 mm; total shell depth at middle of bridge 70.6 mm.

Description. Specimen consists of a complete carapace with articulated plastron; all scutes have been removed and the specimen was highly polished during preparation. No ancillary skeletal components have been retained. The thoracic vertebrae have been lost, likely deliberately removed based on the damage to the rib heads. There is no evidence this specimen was cooked for consumption and was likely collected and prepared curatorially instead.

Dorsally there is an open space previously occupied by a 4th neural bone (at the midline junction of the 3rd and 4th pleurals) which is four-sided and diamond-shaped (following Pritchard 1988; Thomson & Georges 1996); the neural itself was lost when its supporting thoracic centrum was removed. This neural shape is indicative of a breakthrough neural that occurs in occasional specimens of any chelid species that would normally not have any visible neural bones. The carapace is ovoid in shape, typical of *Chelodina rugosa* sensu lato (i.e., including *C. kurrichalpongo* and *C. siebenrocki*). There is a reticulated pattern on the surface of the shell bone. Pleurals 1 through 5 have lateral fontanelles at the rib/gomphosis indicating this is not a fully grown individual. Based on size, growth and generalized shape, it is in all likelihood a subadult female. However, this is not certain.

The plastron is also complete and possesses a reticulated surface patterning resembling that of the carapace. This is a feature of *Chelydera* species. Unusually, the intergular scute is extended forwards and reaches the rim of the plastron. At the same time there is a slight indentation of the anterior edge of the plastron.

Inside the shell, there is significant damage to many rib heads; all the thoracic centra are missing. There is also a small hole drilled into the anterior vertebral arches where the bone sample for our analysis was taken. The pelvic suture insertion is square to oval in general shape and is significantly extending onto the 7th pleural and pygal as well as completely crossing the 8th pleural. This is the typical condition in *C. rugosa* sensu lato. The anterior bridge strut (for terminology, see Thomson *et al*. 1997) is enlarged and robust, angled back at approximately 45° and reaches the halfway point of the 1st rib within the 1st pleural. This is the typical condition of *Chelydera* species (compare Thomson 2000; Thomson *et al*. 2000) and excludes allocation of the holotype to the subgenera *Macrochelodina* or *Chelodina*.

Chelodina rugosa Ogilby, 1890

Holotype: Australian Museum, Sydney (AM R6256), Figure 3

Measurements. Straight carapacial length (midline) 255.8 mm; maximum carapacial width 171.7 mm; carapacial

width at mid-bridge level 160.0 mm; maximum plastral length (from level of paired caudal tips to extreme anterior margin) 211.4 mm; midline plastral length 191.7 mm; plastral width at anterior extremity of bridge 95.7 mm; maximum posterior plastral width 92.9 mm; total shell depth at middle of bridge 93.9 mm.

FIGURE 3. Holotype of *Chelodina rugosa*, Australian Museum, Sydney (AM R6256). Photos: G. Shea.

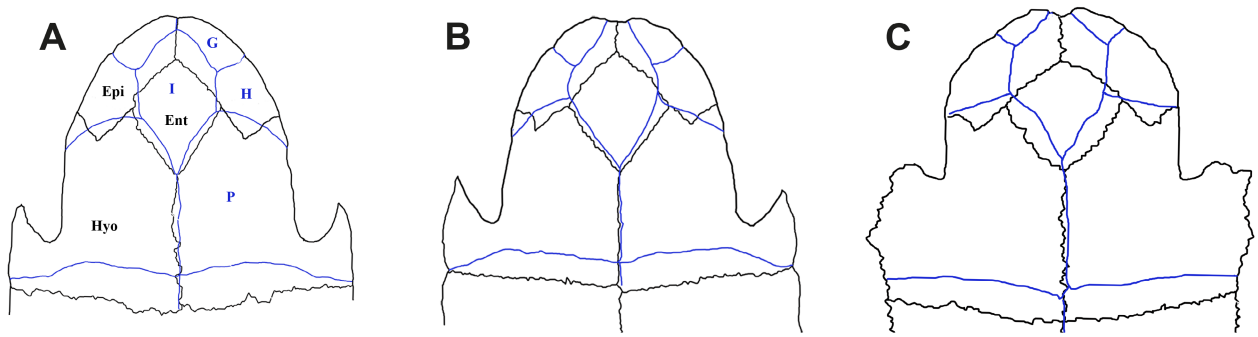

FIGURE 4. Comparison of (A) the holotype of *Chelodina rugosa* (AM R6256), (B) the holotype of *C. intergularis* (AM R6255) and (C) an individual of *C. burrungandjii* sensu stricto (UC 2101; redrawn from Thomson *et al*. 2000). Not to scale. Epidermal scutes (blue): G = gular; H = humeral; I = intergular; P = pectoral. Bony plates (black): Epi = epiplastron; Ent = entoplastron; Hyo = hyoplastron. In AM R6256 the bony sutures are visible at closer inspection through the translucent epidermal scutes. Drawings: S. Thomson.

FIGURE 5. Plastral aspects of *Chelodina kuchlingi*; specimens from the Western Australian Museum, Perth. From left to right: WAM R29411 (holotype), WAM R28116, WAM R28117 (some scute outlines in this specimen highlighted in blue). To scale, midline plastral length of holotype 185 mm. Note that the intergular reaches the anterior plastral rim only in the holotype. Photos: G. Kuchling.

Description. Specimen consists of a complete carapace and articulated plastron, the anterior thoracic centra are in situ as well as the posterior pelvis. Preserved separately are the 7th and 8th cervical vertebrae. The scutes are in situ with this specimen. This specimen was clearly either collected alive or found recently deceased and then prepared curatorially for the museum. The entire carapace has a fine reticulate pattern to the scutes which is more rugose and antero-posteriorly aligned in the 2nd to 4th vertebral scutes. This pattern is typical of *C. rugosa* sensu lato as defined above.

The 4th vertebral scute is reduced in size compared to other specimens of *C. rugosa*, with an extra scute between this and the 5th vertebral which is also reduced. Between the 1st costal on the left side and the 1st vertebral scutes there is an extra anomalous scute which has encroached into the normal size and shape of both scutes that border it. The 2nd marginal is approximately 30% longer than the 3rd, otherwise marginals appear normal in growth (note damage left side below) and number 11 on each side. A pygal scute and cervical scute are also present.

At the left side rear quarter of the carapace there is significant damage above the hind leg. This would appear to be the result of a bite from a predator. This damage has fully healed with overgrown scute material and hence occurred many years before the death of the animal.

The plastron is complete, includes the attached posterior pelvis, and also has a fine reticulate pattern throughout. The museum accession number (R 6256) is written in permanent ink on the left humeral scute. There is some old larger-font-sized handwritten text on the plastron, twice “Cape York” in different orientations, one longitudinal, one transverse. The transverse inscription also has “Thorpe,” additional text is present but illegible. On the left rear of the plastron, within the anal scute, is a break where some bone has been lost, interestingly it is in a similar position to the injury of the carapace. There is evidence of some healing, and hence the injury occurred before the animal died. However, the plastral fracture is far less healed over than the carapace injury, indicating that the plastral damage occurred later.

The scute pattern of the plastron is typical of *C. rugosa* sensu lato. Importantly, this includes the shape, size and extent of the intergular scute. This scute is large, hexagonal though elongated. It partially divides the humerals and separates the pectorals. It is enclosed anteriorly by the gular scutes, which is the typical *Chelodina* condition. There is a small indentation between the epiplastra/gulars at the anterior of the plastron.

Internally, the first four thoracic centra are present. The 4th thoracic centrum is articulated and damaged anteriorly, the other thoracic centra seem to have become disarticulated over time, or during preparation, but were not cut out

as the rib heads are largely undamaged. This differs from the *C. intergularis* type where the centra were removed during preparation as indicated by the extensive rib damage. The pelvis is postero-laterally rotated (sensu Thomson *et al*. 2023) and attached to the 1st and 2nd sacral ribs (ribs 10–11) which are in situ. The pelvis covers the 8th pleural and extends onto both the 7th pleural and the pygal.

Comparisons

Other than the shape and relationships of the intergular scute impression, the holotype of *Chelodina intergularis* closely resembles *C. rugosa* sensu lato, and differs from other extant members of the subgenus *Chelydera*. While it shares with the holotype of *C. kuchlingi* and some *C. burrungandjii* sensu stricto (i.e., from Arnhem Land) contact of the intergular with the anterior plastral margin, the nature of this contact is different. *Chelodina burrungandjii* sensu stricto exhibits shortening of the anterior lobe of the plastron in the underlying bones (Fig. 4). This is presented by the shorter and wider entoplastron and antero-posterior shortening of the hyoplastra. The effect of this on the overlaying scutes is that they are all forced forwards which causes the intergular to divide the gulars and reach the anterior margin of the plastron. In the *C. intergularis* holotype the underlying bones are typical for *C. rugosa* sensu lato, i.e., elongated, and the anterior plastral lobe is approximately trapezoid in general shape. As such it is clear, the extended intergular of the *C. intergularis* type is an individual anomaly rather than a species-specific character. *Chelodina kuchlingi* was long known only by the type and it is a wet specimen, preventing examination of the underlying bony sutures. However, based on the dimensions of the anterior plastron, the intergular reaching the plastral margin is also likely an individual anomaly of the *C. kuchlingi* type. This is supported by two recently identified additional *C. kuchlingi* specimens (see Kuchling 2020) in which the intergular does not reach the anterior plastral rim (Fig. 5).

The holotype of *C. intergularis* additionally differs from *C. burrungandjii* sensu stricto in having the carapace ovoid (narrowed anteriorly) rather than oblong, the marginals not upturned, and the lack of multiple exposed neural bones on the dorsal surface of the carapace (Thomson *et al*. 2000). While the *C. intergularis* holotype lacks the shields of the shell, the underlying bone bears numerous irregular reticulations that are very different in orientation from the radiating rugosities of the carapace shields of *C. kuchlingi*, as reported by Cann (1997) and Cann & Sadlier (2007), and the anal notch is much deeper and more rounded. It differs from *C. parkeri*, type species of *Chelydera* with deeply divergent mitogenome (Kehlmaier *et al*. 2019; Fig. 2), in having a wide nuchal, a deep and rounded anal notch, and a less posteriorly flared carapace (Rhodin & Mittermeier 1976). It differs from *C. expansa* in having an egg-shaped, relatively narrow carapace, the anterior plastral margin more tapered, and the posterior plastral lobe expanded at the level of the femoral shields (Goode 1967).

Acknowledgements

We are indebted to Alicia Grealy (CSIRO, Canberra) for extracting the bone sample from the holotype of *Chelodina intergularis* under ultraclean conditions. Jodi Rowley and Dane Trembath (Australian Museum, Sydney) helped during the work with the type specimens. Paul Doughty and Jenelle Ritchi (Western Australian Museum, Perth) helped with shipping the bone sample to Dresden and allowed access to the *C. kuchlingi* specimens. The manuscript of this study profited from the comments by Anders Rhodin. Aaron Bauer is acknowledged for handling the manuscript.

Supporting Materials

Tables S1–S6 and the alignment used for building the trees of Figure 2 are available from figshare using the link https://doi.org/10.6084/m9.figshare.25133879.

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APPENDIX 1. Likely or possible *Chelodina* specimens received by the Australian Museum between November 1854 and 1874, based on monthly donations lists and Annual Reports of the Australian Museum. Monthly lists were not published for April 1860, December 1863, January 1864, September–October 1866, February, September and December 1867, February and June 1869, February, May, June, August, September and November 1870, January, February, August and September 1871, November–December 1872, January, July and December 1873, January–March, May–June, August and October–November 1874, and February, April and August–September 1875. Rejection as possible type of *Chelodina intergularis* (a dry shell of an adult, of a species distributed in northern Australia) due to (A) being living, (B) locality outside of range, (C) donor a child or woman living in Sydney (and hence unlikely to have obtained a turtle specimen from far northern Australia), (D) young or small turtle.

Month/Year	Nominal and original identification	Donor	Locality (if provided)	Reference	Reason for rejecting record
Dec 1854	A long-necked tortoise	Master Geoffrey Eagar		Anonymous (1855a)	C
Mar 1855	A long-necked tortoise (*Testudo longicollis*)	Miss Margaret Moran		Anonymous (1855b)	C
Jun 1855	Eight specimens of *Chelodina* or fresh water turtle (six of the species being undescribed)	Samuel Stutchbury, Government Geologist	Northern Districts? (Locality unclear from the presentation as part of a large collection)	Anonymous (1855c)	B (Stutchbury did not travel further north than Gladstone, Qld; Branagan & Vallance 1976)
Feb 1856	Two long-necked tortoises	Master J. Ockman		Anonymous (1856)	C
Sep 1857	A long-necked tortoise (*Emys longicollis*)	Master F. Houston		Anonymous (1857a)	C
Oct 1857	A long-necked tortoise (*Emys longicollis*) with its eggs	Master Mannhauskings		Anonymous (1857b)	C
Mar 1858	A long-necked tortoise (*Emys longicollis*)	Mr John Hanlon		Anonymous (1858), Angas (1859)	
Feb 1859	A small living tortoise found embedded in rock	Governor-General	Between Maitland and Stoney Creek bridges [NSW]	Anonymous (1859a), Angas (1860)	A, B, D
Nov 1859	Two living fresh water tortoises (*Emys*)	Captain O'Reilly, S.S. *Telegraph*	Moreton Island [Qld]	Anonymous (1859b), Angas (1860)	A, B
Jan 1860	A freshwater tortoise (*Emys longicollis*)	Captain Dunning		Anonymous (1860a, 1861a)	
Sep 1860	A turtle from the egg	Mr S. Gray	Double Bay [NSW]	Anonymous (1860b, 1861a)	B, D
Nov 1860	A large fresh water tortoise	Rev J. Hannay	Angaston, SA	Anonymous (1860c, 1861a)	B
Mar 1861	A large tortoise	Mrs Ritchie	Pitt Street [Sydney, NSW]	Anonymous (1861b), Krefft (1862)	C
May 1862	A tortoise (*Emys longicollis*)	Charles Moore (Curator of Botanic and Zoological Gardens)		Anonymous (1862a), Krefft (1863)	
Nov 1862	Two tortoises (*Emys longicollis*)	Mr A. Butt		Anonymous (1862b), Krefft (1863)	
Jan 1863	Long-necked tortoise (*Emys longicollis*)	Mr Adams		Anonymous (1863a), Krefft (1864)	
Feb 1863	A long-necked tortoise (*Emys longicollis*)	Messrs H.R. Hurford & Co.		Anonymous (1863b), Krefft (1864)	

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APPENDIX 1. (Continued)

Month/Year	Nominal and original identification	Donor	Locality (if provided)	Reference	Reason for rejecting record
Aug 1863	A long-necked tortoise (*Emys longicollis*)	Master Henry Foster		Anonymous (1863c), Krefft (1864)	A
Dec 1864	Two tortoises (*Emys longicollis*)	R. Ronald Esq.		Anonymous (1865a)	
Feb 1865	A tortoise (*Emys longicollis*)	Mr Charles Manton		Anonymous (1865b), Krefft (1866)	
Jan 1866	A long-necked tortoise (*Chelodina longicollis*)	Dr Rattray, R.N., H.M.S. *Salamander*		Anonymous (1866a), Krefft (1867)	
Apr 1866	A long-necked tortoise (*Chelodina longicollis*)	Mrs O'Neil		Anonymous (1866b), Krefft (1867)	B
Jun 1866	A small tortoise (*Chilodina longicollis*) [sic]	Mrs Pickard		Anonymous (1866c), Krefft (1867)	C, D
Nov 1868	A tortoise (*Chelodina longicollis*)	Mr John Gould		Anonymous (1869), Krefft (1869)	

APPENDIX 2. Chronology of movements of the ship H.M.S. *Salamander* between 1864 and January 1866.

Location	Date of Arrival	Date of Departure	Reference
Sydney	4 June 1864	22 June 1864	Anonymous (1864b, 1864c)
Brisbane	27 June 1864	14 July 1864	Anonymous (1864d, 1864e)
Rockingham Bay	21 July 1864	22 September 1864	Anonymous (1864f)
Somerset	29 July 1864	7 September 1864	Anonymous (1864f)
Brisbane	19 September 1864	24 September 1864	Anonymous (1864g, 1864h)
Sydney	27 September 1864	20 November 1864	Anonymous (1864i, 1864j)
Brisbane	29 November 1864	8 December 1864	Anonymous (1864k, 1864l)
Rockingham Bay	14 December 1864	16 December 1864	Anonymous (1865e)
Somerset			
Brisbane	6 February 1865	16 February 1865	Anonymous (1865f, 1865g)
Sydney	21 February 1865		Anonymous (1865h)
Brisbane	17 April 1865	27 April 1865	Anonymous (1865i)
Port Denison	2 May 1865	3 May 1865	Anonymous (1865j)
Rockingham Bay	7 May 1865	9 May 1865	Anonymous (1865k)
Somerset		21 May 1865	Anonymous (1865l)
Brisbane	17 June 1865	30 June 1865	Anonymous (1865m, 1865n)
Sydney	4 July 1865	29 August 1865	Anonymous (1865o, 1865p)
Brisbane	1 September 1865	13 September 1865	Anonymous (1865q, 1865r)
Rockingham Bay	23 September 1865	24 September 1865	Anonymous (1865s)
Somerset		27 October 1865	Anonymous (1865t)
Rockingham Bay	18 November 1865	19 November 1865	Anonymous (1865t)
Port Denison	21 November 1865	21 November 1865	Anonymous (1865u)
Brisbane	30 November 1865	3 December 1865	Anonymous (1865v, 1865w)
Sydney	7 December 1865	13 January 1866	Anonymous (1865x, 1866f)

APPENDIX 3. Likely or possible *Chelodina* specimens received by the Australian Museum between 1875 and 1911, based on monthly donations lists and Annual Reports of the Australian Museum. Rejection as possible type of *Chelodina intergularis* (a dry shell of an adult, of a species distributed in northern Australia) due to (A) being living, (B) locality outside of range, (C) donor a child or woman living in Sydney (and hence unlikely to have obtained a turtle specimen from far northern Australia), (D) young or small turtle.

Date	Registration No.	Details	Donor	Locality	Reference	Reason for rejecting record
June 1876	A register, p. 29	One *Chelodina longicollis*/*Euchelymys sulcifera**	Mr Hickey	(Riley St), Sydney (register entry)	Anonymous (1876), Ramsay (1877)	A (fide register entry), B
1876	No register entry	One *Chelodina longicollis*	Mr A. Spencer	Sydney	Ramsay (1877), not in monthly lists	B
February 1877	A register, p. 82	One *Chelodina oblonga* and three eggs	E.S. Hill		Not listed in donation lists (monthly or annual)	
December 1878	A3334	One *Chelodina longicollis/Chelonia* [sic] *oblonga* (ID differs between donations lists)	Mr H.T. Drake	Newtown	Anonymous (1879a), Ramsay (1879)	A (register entry), B
April 1879	A5157	One live *Chelodina*	Mr R. Thorpe	Botany Swamps	Anonymous (1879b, 1880a)	A, B
October 1879	A7347	One small live *Chelodina longicollis*. Noted in register as "escaped from museum and returned as a donation"	Mrs J.E. Farraway	Sydney	Anonymous (1879c)	A, B, C, D
November 1879	A7384a	One *Chelodina longicollis*	Mr Lewis Truscott	Hunter's Hill	Anonymous (1880a, 1880b)	B
1879	A5190, A5191	Two young turtles**	Mr Gray	Torres Straits (register)	Anonymous (1880a), not listed in monthly lists	B
October 1881	A10790, now R131326	One *Chelodina longicollis*	Mr J.E. Josephson***	Botany (register)	Anonymous (1881a, 1882a)	B
March 1882	A12525, now R131327	One *Chelodina longicollis*	Mr K.H. Bennett	Fish River (register)	Anonymous (1882b, 1883a)	B
1883	B334	A tortoise	Mrs E. Knight		Anonymous (1884a), not listed in monthly lists	C
July 1884	B, entry between B3270 and B3271	One *Chelodina oblonga* (noted in registration entry as "useless" and hence presumably not registered and discarded)	Mrs Smith		Anonymous (1884b, 1885)	C
February/March 1887****	R107	One *Chelodina oblonga*	Mr J. M'Lean		Anonymous (1887, 1888)	

* Recorded as *Chelodina longicollis* in Ramsay (1877) but as *Euchelymys sulcifera* in Anonymous (1876). *Euchelymys sulcifera* Gray, 1872 is a synonym of *Emydura macquarii* (fide Cogger *et al.* 1983)—this is possibly a *lapsus* for *Chelodina sulcifera* Gray, 1856.

** Generic identity not reported, and hence possibly sea turtles.

*** Annual list (Anonymous 1882a) gives donor as Mr F.K.T. Walker.

**** Donation lists record the specimen as received in February, but registered in March.