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A NEW LOOK AT THE FRESHWATER TORTOISES OF AUSTRALIA

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Research into Australian freshwater turtles has greatly advanced during the last decade. Numerous new forms have been formally described, and many papers describing turtles have been submitted or are in their final stages of preparation. This new work has been driven by extensive surveys for new forms, renewed interest in turtle taxonomy by some bright students, and the introduction of some modern molecular techniques to the problem of defining species' boundaries objectively.

This work has confirmed many early ideas on what species were new, as outlined in the literature, but it has also yielded some surprises. The cryptic species pair of saw-shell turtles, Elseya georgesi from the Bellinger of coastal New South Wales and Elseya purvisi from the coastal Manning River, is one example. Three instances of natural hybridisation among the snake-necked turtles other examples. (Chelodina) provide Chelodina novaequineae is hybridising with Chelodina longicollis where their ranges meet in central coastal Queensland, and C. novaeguineae is hybridising with C. rugosa in the gulf country, despite their distant relationship. Backcrossed individuals have been found, providing a real challenge to our ideas of what a Chelodina species is.

Whatever the final figure is for the number of Australian freshwater turtle species, this critical information is coming to light at a time when many populations of turtle are in decline as human and aquatic wildlife populations compete for a very limited resource in Australia – water. This fundamental taxonomic work is critical if we are to balance conservation concerns with development.

Introduction

The freshwater turtle fauna of Australia and adjacent regions is dominated by the family Chelidae, which occurs only in Australia, New Guinea, the island of Roti in Indonesia, and South America. Their fossil record extends back to the Upper Cretaceous of South America (de Broin 1987) and the Miocene of Australia (Gaffney, Archer et al. 1989), but no fossil chelids are known from outside the present range of the family (Williams 1953; Williams 1953; Gaffney 1991). The family is therefore considered to be of Gondwanal origin (Burbidge, Kirsch et al. 1974).

The classification of Australasian chelid turtles is poorly founded, and in drastic need of review (Cogger 2000). This has been a major impediment to conservation. The situation has changed recently, with detailed surveys and analysis of species boundaries using allozyme electrophoresis (Georges and Adams 1996; Georges, Adams et al. submitted) and the subsequent formal description of a number of new species (Cann 1997; Cann 1997; Cann 1997; Thomson, White et al. 1997; Thomson, Kennett et al. 2000). Further descriptions are imminent.

In this paper, we give an account of the current status of knowledge of the taxonomy of Australian turtles.

Short-Necked River Turtles

Species of *Emydura* are widespread and abundant in eastern and northern Australia, where they occupy rivers and the larger, permanent waterholes and billabongs of their flood plains. They are omnivorous short-necked species and are general in their habitat requirements, provided the water is permanent. Electrophoretic surveys found no clear distinctions between *Emydura signata*, *E. krefftii* and *E. macquarii* and, in the absence of clear morphological characters to separate them, they should be regarded as a single biological species, *Emydura macquarii* (Georges and Adams 1992; Georges and Adams 1996). A case can be made for sub-specific recognition using morphology, coloration and geographic range. Populations of the Murray-Darling drainage and coastal rivers from the Brisbane River to the Hawkesbury-Nepean (*Emydura macquarii macquarii*), populations from coastal Queensland north from the Mary River to the vicinity of Princess Charlotte Bay (*Emydura macquarii krefftii*), from Fraser Island, and from Cooper Creek in central Australia can each be regarded as subspecies (that latter two as yet unnamed). A number of other subspecies have been described for this widespread southern *Emydura* (Cann 1998).

In the north, there are a number of closely related species. The Northern Red-Faced Turtle, *Emydura victoriae*, ranges from the Fitzroy River of Western Australia east to the Daly River of the Northern Territory. It may be more than one species, and probably includes *Emydura australis* (Cann, 1998). Worrell's Turtle or the Diamond-head is found in the rivers from the Daly River in the west to the rivers flowing into the Gulf of Carpentaria along the west coast of Cape York. This form is electrophoretically indistinguishable from populations of *Emydura subglobosa* in New Guinea, but lacks the red suffusion of the New Guinea populations.

It is best referred to as *Emydura subglobosa worrelli*. *Emydura subglobosa subglobosa* is found in the Jardine River at the tip of Cape York and is widespread in the southern flowing rivers of the island of New Guinea. The Northern Yellow-faced Turtle, *Emydura tanybaraga*, is widespread across northern Australia. All three species of *Emydura* are found in the Daly River.

Australian Snappers

The species of *Emydura* are all very closely related, differing at most by few fixed allozyme differences, and are presumably a recent radiation. This is not the case for the genus Elseya - the Australian Snappers. What was until recently regarded as a single widespread species, the Northern Snapping Turtle Elseya dentata, is now known to be a series of highly divergent allopatric species (Georges and Adams 1996). They are river turtles and largely herbivorous. Elseya dentata is restricted to the northern rivers west of, but not including, the Alligator Rivers region of the Northern Territory. A distinct undescribed species occurs in the Alligator Rivers region and the rivers flowing north from the Arnhem Land plateau (Elseya sp. [Sth Alligator] of Georges and Adams, 1996). The Gulf Snapping Turtle, Elseya lavarackorum, is poorly known, but its distribution is thought to extend from the Roper River of the Northern Territory in the west to at least as far east as the Gregory-Nicholson drainage in Queensland. There is an undescribed species in the Johnstone Rivers region near Cairns, Elseya irwini restricted to the Burdekin, and there is a third undescribed species in the Mary, Burnett and Fitzroy Rivers of south-eastern Queensland (Georges and Adams 1996). A related form, the New Guinea Snapping Turtle Elseya novaeguineae, is widespread in New Guinea. Elseya branderhorsti is found in the southern rivers of New Guinea. It is likely that many more species will be discovered there (Rhodin and Genorupa, 2000; Samedi and Iskandar, 2000) and in the Kimberley region (Cann, 1998).

Saw-shelled Turtles

A second lineage of carnivorous and omnivorous species is currently grouped within *Elseya*. They tend to be most abundant in the upper reaches of rivers and their tributaries. The Common Sawshell, *Elseya latisternum*, is the most widespread. It occurs in the coastal rivers from the Richmond River of northern New South Wales, to the Jardine River on the tip of Cape York, in the rivers discharging into the Gulf of Carpentaria, and in the

headwaters of rivers that discharge from the Arnhem Land plateau. Other species in this group are very restricted. The Bellinger River Turtle, *Elseya georgesi*, and the Manning River Turtle, *Elseya purvisi*, are restricted to the coastal New South Wales rivers that give them their common names. They are of particular interest because they are a sibling or cryptic species pair, morphologically difficult to distinguish on external examination, but deeply divergent genetically (Georges and Adams 1996). Once thought to be a single species, the genetic examination prompted a closer look at their morphology and revealed that *Elseya purvisi* has well-developed series of exposed neural bones, consistently lacking in *Elseya georgesi* (Thomson and Georges 1996). Neural bones in most chelid turtles are reduced subsurface bony elements of the carapace lying immediately above the vertebral column (Thomson and Georges 1996). A fourth species in this group, *Elseya bellii*, is found in the granitic headwaters of the Namoi, Gwydir and Severn tributaries of the Darling River in inland New South Wales. Those from the upper reaches of the Severn have small but distinctive morphological differences from the Namoi/Gwydir populations, and may prove to have a similar relationship to that between *Elseya purvisi* and *E. georgesi* (Cann, 1998).

Snake-necked Turtles

Australia is well known for its snake-necked chelid turtles, genus *Chelodina*, because their necks can be spectacularly long in relation to their bodies, an innovation rare among the cryptodiran turtles that dominate the turtle fauna of the Northern Hemisphere. Their long necks have evolved through the benefits of attenuated strike and gape feeding that enables these animals to secure fast-moving prey not available to their short-necked cousins. When feeding, the head and neck are thrust out against the inertia of the body. At the same time, the floor of the mouth is lowered causing an in-rushing of water to suck in the prey.

Species of *Chelodina* fall into three sub-generic groups (Burbidge, Kirsch et al. 1974). *Chelodina longicollis* and *C. steindachneri* of Australia, *C. pritchardi* and *C. reimanni* of New Guinea, *C. mccordi* of Roti and *C. novaeguineae* of Australia and New Guinea belong to Group A. They are carnivorous foragers with relatively narrow heads, shorter thinner necks and broader plastrons (Goode 1967; Rhodin 1994; Rhodin 1994). *Chelodina expansa*, *C. burrungandjii* and *C. rugosa* of Australia, and *C. siebenrocki* and *C. parkeri* of New Guinea belong to Group B are ambush predators with relatively broad heads, longer thicker necks and narrower plastrons (Goode 1967; Rhodin and Mittermeier 1976). *Chelodina rugosa* and *C. siebenrocki* are indistinguishable using allozyme electrophoresis,

and are morphologically very similar. We regard them as a single taxon, Chelodina rugosa.

Chelodina colliei of southwestern Australia (formerly C. oblonga, Thomson 2000) is superficially similar to species of the Group B, and has often been placed in that group (Goode 1967; Legler 1981).

However we follow Burbidge et al. (1974) and place it in a third sub-generic group, Group C. It is distinguished from other described *Chelodina* by a consistent set of well developed of neural bones (Burbidge, Kirsch et al. 1974; Thomson and Georges 1996).

Monotypic Genera

The remaining genera are monotypic. *Rheodytes leukops* is restricted to the Fitzroy-Dawson drainage, *Elusor macrurus* is found only in the Mary River of coastal Queensland, and *Pseudemydura umbrina* is restricted to coastal swamps near Perth. The cryptodire, *Carettochelys insculpta*, is found in the Victoria River, Daly River and Alligator Rivers region of the Northern Territory.

Natural Hybridisation

Hybridisation presents particular problems for any species concept, as substantial gene flow between taxa acts against their divergent evolution and blurs their separation as discrete entities. Traditionally, hybridisation is interpreted as contributing to a final stage in speciation, whereby introgression leads to reduced fitness and positive selection for traits limiting further hybridisation (Dobzhansky 1940; Dobzhansky 1970). When two diagnosable taxa are in long-standing allopatry, the possibility exists that despite substantial genetic divergence, reproductive incompatibility may not be fully effected, with the final stage of reproductive character displacement requiring a period in sympatry. Recent studies soon to be published demonstrate that reproductive compatibility, a pleisiomorphic trait by definition, can persist for substantial periods in a phylogeny derived from morphological and molecular data. Chelodina rugosa (Fig. 1) and C. novaeguineae (Fig.2) are distant phylogenetically, and may soon be placed in separate genera (Legler 1985), yet they hybridise in the Gulf region of Queensland with evidence of introgression (Georges, Adams et al. submitted). Chelodina longicollis (Fig. 3) and C. novaeguineae are not sister taxa, yet they hybridise in central coastal Queensland. Strict application of the Biological Species Concept (Mayr 1969) would have us regard these as single species, but in practice, all species concepts must be relaxed to include the possibility that species can form natural hybrids (Arnold 1997).

When the hybrids from central coastal Queensland were found, it was clear that cross-breeding was taking place on the boundary of the distributions of the two parent *Chelodina novaequineae* and *C. longicollis* (Cann, 1998). Not so with the hybrids (Fig. 4) between *C. novaeguineae* and *C. rugosa*. They were initially thought to be a new species, and a description was being prepared (Cann, 1998). They were found in a dam made for mining over 80 years ago, which gathers water only in the tropical wet. This dam is toxic, with warnings on water use, so it is interesting to speculate whether this has in some way interfered with the normal barriers to reproduction between the two species. High on the list of research questions then is whether this hybridisation is more widespread. Does it occur in the Gilbert River proper, some 6 km away? To what extent is backcrossing occurring and is there persistent gene transfer between the two fairly distantly related species?

Conclusion

The current Australian turtle fauna appears to comprise a series of distinct lineages, each of considerable antiquity, and possibly relicts of a more diverse fauna that existed when wetter climes prevailed. Half of the extant genera are monotypic, and many species are restricted to single drainage basins. The recent work on taxonomy will allow a more reasoned analysis of the conservation status of freshwater turtles in Australia and will allow us to identify hotspots of biodiversity and endemism that deserve special management attention (Georges and Thomson, 2001).

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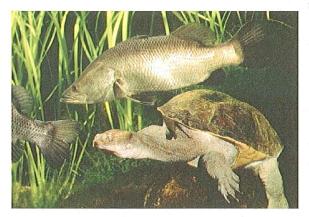


Fig.1. *Chelodina rugosa* from the Gilbert River, Gulf Country, Northern Territory, Queensland. All photos by the authors.

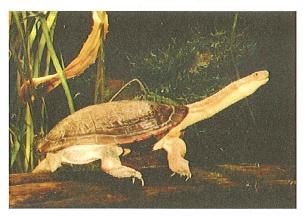


Fig. 2. Chelodina novaeguineae sp.



Fig. 3. Chelodina longicollis



Fig. 4. A fertile hybrid between *C. rugosa* and *C. novaeguineae sp.*



Fig. 5. A collection of shells from central coastal Queensland where *C. longicollis* and *C. novaeguineae sp.* meet.



Fig. 6. Top to bottom: *C. rugosa, C. novaeguinaea sp,* and *C. hybrid.*