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Chelodina expansa Gray 1857 – Broad-Shelled Turtle, Giant Snake-Necked Turtle

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SUMMARY.-Australia's largest snake-necked turtle, *Chelodina (Macrochelodina) expansa* (Family Chelidae), occurs broadly through the inland rivers and billabongs of eastern and southeastern Australia. The species is cryptic in habit, yet occupies waters heavily exploited and regulated by humans. Traditionally considered a riverine species, recent studies demonstrate that it is more frequently represented in permanent lakes and billabongs connected to main river channels. Typical of many freshwater turtles, *C. expansa* displays delayed maturity and high adult survivorship. It is carnivorous and feeds primarily on fast-moving prey such as crustaceans and fish, but will also consume carrion. The reproductive biology of *C. expansa* sets it apart from most other turtles; in response to low temperatures, embryos enter a diapause, which enable them to survive over winter in nests, resulting in a year-long incubation period. *Chelodina expansa* has lower population densities than sympatric turtle species, which may increase its vulnerability to threats. Persistence of *C. expansa* relies on habitat quality and longitudinal connectivity of freshwater systems in southeastern Australia.

DISTRIBUTION. – Australia. Found throughout southeastern Australia, in the Murray-Darling Basin, and coastal rivers of southeastern Queensland from the Logan-Albert drainage in the south to the Fitzroy drainage in the north. Offshore populations occur on Fraser, Moreton, and Stradbroke islands, Queensland.

SYNONYMY.–Chelodina expansa Gray 1857, Chelodina oblonga expansa, Macrochelodina expansa, Chelodina (Macrochelodina) expansa.

SUBSPECIES. – None currently recognized.

STATUS. – IUCN 2013 Red List: Not Listed [Least Concern, LC, assessed 1996], TFTSG Draft Red List: Near Threatened (NT, assessed 2011); CITES: Not Listed; Australian EPBC Act: Not Listed.

Taxonomy. — *Chelodina* (Fitzinger 1826) is one of seven genera endemic to the Australian region, and arose in the mid-Eocene approximately 47 million years ago (Near et al. 2005). *Chelodina* represents a clearly defined monophyletic group and is characterized by exceptionally long necks that have evolved independently of other South American long-necked genera (Georges et al. 1998). *Chelodina* species fall into three long-standing natural (monophyletic)



Figure 1. Gravid female *Chelodina expansa* negotiates a sandy dirt road in search of suitable nesting habitat, Paringa, South Australia, Australia. Photo by Claire Treilibs.

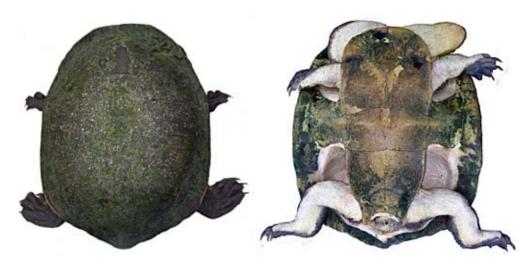


Figure 2. Dorsal and ventral views of an adult female *Chelodina expansa*. Note the narrow plastron and the inability of the animal to fully conceal its neck and limbs inside the shell. Photos by Deborah Bower.

divisions first proposed (but not named) by Goode (1967); later confirmed using serological (Burbridge et al. 1974), morphological (Thomson et al. 1997), and allozyme data (Georges and Adams 1992; Georges et al. 2002); and finally named as subgenera by Georges and Thomson (2010). These are *Chelodina*, *Macrochelodina* (genus proposed by Wells and Wellington 1985), and *Macrodiremys* (genus proposed by McCord and Joseph-Ouni 2007). *Chelodina expansa* falls within the *Macrochelodina* subgenus with *C. rugosa*, *C. parkeri*, and *C. burrungandjii*. These taxa are all characterized by a broad head, narrow plastron, and a robust and exceptionally long neck.

There are morphological differences between mainland *C. expansa* populations and those on Fraser Island (insular



Figure 3. Front and side of *Chelodina expansa* head. Photos by Deborah Bower (top) and Kate Hodges (bottom).

adults are smaller and darker). Furthermore, Cann (1998) suggested that morphological differences between populations east and west of the Great Dividing Range might be accorded subspecific status. Actual or suggested morphological differences are not supported by genetic analysis (Hodges et al., in press) and subspecific status of eastern and western populations has not been formally proposed and is not generally accepted.

Chelodina expansa is broadly sympatric with, but ecologically distinct, from *Chelodina longicollis*. There is evidence to suggest the two species have hybridized and backcrossed on multiple occasions in the past. *Chelodina expansa* exhibits mitochondrial genome variation typical of *C. longicollis* populations, consistent with introgressive hybridization, probably during the Pleistocene. The two species share haplotypes, yet maintain distinctive genetic identity at nuclear genetic markers (Hodges et al., in press).

Description. — *Chelodina expansa* is one of Australia's largest chelids, though the species displays marked sexual dimorphism, with smaller males that mature earlier than females (Spencer 2002). Males are distinguished by an elongate tail that extends beyond the margin of the carapace when mature. Maximum adult female size can reach a



Figure 4. *Chelodina expansa* hatchling, seven days old, from Wentworth, New South Wales. Photo by Kate Hodges.

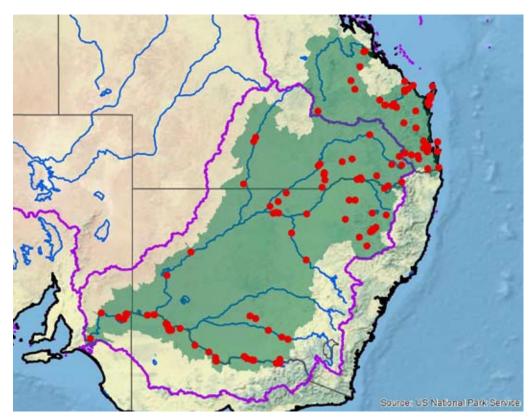


Figure 5. Distribution of *Chelodina expansa* in Australia. Purple lines = boundaries delimiting major watersheds (level 3 hydrologic unit compartments – HUCs); red dots = museum and literature occurrence records of native populations based on Iverson (1992), plus more recent and authors' data; green shading = projected native distribution based on GIS-defined HUCs constructed around verified localities and then adding HUCs that connect known point localities in the same watershed or physiographic region, and similar habitats and elevations as verified HUCs (Buhlmann et al. 2009), and adjusted based on authors' and others' subsequent data, including data provided by A. Georges of the Australian Ecology Research Group, University of Canberra.

carapace length (CL) of 500 mm, with an additional neck length of about 65–75% of the CL (Cann 1998). Females attain a maximum mass of 6 kg and males grow to 4 kg (Bower 2012). Males reach maturity at 9–11 yrs and females at 14–15 yrs (Spencer 2002).

Chelodina expansa has a cream-colored plastron and brown carapace, though the latter often appears green from filamentous algal attachment. Skin colors correspond to the plastron and carapace; dark and light colors meet in a distinct line that is evident when viewed laterally. The carapace is broadest at two-thirds of its length and ends in a triangular, shield-shaped posterior. A distinct dorsal ridge is evident in the carapace of subadult turtles but this flattens over time. The head is broad, long, and flat, with eyes that sit atop a pointed face. Two small barbels are often present on the front of the chin.

The species cannot completely retract into its shell like *C*. *longicollis*; therefore, the dorsal view clearly shows exposed limbs and neck. Neck and legs are broad with loose skin and armor-like ridges running horizontally across the anterior section of arms and legs. Feet are large with four claws on both hind and front feet, with heavily webbed toes. *Chelodina expansa* releases odorless (to humans) yellow fluid from its inguinal and axillary scent glands when disturbed.

Distribution. — Chelodina expansa is distributed throughout the inland rivers of southeastern Australia's Murray-Darling Basin. It is not known south of the Murray River proper, except for a population in the Goulburn River tributary (Cann 1998). Coastal populations occur in southeast



Figure 6. Sub-adult male *Chelodina expansa*, Lake Mackenzie, Fraser Island, Queensland. These insular animals are generally smaller and darker-colored than those in mainland populations. Photo by Kate Hodges.

Queensland in the Fitzroy, Burnett, Mary, Brisbane, Pine, and Albert-Logan river catchments. Offshore populations occur in the dune lakes of Fraser, Moreton, and Stradbroke islands off the southeast coast of Queensland.

Chelodina expansa occurs in sympatry with C. longicollis and Emydura macquarii throughout much of the western part of its range in the Murray Darling Basin; and with Elseya albagula, Myuchelys latisternum, Emydura krefftii, Elusor macrurus, and C. longicollis east of the Great Dividing Range in the coastal catchments (Georges 1982).

Habitat and Ecology. – Chelodina expansa leads a cryptic life as a highly aquatic freshwater turtle that occurs mostly in lacustrine habitats too turbid to permit underwater observation and is rarely seen basking (Chessman 1978; Cann 1998). Despite its description as a riverine turtle (Cann 1998; Cogger 2000), in most river studies C. expansa comprises a very small proportion of the combined species abundance (Chessman 1988b; Limpus et al. 2002; Hamann et al. 2008). Instead, C. expansa is more substantially represented in freshwater turtle communities sampled in permanent lakes and billabongs (Chessman 1988b; Spencer and Thompson 2005; De Lathouder et al. 2009; Bower 2012), which probably reflects their preference for slow flowing water bodies. However, in some lakes within their range they are poorly represented (Chessman 1988b; Georges 1982). Chelodina expansa generally occurs in low densities (Chessman 1988b; Limpus et al. 2002; Hamann et al. 2008); at least some populations are five times less abundant than the sympatric short neck turtle, E. macquarii (Spencer and Thompson 2005).

Chelodina expansa appears to prefer habitats with structural complexity (Legler 1978; Meathrel et al. 2002); however, drivers of habitat choice remain unclear. Its habitat niche is intermediate between *C.longicollis* and *E.macquarii* (Chessman 1988b). In some river systems, niche segregation appears to occur vertically among *C. expansa* and other turtle species; *C. expansa* occurs in the mid-water column or where vegetative debris is abundant, but this is not consistent among sites (Legler 1978). Behavioral observations of captive animals support these data, as *C. expansa* individuals immerse in upright vegetation in aquarium tanks where they attempt to conceal themselves (Legler 1978).

In the Murray River, unlike the other sympatric turtle species that show strong affinities with environmental variables, *C. expansa* abundance is only weakly correlated with water depth and distance from the river (Chessman 1988b). In Brisbane's urban lakes, *C. expansa* represents 11.1% of the total turtle assemblage and abundance correlates positively with the abundance of introduced fish and levels of disturbance (De Lathouder et al. 2009).

Chelodina expansa has delayed maturity and survival rate increases between the egg and adult stage (Spencer and Thompson 2005); this life history strategy is typical of many freshwater turtles (Shine and Iverson 1995). One closed population of C. *expansa* that has been studied in detail demonstrates that annual survivorship is high (females 0.92, male 0.88, and juveniles 0.84), and does not vary temporally or spatially among lagoons (Spencer and Thompson 2005).

In the Murray River, *C. expansa* is caught in baited traps between October and April, when water temperatures are above 18°C (Chessman 1988a). It is the least cold-adapted of the three sympatric species but has been observed moving at temperatures as low as 16°C (Chessman 1988a). Radiotelemetry has revealed that females occupy discrete linear home ranges of 1.43 ± 1.73 km; whereas, males have larger linear home ranges 11.18 ± 4.10 km and are capable of movements > 25 km upstream (Bower et al. 2012b). In the laboratory, the diel activity of *C. expansa* is weakly bimodal in adults, peaking early in the night, but activity is erratic in juveniles (Chessman 1988a). Capture rates of wild animals reflect weak bimodal patterns with peaks near dawn and in the afternoon or evening (Chessman 1988a).

Chelodina expansa exhibits periodic growth annuli on the plastral scutes (Chessman 1978) but these are unreliable for age determination (Spencer 2002). Instead, growth in *C*. *expansa* is best described by the logistic model (Spencer 2002); slow growth for the first two years is followed by rapid growth between three and five years of age, after which growth slows (Spencer 2002). Changes in diet may explain this pattern, if prey choice changes ontogenetically (Spencer 2002).

Chelodina expansa is carnivorous and acquires food by ambush or active foraging (Chessman 1983). Ambushed prey is obtained by rapid extension of the long neck in a forceful strike from a semi-retracted to an extended position (Chessman 1983) and food is consumed by the gape and suck method (Legler 1978; Cann 1998). Diet is similar in juveniles, females, and males, and may overlap with sympatric species at specific times of the year (Chessman 1983). Diet consists primarily of decapod crustaceans (Chessman 1983) and fish (Meathrel et al. 2002) and may include aquatic bugs, terrestrial invertebrates, and carrion (Chessman 1983). While C. expansa is often considered an obligate carnivore, 80% of gut contents were comprised of plant debris (n = 15) in C. expanse inhabiting an isolated billabong with C. longicollis and E. macquarii (Meathrel et al. 2002). This suggests that the addition of vegetation in its diet may be significant, especially during periods of low resource availability (Meathrel et al. 2002).

Behavior of *C. expansa* has not been well documented in natural settings but wild caught and captive animals lend small insights into the nature of this cryptic turtle. *Chelodina expansa* are not usually aggressive or pugnacious to humans when captured (Legler 1978) or handled. Individuals do not attempt to conceal the head and neck when handled; rather, they occasionally violently thrash their neck and limbs (Legler 1978). Head bobbing occurs among individuals when feeding; while potential communicative meanings are unclear, it has been suggested that this behavior may demonstrate interspecific recognition (Legler 1978). In captivity, C. expansa groom themselves regularly by scratching and biting to remove dead skin (Legler 1978; Green 1996). It has been hypothesized that grooming is important for turtles that rarely bask (Legler 1978). Under severe heat discomfort C. expansa will expel tears, pant, froth at the mouth, and shade their limbs under their shell (Webb 1978).

The physiology of C. expansa is linked to their highly aquatic existence in Australian freshwaters. The internal surface area of their cloacal bursae is comparatively smooth, suggesting that they do not achieve a high level of cloacal respiration (Legler and Georges 1993). Their resistance to desiccation is intermediate between the more terrestrial C. longicollis and the highly aquatic E. macquarii (Chessman 1984). In the laboratory, C. expansa survived 26 days immersion in sea water, which suggests a tolerance to saline habitats (Scheltinga 1991). Wild populations of C. expansa continue to inhabit secondarily brackish habitats with little physiological change, but hypersaline areas may present a challenge (Bower et al. 2012a). Hatchlings that emerged from eggs in saline treatments were smaller with higher concentrations of plasma sodium, chloride, urea, and potassium (Bower et al. 2013).

Nesting occurs predominantly through autumn and winter and occasionally in spring (Goode and Russell 1968; Georges 1984; Booth 1998a); however, it is not known whether spring nests represent a second clutch (Booth 1998a). Chelodina expansa nests during the day, after rainfall, but avoids nesting on days when air temperature is low (Bowen et al. 2005). The diurnal nesting habits result in predation rates much lower (50–70%) than sympatric species (E. macquarii), which are heavily preyed upon by foxes (Spencer and Thompson 2005). Nests are typically constructed $42.1 \pm$ 12.8 m from shore (Spencer and Thompson 2005), and have a vertical shaft 7.5-9 cm deep leading into an egg chamber 7-13 cm deep (Banks 1983; Booth 2002b). Females use their hind legs to dig in an alternative scooping motion and complete nesting in 20-180 minutes, using their body to compact the nest plug (Booth 2010). At the conclusion of oviposition, females create a plug by releasing liquid while compressing the substrate (Goode and Russell 1968). The continuation of nesting behavior is exhibited in animals that have been induced with oxytocin after they have already laid in captivity, suggesting that complex behavioral and hormonal cues interact with nesting behavior (McCosker 2002).

Hatchlings emerge after rain and emergence can be unsuccessful in dry conditions (Goode and Russell 1968).

Figure 7. Nesting crawl of a Chelodina expansa on a sand dune leading to an agricultural field, Wentworth, New South Wales. Photo by Deborah Bower.

After entering aquatic habitats, hatchlings may be preyed upon by large fish (Phillott and Parmenter 2000).

There has been substantial research into physiological aspects of the embryonic biology of C. expansa, resulting from the species' unique reproductive strategy (Booth 1998a,b, 1999, 2000, 2002a,b, 2003). Embryos of C. expansa enter a diapause cued by low temperatures (Booth 2000, 2002a), which enable them to overwinter in the nest (Goode 1966). Consequently, the eggs of C. expansa have unusually long incubation times, though they vary considerably from 192 to 522 days (Goode and Russell 1968). In addition, incubation times are comparatively longer than those of most other species, owing to the flat shell and long neck of Chelodina species, which restricts the viscera and slows the yolk ingestion rate (Goode and Russell 1968).

Chelodina expansa lays large, brittle, ovoid eggs (Woodall 1984) ranging from 32–45.2 mm in length, 23.4–30.8 mm in width and 0.4-24.9 g in mass (Booth 1999), with clutch sizes of 5-28 eggs (Goode and Russell 1968; Banks 1983; Georges 1984; Booth 1999). Chelodina expansa eggs tolerate a wide





Figure 8. *Chelodina expansa* egg showing the white patch that occurs on the dorsal surface during early development. Photo by Kate Hodges.

temperature range from 4.9–29.6°C (Goode and Russell 1968), and the species likely exhibits genetic sex determination (GSD) similar to the other Chelids, such as *C. longicollis* (Ezaz et al. 2006) and *Emydura macquarii* (Martinez et al. 2008), though this has not yet been explicitly tested. Hatchlings measure 34.5–37.9 mm CL, with masses ranging from approximately 7.9–12.88 g (Booth 2000, 2002a); their size and mass are influenced by both the hydric environment of the nest and the clutch of origin (Booth 2002b).

Population Status. — *Chelodina expansa* populations appear to have tolerated the initial regulation of the Murray Darling Basin (Chessman 1978), which has created slow moving, permanent weir pools within a previously dynamic desert river system (Walker 2001). While populations of two sympatric turtle species (*E.macquarii* and *C.longicollis*) have declined between 1986–2009, the relative abundance and population structure of *C. expansa* has remained consistent (Chessman 2012).

Threats to Survival. — Low densities of *C. expansa* make populations susceptible to negative perturbations at specific life stages (Spencer and Thompson 2005). Survivorship of adult *C. expansa* is high and most mortality occurs in adult females during nesting forays (Spencer and Thompson 2005). The propensity to nest far from shore increases the probability of harmful encounters with vehicles and predators (Spencer and Thompson 2005). Therefore, conservation managers should be mindful of development around nesting areas.

The future health of the Murray-Darling Basin is under threat (Leblanc et al. 2012). River regulation and seasonal flow inversion has resulted in salinization, algal blooms, sedimentation, and the establishment of exotic species, all of which threaten freshwater species such as turtles (Walker 2001). In the wake of anthropogenic activity, the poor health of the Murray-Darling Basin and the Murray River in particular, threatens the persistence of native freshwater fauna (Walker 2001).

Climate change may be problematic for *C. expansa* because nesting, diapause, and possibly hatching, rely on climatic cues (Booth 2002a; Bowen et al. 2005). Additionally, the morphology of hatchlings is influenced by the hydric environment experienced throughout incubation (Booth

2002b) and may cause further vulnerability to populations of *C.expansa* if aridity or salinization increases in southeastern Australia (Dunlop and Brown 2008).

Conservation Measures Taken. — The species is not listed as threatened under the Australian Environmental Protection and Biodiversity Conservation Act (1999), though is protected, thus requiring a licence to be kept in all states and territories. Local community efforts undertaken in South Australia have focused on providing predator-free nesting areas and control of introduced species (Goodwin and Hopkins 2005). No recovery plan has been compiled for *C. expansa*, as they are not considered a priority for conservation.

To conform to the precautionary principle and owing to a paucity of information, *C. expansa* is listed as Vulnerable in South Australia under the National Parks and Wildlife Act (1972) and Threatened in Victoria under the Flora and Fauna Guarantee Act (1988). However, these listings may reflect their cryptic nature rather than their population vulnerability (Spencer and Thompson 2005). The species is not formally on the IUCN Red List; however, the TFTSG preliminarily assessed it as Near Threatened under IUCN criteria in 2011.

The species occurs in the following Protected Areas: Murray River National Park, Murray Sunset National Park, Hattah-Kulkyne National Park, Gunbower National Park, Lower Goulburn National Park, Warby-Ovens National Park, Barmah National Park, Kinchega National Park, Paroo-Darling National Park, Macquarie Marshes Nature Reserve, Great Sandy National Park, Fraser Island World Heritage Area, and Moreton Island National Park.

Conservation Measures Proposed. — Priority conservation actions should be focused on restoring river health through environmental flows and the reduction of pest predatory species (foxes and ravens). Research should focus on determining the environmental factors that regulate turtle densities and evaluating how these relate to river management.

Captive Husbandry. — *Chelodina expansa* is common in the international pet trade, notably in the USA; however, it can only be kept as a pet in Australia under a special licence. The species is sensitive to overcrowding and pairs of adults require a water area of at least 150×200 cm with a depth of 50 cm (Weigal 1998). Juveniles require water temperatures of 22–26°C, and captive animals eat raw meat, insects, small mice, and small fish (Weigal 1998).

Current Research. — Demographic studies on freshwater turtles in the Murray Darling Basin are ongoing with researchers at the Arthur Rylah Institute and Charles Sturt University.

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LITERATURE CITED

- BANKS, C.B. 1983. Breeding Australian chelids at the Royal Melbourne Zoo. ASRA Journal – The Journal of the Association for the Study of Reptilia and Amphibia 2:2–21.
- BOOTH, D.T. 1998a. Egg size, clutch size and reproductive effort of the Australian Broad-shelled turtle, *Chelodina expansa*. Journal of Herpetology 32:592–596.
- BOOTH, D.T. 1998b. Nest temperature and respiratory gases during natural incubation in the broad-shelled river turtle, *Chelodina expansa* Testudinata : Chelidae. Australian Journal of Zoology 46:183–191.
- BOOTH, D.T. 1999. Size, water and energy content of freshwater turtles, *Emydura signata* and *Chelodina expansa*. Proceedings of the Linnean Society of New South Wales 121:52–59.
- BOOTH, D.T. 2000. Incubation of eggs of the Australian broad-shelled turtle, *Chelodina expansa* (Testudinata: Chelidae) at different temperatures: effects on pattern of oxygen consumption and hatchling morphology. Australian Journal of Zoology 48:369–378.
- BOOTH, D.T. 2002a. The breaking of diapause in embryonic broadshelled river turtles *Chelodina expansa*. Journal of Herpetology 36:304–307.
- BOOTH, D.T. 2002b. Incubation of rigid-shelled turtle eggs: do hydric conditions matter? Journal of Comparative Physiology B 172:627–633.
- BOOTH, D.T. 2003. Composition and energy density of eggs from two species of freshwater turtle with two fold ranges in egg size. Comparative Biochemistry and Physiology - Part A: Molecular and Intergrative Physiology 134:129–137.
- BOOTH, D.T. 2010. The natural history of nesting in two Australian freshwater turtles. Australian Zoologist 35:198–203.
- BOWEN, K.D., SPENCER, R.J., AND JANZEN, F.J. 2005. A comparative study of environmental factors that affect nesting in Australian and North American freshwater turtles. Journal of Zoology 267:397–404.
- BOWER, D.S. 2012. Conservation biology of freshwater turtles in the lower Murray River. Ph.D. Dissertation, University of Canberra.
- BOWER, D.S., DEATH, C., AND GEORGES, A. 2012a. Ecological and physiological impacts of salinisation on freshwater turtles of the lower Murray River. Wildlife Research 39:705–710.
- BOWER, D.S., HUTCHINSON, M., AND GEORGES, A. 2012b. Movement and habitat use of Australia's largest snake-necked turtle: implications for water management. Journal of Zoology 287:76–80.
- BOWER, D.S., HODGES, K.M., AND GEORGES, A. 2013. Salinity of incubation media influences embryonic development of a freshwater turtle. Journal of Comparative Physiology B 183:235–241.
- BURBIDGE, A., KIRSCH, J.A.W., AND MAIN, A.R. 1974. Relationships within the Chelidae (Testudines: Pleurodira) of Australia and New Guinea. Copeia 1974:392–409.
- CANN, J. 1998. Australian Freshwater Turtles. Sydney and Singapore: Beaumont Publishing, 292 pp.
- CHESSMAN, B.C. 1978. Ecological studies of freshwater turtles in southeastern Australia. Ph.D. Dissertation, Monash University, Melbourne.
- CHESSMAN, B.C. 1983. Observations on the diet of the broad-shelled turtle, *Chelodina expansa* Gray (Testudines: Chelidae). Australian Wildlife Research 10:169–172.
- CHESSMAN, B.C. 1984. Evaporative water loss from three south-eastern Australian species of water turtle. Australian Journal of Zoology 32:649–655.
- CHESSMAN, B.C. 1988a. Seasonal and diel activity of freshwater turtles in the Murray Valley, Victoria and New South Wales. Australian Wildlife Research 15:267–276.
- CHESSMAN, B.C. 1988b. Habitat preferences of freshwater turtles in the

Murray Valley, Victoria and New South Wales. Australian Wildlife Research 15:485–491.

- CHESSMAN, B.C. 2012. Declines of freshwater turtles associated with climatic drying in Australia. Wildlife Research 38:664–671.
- Cogger, H. 2000. Reptiles and Amphibians of Australia. Sydney: Reed New Holland, 808 pp.
- DE LATHOUDER, R., JONES, D.N., AND BALCOMBE, S.R. 2009. Assessing the abundance of freshwater turtles in an Australian urban landscape. Urban Ecosystems 12:215–231.
- DUNLOP, M. AND BROWN, P. 2008. Implications of climate change for Australia's National Reserve System: a preliminary assessment. Prepared for the Federal Government by CSIRO scientists. Available at: http://www.climatechange.gov.au/impacts/publications/ nrs-report.html.
- EZAZ, T., VALENZUELA, N., GRÜTZNER, F., MIURA, I., GEORGES, A., BURKE, R. L., AND MARSHALL-GRAVES, J.A. 2006. An XX/XY sex microchromosome system in a freshwater turtle, *Chelodina longicollis* (Testudines: Chelidae) with genetic sex determination. Chromosome Research 14:139–150.
- FITZINGER, L.J. 1826. Neue Classification der Reptilien, nach ihren Natürlichen Verwandtschaften nebst einer Verwandtschaftstafel und einem Verzeichnisse der Reptilien-Sammlung des k.k.Zoologischen Museum zu Wien. J.G. Hübner Verlagen, Wien.
- GEORGES, A. 1982. Ecological studies of Krefft's River Tortoise, *Emydurakrefftii*, from Fraser Island, Queensland. Ph.D.Dissertation, University of Queensland, Brisbane.
- GEORGES, A. 1984. Observation on the nesting and natural incubation of the long-necked tortoise *Chelodina expansa* in south-east Queensland. Herpetofauna 15:27–31.
- GEORGES, A. AND ADAMS, M. 1992. A phylogeny for Australian chelid turtles based on allozyme electrophoresis. Australian Journal of Zoology 40:453–476.
- GEORGES, A. AND THOMSON, S.A. 2010. Diversity of Australasian freshwater turtles, with an annotated synonymy and keys to species. Zootaxa 2496:1–37.
- GEORGES, A., BIRRELL, J., SAINT, K.M., MCCORD, W., AND DONNELLAN, S.C. 1998. Aphylogeny for side-necked turtles (Chelonia: Pleurodira) based on mitochondrial and nuclear gene sequence variation. Biological Journal of the Linnean Society of London 67:213–246.
- GEORGES, A., ADAMS, M., AND MCCORD, W. 2002. Electrophoretic delineation of species boundaries within the genus *Chelodina* (Testudines: Chelidae) of Australia, New Guinea and Indonesia. Zoological Journal of the Linnean Society 134:401–421.
- GOODE, J. 1966. Notes on the artificial incubation of eggs of Victorian chelid turtles. Victorian Naturalist 83:280–286.
- GOODE, J. 1967. Freshwater Tortoises of Australia and New Guinea (in the Family Chelidae). Melbourne: Lansdowne Press, 154 pp.
- GOODE, J. AND RUSSELL, J. 1968. Incubation of eggs of three species of chelid tortoises and notes on their embryological development. Australian Journal of Zoology 16:749–761.
- GOODWIN, C. AND HOPKINS, G. 2005. More Turtles: Murray River Protection Manual. Berri: Riverland Animal Plant Control Board.
- GRAY, J.E. 1857. Description of a new species of *Chelodina* from Australia. Proceedings of the Zoological Society of London 1856[1857]:369–371.
- GREEN, D. 1996. Observations of grooming in some captive Australian chelid turtles. Herpetofauna 26:46.
- HAMANN, M., SCHAEUBLE, C.S., EMERICK, S.P., LIMPUS, D.J., AND LIMPUS, C.J. 2008. Freshwater turtle populations in the Burnett River. Memoirs of the Queensland Museum 52:221–232.
- HODGES, K., DONNELLAN, S., AND GEORGES, A. In press. Phylogeography of the Australian freshwater turtle *Chelodina expansa* reveals complex relationships among inland and coastal bioregions.

Biological Journal of the Linnean Society.

- LEBLANC, M., TWEED, S., VAN DIJK, A., AND TIMBAL, B. 2012. A review of historic and future hydrological changes in the Murray-Darling Basin. Global and Planetary Change 80:226–246.
- LEGLER, J.M. 1978. Observations on behavior and ecology in an Australian turtle, *Chelodina expansa* (Testudines: Chelidae). Canadian Journal of Zoology 56:2449–2543.
- LEGLER, J.M. AND GEORGES, A. 1993. Family Chelidae. In: Glasby, C.J. Ross, Graham J.B., and Beesley, P.L. (Eds.). Fauna of Australia. Vol. 2A. Amphibia and Reptilia. Canberra: Australian Government Publishing Service, pp. 142–152.
- LIMPUS, C.J., LIMPUS, D.J., AND HAMANN, M. 2002. Freshwater turtle populations in the area to be flooded by the Walla Weir, Burnett River, Queensland: baseline study. Memoirs of the Queensland Museum 48:155–168.
- MARTINEZ, P., EZAZ, T., VALENZUELA, N., GEORGES, A., AND MARSHALL-GRAVES, J. 2008. An XX/XY heteromorphic sex chromosome system in the Australian Chelid turtle *Emydura macquarii*: a new piece in the puzzle of sex chromosome evolution in turtles. Chromosome Research 16:815-825.
- MCCORD, W.P. AND JOSEPH-OUNI, M. 2007. A new genus of Australian longneck turtle (Testudines: Chelidae) and a new species of *Macrochelodina* from the Kimberley region of Western Australia (Australia). Reptilia (GB) (Barcelona) 55:56–64.
- McCosker, J. 2002. *Chelodina expansa* broad-shelled river turtle and *Emydura signata* Brisbane short-neck turtle. Reproduction. Herpetological Review 33:198–199.
- MEATHREL, C.E., SUTER, P.J., AND RADFORD, N.M. 2002. Niche segregation between three species of freshwater turtle in a large billabong during flood. Victorian Naturalist 119:160–173.
- NEAR, T.J., MEYLAN, P.A., AND SHAFFER, H.B. 2005. Assessing concordance of fossil calibration points in molecular clock studies: an example using turtles. The American Naturalist 165:137–146.
- PHILLOTT, A.D. AND PARMENTER, J.C. 2000. Predation on *Emydura krefftii* and *Chelodina expansa* hatchlings in central Queensland. Herpetofauna 30:22–25.
- SCHELTINGA, D. 1991. Salt glands and the tolerance of *Chelodina* longicollis and *C. expansa* for saline water. Honours Thesis,

University of Queensland, Brisbane.

- SHINE, R. AND IVERSON, J.B. 1995. Patterns of survival, growth and maturation in turtles. Oikos 72:343–348.
- SPENCER, R.J. 2002. Growth patterns of two widely distributed freshwater turtles and a comparison of common methods used to estimate age. Australian Journal of Zoology 50:477–490.
- SPENCER, R.J. AND THOMPSON, M.B. 2005. Experimental analysis of the impact of foxes on freshwater turtle populations. Conservation Biology 19:845–854.
- THOMSON, S., WHITE, A., AND GEORGES, A. 1997. A re-evaluation of *Emydura lavarackorum*: identification of a living fossil. Memoirs of the Queensland Museum 42:327–336.
- WALKER, K.F. 2001. A river transformed: the effects of weirs on the River Murray. In: Blanch, S.N. and Baird, K. (Eds.). The Proceedings of The Way Forward on Weirs. Sydney: Inland Rivers Network, 233 pp.
- WEBB, G.J. 1978. Observations on basking in some Australian turtles (Reptilia: Testudines: Chelidae). Herpetologica 34:39–42.
- WEIGAL, J. 1998. Care of Australian Reptiles in Captivity. Gosford: McPherson's Printing Group, 144 pp.
- WELLS, R. AND WELLINGTON, R. 1985. A classification of the Amphibia and Reptilia of Australia. Australian Journal of Herpetology, Supplementary Series 1:1–61.
- WOODALL, P.F. 1984. The structure and some functional aspects of the eggshell of the broad-shelled river tortoise *Chelodina expansa* (Testudinata: Chelidae). Australian Journal of Zoology 32:7–14.

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