



FAUNA *of* AUSTRALIA



15. GENERAL DESCRIPTION AND DEFINITION OF THE ORDER CHELONIA

John M. Legler

15. GENERAL DESCRIPTION AND DEFINITION OF THE ORDER CHELONIA

Turtles are members of the order Chelonia (also termed Testudinata). There is general agreement on the monophyly of turtles and their distinction as an order within the Reptilia (Gaffney & Meylan 1988; Romer 1956). At all levels of knowledge the distinction of turtles is unequivocal. Turtles are familiar to humans. There is a word for 'turtle' in most languages and many children can draw a crude, but diagnostic picture of a turtle before they can spell the word. If turtles were known only from fossils, they would be regarded with substantially more awe than they are as familiar animals. The most common English names for chelonians are turtle, tortoise, and terrapin. Each may have special significance in local areas. For example, 'tortoise', as generally used by turtle biologists, refers to the completely terrestrial testudinid chelonians. In Australia, the term is used for any member of the family Chelidae.

Chelonians are toothless, oviparous, quadrupedal, pentadactyl reptiles with a shell and a unique trochlear system for the common tendon of the jaw adductor muscles. The principal and unequivocal diagnostic features of the Chelonia are the shell and the changes in related anatomy that accompany it. The carapace (upper shell) consists of costal bones fused to ribs, neural bones fused to vertebrae, and peripheral bones. The interclavical, clavicals and plates of dermal bone on the belly are incorporated in the plastron. The carapace and plastron articulate laterally and enclose the limb girdles. The limb girdles therefore are surrounded by the axial skeleton, unlike all other amniotes. The evolution of the chelonian shell was a major early modification of the basic amniote body plan. It has served the chelonians well as they have survived and prospered with a minimum of modification, while most of the major events in reptilian evolution went on around them (see Carr 1952 for a delightful account).

There have been a few other reptilian experiments with a 'shell'. *Eunotosaurus* of the Permian of South Africa had broadened ribs, and certain placodont reptiles, especially *Henodus* of the Upper Triassic of Europe, had dermal elements fused to the axial skeleton, but none of these is a turtle nor is any involved in turtle ancestry (Carroll 1988). The homologies and the embryonic development of the chelonian carapace are reasonably well known, but the evolution of the carapace is seemingly still an open issue.

Aside from a drastic modification of the skeleton, turtles have remained quite generalised in most other aspects of anatomy, physiology and behaviour. Some adaptive modification has accompanied radiation, over approximately 200 million years, into a wide variety of habitats, ranging from complete

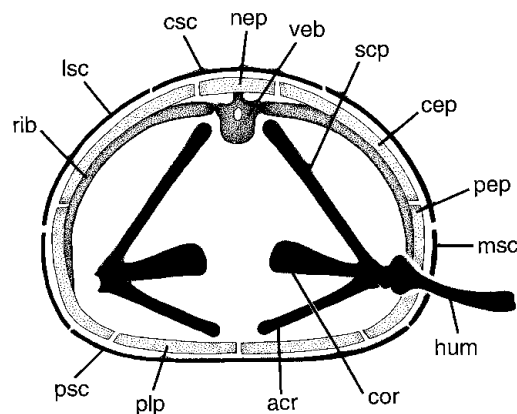


Figure 15.1 Diagrammatic cross-section through middle of a chelonian shell showing relative positions of skeletal and epidermal elements. **acr**, acromion; **cep**, costal plate; **cor**, coracoid; **csc**, central scute; **hum**, humerus; **lsc**, lateral scute; **msc**, marginal scute; **nep**, neural plate; **pep**, peripheral plate; **plp**, plastral plate; **psc**, plastral scute; **rib**, rib; **scp**, scapula; **veb**, vertebra.

[T. Wright]

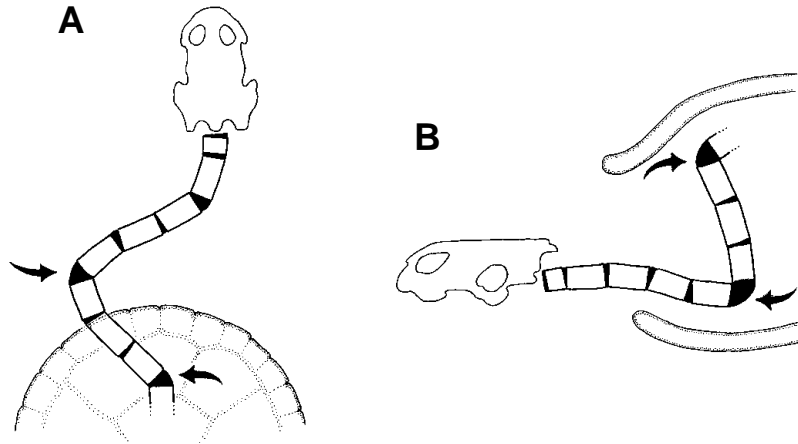


Figure 15.2 Differences in neck flexion and retraction in the two suborders of turtles. **A**, Pleurodira; **B**, Cryptodira. Arrows show points of greatest flexure. (After Williams 1950) [T. Wright]

terrestrialism in land tortoises (family Testudinidae) to an almost complete adaptation to aquatic life in the marine turtles (families Cheloniidae and Dermochelyidae). Land tortoises have elephantine feet, with short digits and no webbing, and are poor swimmers. Marine turtles are so specialised for swimming that they have difficulty with tetrapodal locomotion on land. However, the changes that occurred during these radiations are relatively small when compared to the initial evolution of the shell.

CLASSIFICATION

The two basic forms of living turtles are grouped in the suborders Cryptodira and Pleurodira. Cryptodires retract the neck straight back, in a sigmoidal curve in the vertical plane. Pleurodires flex the neck laterally, in either direction, in the horizontal plane and tuck it between the carapace and plastron. The pelvis is fused to the plastron in pleurodires but is free in cryptodires. Pleurodires occur only on southern continents and are less diverse than the worldwide cryptodires.

Living turtles comprise 12 or 13 families; recent classifications include about 90 genera and some 260 species. The best checklist is that of Iverson (1992) which includes maps and cladograms, but no drawings. The checklist of Wermuth & Mertens (1961) lacks maps but has useful line drawings of many taxa. King & Burke (1989) also provided a useful checklist. There are two compendia entitled 'Turtles of the World' (Pritchard 1967; Ernst 1989).

There is general agreement on the equal subordinal rank of cryptodires and pleurodires, on extant families, and on suprafamilial groupings. The most recent, most complete, most complex, and probably best classification and phylogeny of turtles is that of Gaffney & Meylan (1988). They included all known fossil and living taxa and invoked many non-traditional taxonomic ranks, such as 'parvorder', 'capaxorder' and 'microorder'. As their work is of great value to a specialist but not a lucid source of general knowledge, I have taken liberties in simplifying their classification. The following classification is based on living taxa, and the present superfamilies differ slightly from those of Gaffney & Meylan.

Suborder Cryptodira

The lateral and posterior emargination of the dermal skull is moderate. There is nearly always a well-defined temporal (zygomatic) arch from the posterior orbital rim to the anterior rim of the tympanic aperture. The trochlear apparatus

15. GENERAL DESCRIPTION AND DEFINITION OF THE ORDER CHELONIA

for the mandibular adductor tendon is formed by the antero-dorsal ridge of the otic capsule, comprising the prootic, the quadrate or both, and is a true synovial joint. The neck flexes in a vertical (sagittal) curve and is usually retractile. The cervical central articulations are well-developed, always broad and are typically double on posterior cervicals. The pelvis is not fused to the plastron. The mesoplastron is never present. The posterior cervical spines are low, and the postzygopophyses are wide apart.

Superfamily Chelydroidea. The North American family Chelydridae includes two monotypic genera of snapping turtles. Inclusion of the big-headed turtles of Asia (family Platysternidae, one monotypic genus) in this superfamily is moot.

Superfamily Chelonioidae. The typical marine turtles occur in all temperate and tropical seas. The family Cheloniidae includes five genera, all of which are present in Australian waters.

Superfamily Dermocheloidea. The family Dermochelyidae includes only the monotypic genus *Dermochelys*. The leatherback turtle, *Dermochelys coriacea*, has a cosmopolitan distribution in arctic, temperate and tropical seas.

Superfamily Trionychoidea. The softshelled turtles of North America, Asia and Africa are placed in the family Trionychidae. Seven genera are recognised. The pig-nosed turtle *Carettochelys insculpta*, sole member of the family Carettochelyidae, is the only freshwater cryptodire in Australia. It occurs also in New Guinea.

Superfamily Kinosternoidea. One species, the River Turtle, *Dermatemys marwi*, is placed in the Family Dermatemydidae, of central America. Four genera of the related musk turtles, family Kinosternidae, occur in North, Central and South America.

Superfamily Testudinoidea. Most of the pond turtles of the family Emydidae are partly aquatic. Nine of the 10 genera occur in North America, and *Emys* occurs in Europe. The closely related batagurid pond turtles, family Bataguridae, are mostly Oriental (22 genera), but *Rhinoclemys* occurs in central and adjacent South America. Australia is the only continent lacking any land tortoises of the widespread family Testudinidae. This family comprises 11 genera, five of which occur only in Africa.

Suborder Pleurodira

The lateral emargination of the dermal skull roof is usually extreme, and the posterior emargination is absent or slight. The temporal arch is variable, absent or posteriorly displaced in most chelids. The trochlear apparatus for the mandibular adductor tendon is formed by the lateral pterygoid process; the lubricatory capsule is an evagination of the buccal mucosa and not truly synovial. The neck flexes laterally to either side and is tucked under the anterior edge of the carapace, but is not truly retractile. The cervical central articulations are well-developed, but are never double. The pelvis is always fused to the plastron. Mesoplastra may be present or not. The posterior cervical spines are relatively high, and the postzygopophyses are closely approximated or fused.

Members of the family Pelomedusidae lack nasal bones, and the vomer is absent in extant forms. The lateral temporal arch includes the jugal and quadratojugal bones. The second cervical centrum is biconvex, and the remainder are procoelous or have saddle articulations. A mesoplastron is present in some taxa. The normal number of chromosomes is $2n = 26$ to 36 (by virtue of microchromosomal reduction) (Bull & Legler 1980). There are seven species in two genera in South America, two genera and 16 species in Africa, and one monotypic genus in Madagascar.

15. GENERAL DESCRIPTION AND DEFINITION OF THE ORDER CHELONIA

In the family Chelidae, nasal bones are present in all genera but *Chelus*, and the vomer is present. A posterior parietosquamosal arch is present (absent in *Chelodina*), and the quadratojugal is absent. The centra of the fifth and eighth cervical vertebrae are biconvex, and saddle joints are never present. A mesoplastron is absent. The normal chromosome number is $2n = 50$ to 64 (96 in triploid *Platemys*), $2n = 50$ in Australian shortnecks and $2n = 54$ in Australian longnecks (Bull & Legler 1980). The family occurs in South America, Australia, New Guinea and Roti (Lesser Sunda Islands). There are eight genera and approximately 29 species in Australia; four of these genera and six endemic species are present in New Guinea. Five genera and approximately 20 species occur in South America.

KEY TO THE GENERA OF AUSTRALIAN TURTLES

Keys can consist of characters that diagnose the taxa or simply of characters which identify a taxon within geographic limits. Diagnostic characters of Chelonia are often internal. The following key is utilitarian and uses characters that may have significance only within Australia. Internal characters, when used, are coupled with external characters. Three of the eight genera of freshwater chelids recognised in Australia are undescribed (Legler in press); two are provisionally referred to as ‘groups’, and one is termed the ‘shortnecked alpha’.

Key to the genera of Australian turtles

- 1(a) Forelimbs flipperlike; claws reduced and atypical; neck retracted vertically; pelvis not fused to plastron. Cryptodira.2
- (b) Forelimb bearing a webbed hand with four or five claws, not flipperlike; neck retracted laterally; pelvis fused to plastron. Pleurodira: Chelidae8
- 2(a) Shell bearing discrete, regular, enlarged cornified scutes. Cheloniidae4
- (b) Shell lacking discrete scutes or covered with numerous small, pebblelike osteoderms (Fig. 15.3E), not discrete enlarged scutes.3

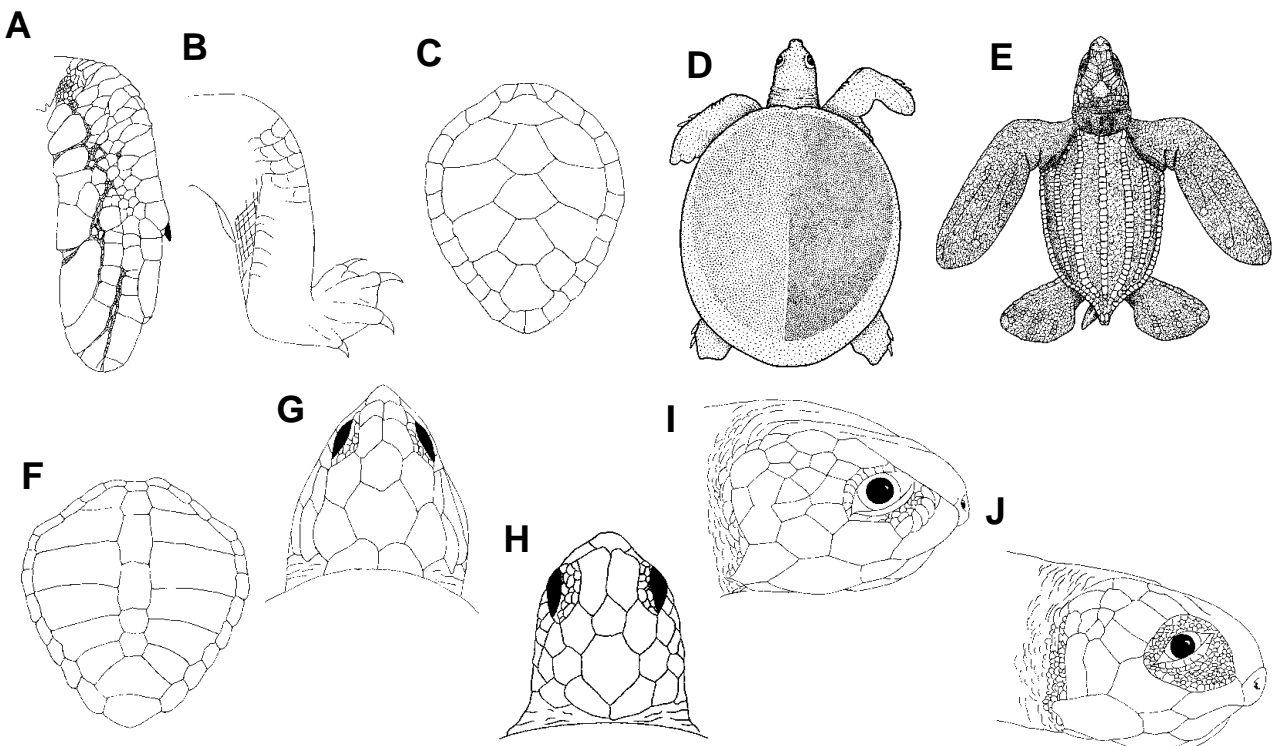


Figure 15.3 Key characters for chelonians. Pertinent features of elements A–J are noted in the key above and on the previous page. [A-C, F, G, I, J, H.G. Cogger; D, E, H, D. Wahl]

15. GENERAL DESCRIPTION AND DEFINITION OF THE ORDER CHELONIA

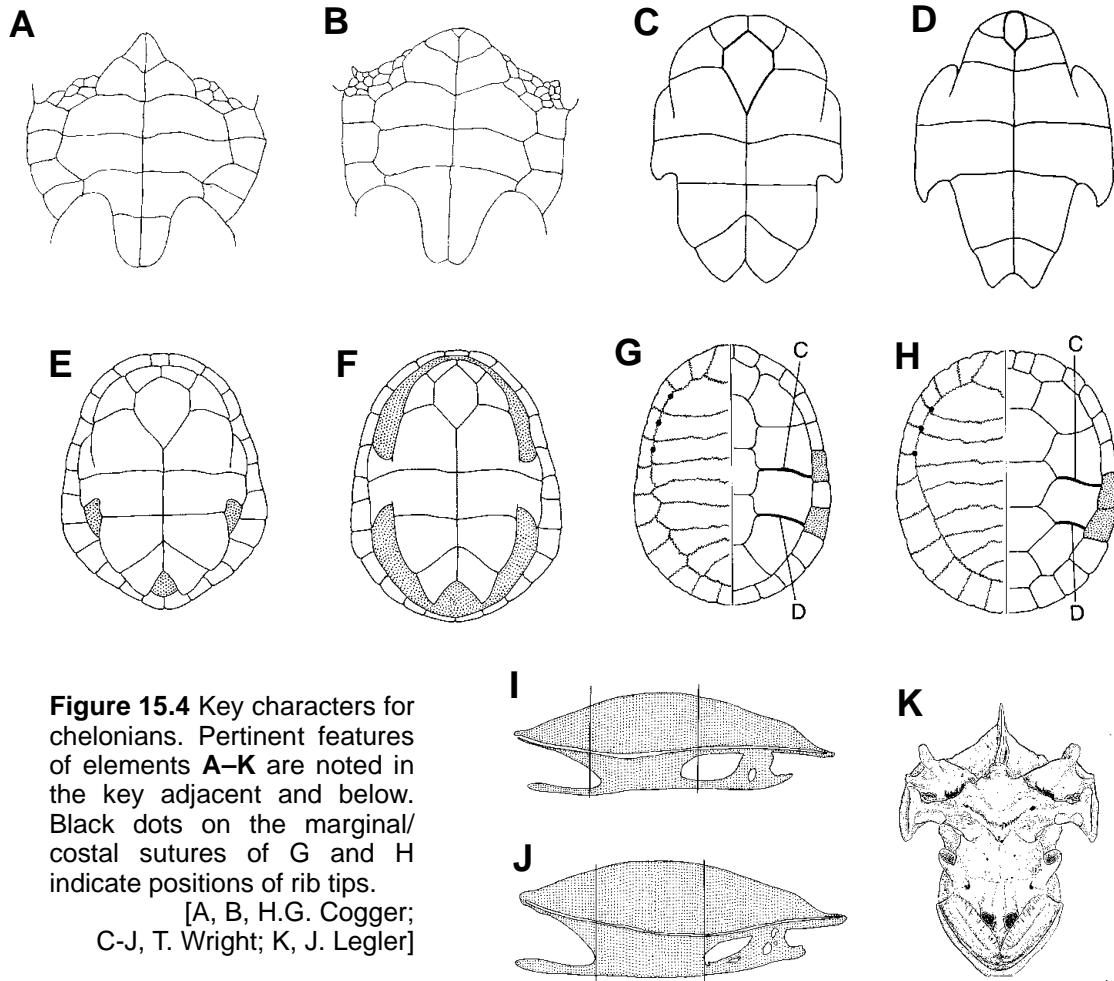


Figure 15.4 Key characters for chelonians. Pertinent features of elements **A–K** are noted in the key adjacent and below. Black dots on the marginal/costal sutures of **G** and **H** indicate positions of rib tips.

[**A, B**, H.G. Cogger; **C–J**, T. Wright; **K**, J. Legler]

- 3(a) Nostrils at tip of fleshy pig-like proboscis; entire shell covered by undivided soft skin; no discrete scales on top of head; freshwater and estuarine habitats of north-western Australia and New Guinea. *Carettochelyidae*
..... *Carettochelys insculpta* (Pl. 3.9)
- (b) Nostrils flush with surface of snout; no proboscis; head bearing discrete enlarged scales; shell covered with many small osteodermal scales; northern Australia (*Dermochelyidae*) *Dermochelys coriacea* (Pls 3.7, 3.8)
- 4(a) Four lateral scutes on each side of carapace5
- (b) More than four lateral scutes on each side of carapace7
- 5(a) Anterior part of head narrow, attenuated and beak-like in profile; two pairs of prefrontal scales (Fig. 15.3G) *Eretmochelys* (Pl. 3.2)
- (b) Anterior part of head rounded and blunt in profile; one pair of prefrontal scales.6
- 6(a) Four or more postocular scales; large scales on eyelid; anterior surface of antebrachium covered by medium to large scales (no broad central band of minute scales) *Chelonia* (Pl. 3.5)
- (b) Three postocular scales; many small scales on eyelid; anterior antebrachium with a perimeter of large scales surrounding a broad median area of minute scales or wrinkled skin *Natator* (Pl. 3.4)
- 7(a) Four enlarged inframarginal scales on each bridge, each usually bearing a pore near posterior border (Fig. 15.4A); six or more lateral scutes on each side; mandibular rami bow outward; maxillary bones separated by vomer; predominantly greyish (young almost black) *Lepidochelys* (Pl. 3.6)

15. GENERAL DESCRIPTION AND DEFINITION OF THE ORDER CHELONIA

- (b) Three enlarged inframarginals on each bridge, never with pores; less than six lateral scutes on each side; mandibular rami straight or bowed inward slightly; maxillary bones in contact; dorsal colouration predominantly reddish brown *Caretta* (Pl. 3.1)
- 8(a) Manus with four claws; gulars in contact; intergular not on anterior edge of plastron (longnecked chelids) 9
- (b) Manus with five claws; gulars not in contact, intergular on anterior edge of plastron (shortnecked chelids). 10
- 9(a) Plastron extensive, almost covering the anterior orifice of shell (or retracted soft parts) in ventral view (Fig. 15.4E); neck shorter in comparison to shell; dorsum of neck with many blunt conical tubercles; musk secretion copious and strongly odoriferous *Chelodina longicollis* group (Pl. 3.11)
- (b) Plastron less extensive, covering only about half of anterior orifice of shell (or retracted soft parts) in ventral view; neck longer in comparison to carapace; skin of neck lacking obvious tubercles; musk secretion slight, odour noticeable, but not strong *Chelodina expansa* group
- 10(a) Intergular excludes both gulars and humerals from midline contact; temporal roofing of skull extensive; head shield covers most of head *Pseudemydura* (Pl. 3.13)
- (b) Intergular separates only gulars, humerals in contact; temporal roofing of skull substantially emarginate from below; head shield variable but never covering most of head 11
- 11(a) Interlateral seams C and D contact posterior parts of marginals 6 and 8; rib tips of costals 2 to 4 articulate with gomphoses in centres of peripherals 4 to 6; a distinct white, ivory or silver iris at all ages. *Rheodytes* (Pl. 3.12)
- (b) Interlateral seams C and D contact marginals 7 and 8; rib tips of costals 2 to 4 articulate in or near interperipheral sutures ; iris variable, if pale then yellowish, not white or ivory. 12
- 12(a) Shell shallower and/or bridge shorter; always a pale contrasting iris; never any median ridging on the triturating surfaces of jaw sheaths 13
- (b) Shell deep and spacious; bridge long. Eye dark and lacking contrast at all ages; a well-defined median ridge on the triturating surfaces of the jaw sheaths *Elseya dentata* group
- 13(a) Tail distinctive and large: precloacal length greater than postcloacal length at all ages; tail laterally compressed; cloacal orifice a longitudinal slit; tail length up to 53% of carapace length in adult males ‘Shortnecked alpha’
- (b) Tail normally chelid: precloacal length greater than postcloacal length only in adult males; tail rounded in cross section, not laterally compressed; cloacal orifice round; maximum tail length always less than half carapace. 14
- 14(a) A well-defined head shield at all ages; dorsum of neck bearing many sharp tubercles; gular barbels always well-defined and longer than wide; rear edge of carapace may be denticulate at any age *Elseya latisternum* group
- (b) Distinguishable headshield only in the largest adults; neck usually smooth, low rounded tubercles at most; gular barbels absent, never longer than wide; rear edge of carapace never denticulate. *Emydura* (Pl. 3.10)