A NEW STEM TURTLE FROM THE MIDDLE JURASSIC OF THE ISLE OF SKYE, SCOTLAND, AND A REASSESSMENT OF BASAL TURTLE RELATIONSHIPS

BY

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DECLARATION

I, Jérémy Anquetin, confirm that the work presented in this dissertation is my own. Where information has been derived from other sources or from work done in collaboration, I confirm that this has been indicated in the text.

ABSTRACT

A recent phylogenetic analysis of turtle interrelationships suggests that the Middle Jurassic was a crucial time period for understanding the evolution of crown-group turtles. However, turtle material of this age is scarce worldwide. Here, a new stem turtle, *Eileanchelys waldmani*, from the Middle Jurassic (Bathonian) of the Isle of Skye, Scotland, is described and compared to other basal species. With cranial and postcranial remains of several individuals, this is the most comprehensive Middle Jurassic turtle material known to date. *Eileanchelys waldmani* documents an intermediate stage in the evolution of early turtles between the Early Jurassic *Kayentachelys aprix* and the crown-group. Whereas most stem turtles are interpreted as terrestrial forms, taphonomic evidence suggests that *E. waldmani* may have been aquatic (freshwater), indicating that basal turtles were ecologically more diverse than previously thought.

This new material provides the basis for a reassessment of other Middle Jurassic turtle remains from the UK, especially revisions of material from Kirtlington and Stonesfield (Oxfordshire). The material from Kirtlington is attributed to Paracryptodira and represents the earliest occurrence of this group. The name '*Protochelys blakii*', which had been proposed for the Stonesfield remains, is considered to be a *nomen dubium* as this material lacks diagnostic features. However, this material is remarkable as it consists of fossilised epidermal scales from the carapace.

A new phylogeny is proposed, resulting from a cladistic analysis of a revised and updated version of a previously published data set. Nineteen new species are included in order to achieve a more thorough representation of basal turtle taxa. *Heckerochelys romani* and *Condorchelys antiqua* are found to be more basal than *Eileanchelys waldmani*. Chengyuchelyids (Middle Jurassic of China) may be stem turtles more basal than *Kallokibotion bajazidi*. *Naomichelys speciosa* is closely related to meiolaniids and *Mongolochelys efremovi*, while *Siamochelys peninsularis* is nested within xinjiangchelyids.

TABLE OF CONTENTS

LIST OF ILLUSTRATIONS AND TABLES

Chapter 1: Introduction

Chapter 2: An introduction to turtle anatomy and systematics

Chapter 3: A new stem turtle from the Middle Jurassic of the Isle of Skye, Scotland

Chapter 4: A reassessment of Middle Jurassic turtles from the UK

Chapter 5: Phylogenetic relationships of basal turtles

Appendix 2: Reconstruction of the skull and carapace of *Eileanchelys waldmani*

INSTITUTIONAL ABBREVIATIONS

AMNH—American Museum of Natural History, New York, USA.

BP—Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, South Africa.

BSPG—Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany.

CCG—Chengdu University of Technology Museum, Chengdu, China.

FMNH—Field Museum of Natural History, Chicago, USA.

IVPP—Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China.

MB—Museum für Naturkunde, Humboldt Universität, Berlin, Germany.

MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA.

MNA—Museum of Northern Arizona, Flagstaff, Arizona, USA.

NHM—Natural History Museum, London, UK.

NMS—National Museums of Scotland, Edinburgh, UK.

OXFUM—Oxford University Museum of Natural History, Oxford, UK.

PIN—Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia.

PMU—Museum of Evolution, Palaeontology section, Uppsala University, Uppsala, Sweden.

SMNS—Staatliches Museum für Naturkunde, Stuttgart, Germany.

TMM—Texas Memorial Museum, Austin, Texas, USA.

UCPM—University of California Museum of Paleontology, Berkeley, California, USA.

YPM—Yale Peabody Museum, Yale University, New Haven, Connecticut, USA.

ZDM—Zigong Dinosaur Museum, Zigong, China.

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CHAPTER 1: INTRODUCTION

Amidst the great diversity of the extant animal kingdom, turtles are unique reptiles whose body, encased in a bony shell composed of a dorsal carapace and a ventral plastron, is universally recognised. Even among the far greater diversity of fossil animals, the unique anatomy of turtles stands out. These incredible shelled reptiles have endured since the Late Triassic, have an extensive fossil record and remain a diverse extant clade. However, the origin of the bizarre turtle *bauplan* remains a mystery (e.g., Rieppel, 2008). Due to the absence of temporal fenestration and an archaic appearance, turtles were long considered to be anatomically primitive and to represent an ancient lineage of 'anapsid' reptiles. Consequently, the origins of turtles were sought among Palaeozoic stem reptiles. However, the turtle skull and postcranial skeleton are in fact highly modified structures (Romer, 1956), rendering the search for their relatives among other amniotes difficult (e.g., Rieppel, 2008; see Chapter 5). The debate about the origins of turtles has not yet been settled and two main hypotheses are considered by palaeontologists: for some, the origins of turtles are to be found among the parareptiles either close to pareiasaurs or to procolophonids (Reisz & Laurin, 1991; Lee, 1993, 1995, 1996, 1997; Laurin & Reisz, 1995), while for others turtles are diapsid reptiles whose origins lie within lepidosauromorphs, often closely allied to the marine sauropterygians (Rieppel & deBraga, 1996; deBraga & Rieppel, 1997; Rieppel & Reisz, 1999; Müller, 2004; Hill, 2005). In contrast, the majority of recent molecular studies support archosaurian affinities for turtles (see Rieppel, 2008 for a review).

SYSTEMATICS AND RELATIONSHIPS OF BASAL TURTLES

Since the advent of cladistic methodology the systematics of turtles have been significantly revised. Early works focussed mainly on specific turtle groups (e.g., Gaffney, 1972, 1975b, 1977; Hutchison & Bramble, 1981; Crumly, 1982; Hirayama, 1985), but Gaffney (1975a) proposed a phylogeny of the higher categories of turtles. Building on this work, Gaffney & Meylan (1988) produced a phylogeny of turtles that comprised all extant species and some fossil taxa (Fig. 1.1A). Although slightly outdated, the latter study still represents a benchmark for workers who want to obtain a general overview of turtle relationships. According to Gaffney & Meylan (1988), *Proganochelys quenstedti* Baur 1887 from the Late Triassic of Germany is the most basal turtle. All remaining species (fossil or extant) were classified into two clades that are still represented today: the Pleurodira and the Cryptodira. These names refer to the mechanism of retraction of the neck within the shell: in a horizontal plane (or in a sideways fashion) for pleurodires and in a vertical plane for cryptodires. However, the neck retraction mechanism evolved independently within both

Figure 1.1—A comparison between previous phylogenetic hypotheses of turtle interrelationships. A, simplified phylogeny from Gaffney & Meylan (1988); B, cladogram of Gaffney *et al.* (1991); C, cladogram of Gaffney (1996); D, cladogram of Hirayama *et al.* (2000); E, cladogram of Dryden (1988); F, cladogram of Rougier *et al.* (1995).

clades during the Cretaceous (Gaffney, 1975a). The dichotomy between pleurodires and cryptodires was based on two main character complexes: the jaw closure mechanism (see Chapter 2) and the bracing of the braincase by palatoquadrate elements. In pleurodires, the trochlea of the main adductor muscle of the lower jaw is on the pterygoid and the braincase is braced by the quadrate, whereas in cryptodires the trochlea of the main adductor muscle is on the quadrate and the braincase is braced by the pterygoid (Gaffney, 1975a; Gaffney & Meylan, 1988). Within this context, *Proterochersis robusta* Fraas 1913, also from the Late Triassic of Germany, and *Kayentachelys aprix* Gaffney *et al.* 1987, from the Early Jurassic of North America, were considered to be the most basal pleurodire and cryptodire, respectively (Fig. 1.1A). In the mid 1990s, two new stem turtles were described: *Australochelys africanus* Gaffney & Kitching 1994, from the Early Jurassic upper Elliot Formation of South Africa, and *Palaeochersis talampayensis* Rougier *et al.* 1995, from the Late Triassic of Argentina. These species were interpreted as more derived than *Proganochelys quenstedti* but basal to the pleurodire-cryptodire dichotomy (Gaffney & Kitching, 1994; Rougier *et al.*, 1995).

The aforementioned pattern of relationships has been consistently recovered by most subsequent computational cladistic analyses (Gaffney *et al.*, 1991; Gaffney, 1996; Shaffer *et al.*, 1997; Gaffney *et al.*, 1998; Brinkman & Wu, 1999; Hirayama *et al.*, 2000; Gaffney *et al.*, 2007; Sterli *et al.*, 2007; Fig. 1.1B-D). However, some workers have also recovered a different pattern of relationships for basal turtles. The cladistic analysis of Dryden (1988) resulted in a phylogeny that departed significantly from those of Gaffney & Meylan (1988) and Gaffney *et al.* (1991). According to Dryden (1988), *Kayentachelys aprix*, *Meiolania platyceps* Owen 1886, Pleurosternidae, Baenidae and Plesiochelyidae are all more basal than the pleurodire-cryptodire dichotomy (Fig. 1.1E). However, with the exception of Gauthier *et al.* (1989) and Joyce (2004, 2007), this work went mostly unnoticed as it was never formally published. Rougier *et al.* (1995) proposed a phylogenetic analysis of the relationships among basal turtles and found *Proterochersis robusta* to be a stem turtle rather than a basal pleurodire (Fig. 1.1F).

Joyce (2004, 2007) was the first to propose a broad-scale phylogenetic analysis of turtles in which all terminal taxa were species rather than broader taxonomic categories. This analysis was constructed as a partial consensus of all previous works and the majority of characters were taken from previous analyses. This analysis included considerably more fossil taxa (i.e., 45 species) and more characters (i.e., 136) than previous studies. The results of Joyce (2007) partly confirmed the studies of Dryden (1988) and Rougier *et al.* (1995) in revealing an extensive stem for the turtle crown-group. *Proterochersis robusta*, *Kayentachelys aprix*, *Meiolania platyceps*, *Mongolochelys efremovi* Khosatsky 1997 and *Kallokibotion bajazidi* Nopcsa 1923 were considered to be stem turtles (Fig. 1.2). The age of the turtle crown-group (i.e., the dichotomy between pleurodires and cryptodires) was consequently adjusted from the Late Triassic to the Late Jurassic (Joyce, 2007).

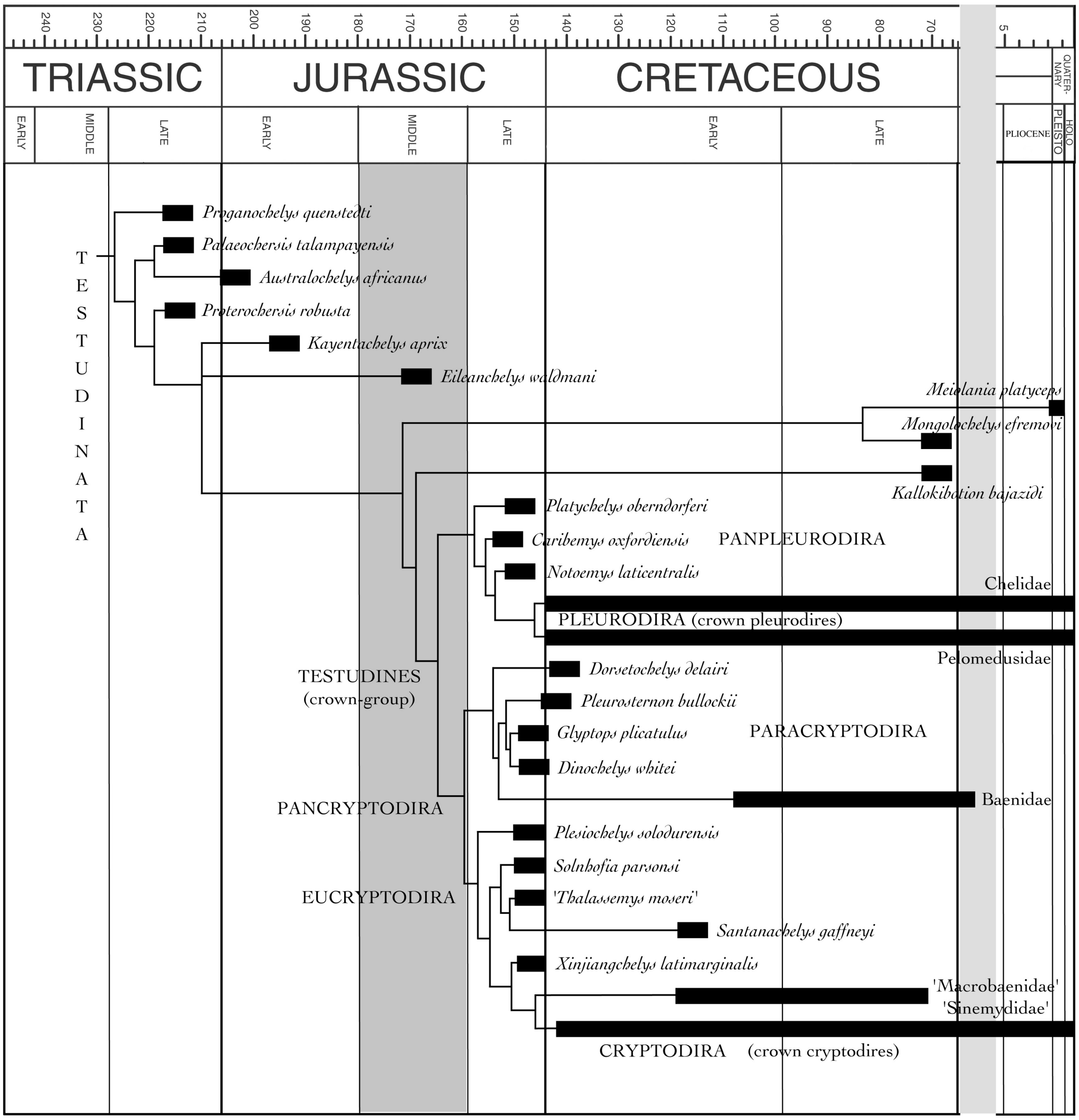

Figure 1.2—Phylogenetic relationships of basal turtles according to Joyce (2007). Placement of *Eileanchelys waldmani* according to Anquetin *et al.* (2009). The heavy grey represents the Middle Jurassic. The light grey indicates a temporal gap in the time scale between the end of the Cretaceous and the Pliocene.

EARLY EVOLUTIONARY HISTORY OF TURTLES

Within the context of Joyce's (2007) cladogram, it appears that all known species from the Late Triassic and Early Jurassic are stem turtles and that crown-group turtles diverged no later than the Late Jurassic. However, there are some indications that crown-group turtles had already diverged during the Middle Jurassic (Gillham, 1994; Nessov, 1995; Tong *et al.*, 2002; Matzke *et al.*, 2005; Danilov & Parham, 2008; Scheyer & Anquetin, 2008; see below and Chapters 4 and 5). This suggests that the Middle Jurassic is a crucial period for understanding the early evolutionary history of turtles. However, turtles from the Middle Jurassic are relatively rare worldwide (Fig. 1.2). When the present study started in 2005, the vast majority of Middle Jurassic turtle remains came from Asia. Sichuan Province in China has yielded several shells that have been attributed to four species: *Chengyuchelys baenoides* Young & Chow 1953, *C. zigongensis* Ye 1982, *'C.' dashanpuensis*

Fang 1987, and *Sichuanchelys chowi* Ye & Pi 1997. *Xinjiangchelys tianshanensis* Nessov 1995 was found in the Callovian strata of the Fergana Depression in Kyrgyzstan. The Junggar Basin of Xinjiang Province in China has also yielded a Callovian species of the genus *Xinjiangchelys*: *X. chowi* Matzke *et al.* 2005. Finally, *Siamochelys peninsularis* Tong *et al.* 2002 was recently described from Middle Jurassic deposits in Thailand. All these species are known exclusively from shell material and have been little studied in a phylogenetic context. Matzke *et al.* (2004) included *Xinjiangchelys tianshanensis* in an analysis of the interrelationships of xinjiangchelyids, whereas Danilov & Parham (2008) included the genus *Chengyuchelys* (based on *C. baenoides* and *C. zigongensis*) in a modified version of the analysis of Joyce (2007) and found it to be the sister group of *Xinjiangchelys latimarginalis* (Young & Chow 1953). Xinjiangchelyids, and consequently also chengyuchelyids, are generally considered to be basal eucryptodire turtles. The relationships of *Sichuanchelys chowi*, *'Chengyuchelys' dashanpuensis* and *Siamochelys peninsularis* have never been investigated.

Apart from Asia, the only other place where Middle Jurassic chelonian remains worthy of interest were found was the United Kingdom. The UK is renowned for its Middle Jurassic deposits that yield a diverse terrestrial microvertebrate assemblage (Evans & Milner, 1994; Benton & Spencer, 1995). The main localities that yielded turtle remains are Kirtlington and Stonesfield in Oxfordshire and Cladach a'Ghlinne on the Isle of Skye, Scotland. These remains are relatively fragmentary and had not been recently assessed, with exception of the Kirtlington material (Gillham, 1994). In 2004, Susan E. Evans (University College London), Paul M. Barrett (the Natural History Museum) and Jason Hilton (University of Birmingham) led fieldwork at the Cladach a'Ghlinne locality and the crew recovered several articulated specimens of a new stem turtle, *Eileanchelys waldmani* Anquetin *et al.* 2009, the study of which constitutes the core of this dissertation. In the meantime, two new stem turtles have been described from Middle Jurassic deposits in Russia and Argentina, respectively: *Heckerochelys romani* Sukhanov 2006 and *Condorchelys antiqua* Sterli 2008. Finally, an exciting new development in the study of early turtles occurred with the description of *Odontochelys semitestacea* Li *et al.* 2008, a Carnian turtle that has teeth on the upper and lower jaws and in which the carapace appears to be in an intermediate stage of development.

AIMS OF THE THESIS

The present dissertation has three main objectives:

- To provide a thorough description of the material from the Isle of Skye, to compare this new material with other taxa and to interpret this new species in the context of the early evolution of turtles.

- To reassess the Middle Jurassic turtle material from the UK, especially from the localities of Kirtlington and Stonesfield, Oxfordshire.

- To reassess the interrelationships of basal turtles by building on the recent phylogenetic analysis of Joyce (2007).

This work begins with an introductory chapter on the anatomy and systematics of turtles (Chapter 2). The unique turtle shell has led to the development of a specific terminology for the various bony plates and epidermal scales that comprise it, and this is summarised briefly herein. Similarly, the terminology of cranial structures has been homogenised in order to ease comparison and part of this terminology differs from that applied to other reptiles. These turtle-specific nomenclatures are used throughout this thesis. Phylogenetic taxonomy (i.e., naming clades rather than ranked categories) has only been applied to turtles recently (Joyce *et al.*, 2004). This work has greatly facilitated the discussion of turtle interrelationships, and comparisons between radically different patterns of relationship; the new taxonomy is followed herein and described in brief in Chapter 2. Descriptions and comparisons of the turtle material from the Isle of Skye, Scotland are presented in Chapter 3. The geological context and the preparation methods used on the material are also described. A thorough description of the material is given, the material is recognised as a new genus and species, and this new species is compared to other relevant basal turtles. The discussion that follows considers several aspects of the anatomy of this new turtle in the context of the clade's early history. Chapter 4 presents a review of the Middle Jurassic turtle material from the UK, including thorough reassessments of the specimens from Kirtlington and Stonesfield, the latter representing the oldest British turtle and a unique example of fossil preservation. A phylogenetic analysis derived from that of Joyce (2007) is proposed in Chapter 5. It focuses on the relationships of basal turtles. The coding of several characters is revised and some additional characters from other studies or personal observations are scored. Nineteen basal species are added to the taxon sample of Joyce (2007) and this is the first time that some of these species have been included in a phylogenetic analysis.

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CHAPTER 2: AN INTRODUCTION TO TURTLE ANATOMY AND SYSTEMATICS

The turtle shell is unique among amniotes. It consists of a mosaic of bony plates and epidermal scales that are organised following a precise geometric pattern. The description of this mosaic requires a specific nomenclature for these plates and scales. The turtle skull is also highly modified compared with that of other amniotes (Romer, 1956). Structures like blood and nerve foramina and canals, as well as the various processes of the skull, are of great use for turtle systematics. The nomenclature of these structures has been standardised in order to ease comparison between turtles, but this terminology often departs from that used in other reptiles. These turtle-specific nomenclatures are briefly detailed below and are used throughout this thesis.

Phylogenetic nomenclature has been applied to turtles recently (Joyce *et al.*, 2004). In a context where phylogenetic analysis has become a universal tool for systematics, this represents a major improvement for the discussion of turtle relationships and the comparison of different patterns of relationship. This nomenclature is briefly discussed and described below.

THE TURTLE SHELL

The turtle shell is a structure that has no equivalent among other tetrapods. It encloses not only the viscera but also accommodates the pectoral girdle, as well as the head and limbs in most cases. The apparent uniformity of the turtle body plan is in some respects illusory and according to Zangerl (1969: 312):

> "there is greater variety among turtles than, for example, among ichthyosaurs or crocodiles."

The turtle shell consists of two parts: a dorsal portion termed the carapace and a ventral part termed the plastron (Zangerl, 1969). Carapace and plastron are usually attached together on each flank of the animal, between the forelimbs and the hindlimbs. This shell area is called the bridge and can be ossified or ligamentous. The turtle shell is made of two distinct types of tissue: internally a layer of dermal bone and externally an epidermal keratinous layer. Both layers are divided into a mosaic of geometric elements (Zangerl, 1969). Of course, in fossils only the bony layer is preserved, except on very rare occasions (see Chapter 4), but the outlines of the keratinous scales are impressed as deep sulci on the dermal bone surface.

The following description of the turtle shell follows the standardised nomenclature established by Zangerl (1969).

The carapace

The carapace is usually composed of 50 dermal bones (Fig. 2.1A). There is a median row of unpaired elements (from anterior to posterior): one nuchal, eight neurals, two suprapygals and one pygal. Each neural is fused to the neural arch of the underlying dorsal vertebra. Lateral to the neurals are the costal bones. Generally, there are eight costals, each fused to the underlying rib. From the nuchal anteriorly to the pygal posteriorly, the perimeter of the carapace is usually composed of eleven rectangular elements, the peripherals. In the bridge area, where peripherals connect the carapace with the plastron, these elements are V-shaped in cross section, whereas other peripherals are wedge-shaped (Zangerl, 1969). Both costals and peripherals are paired elements.

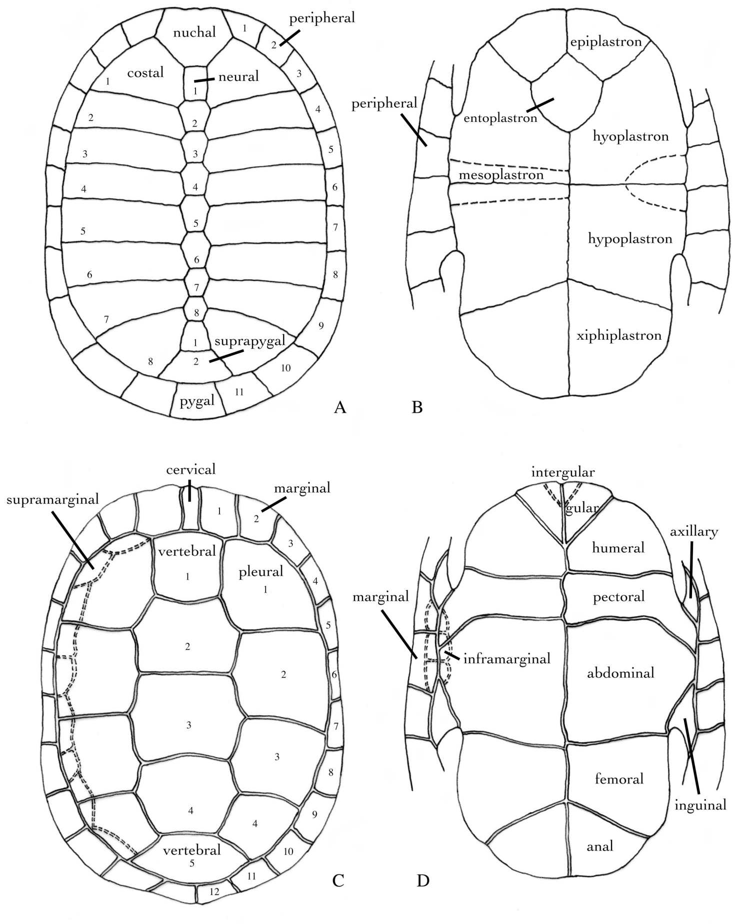

Figure 2.1—Nomenclature of the bony plates and epidermal scales of the turtle shell following Zangerl (1969). A, carapace bony elements; B, plastron bony elements; C, carapace scales; D, plastron scales. Redrawn from Zangerl (1969).

This common pattern is found in most turtles, but there are exceptions (Zangerl, 1969). For example the number of pairs of peripherals is reduced from eleven to ten in kinosternids, whereas it is increased from eleven to twelve in some cheloniids. This can also occur with neurals or costals. The number of suprapygals can also be reduced. A more complex shell (carapace + plastron) anatomy is found in some groups and consists of the acquisition of a secondary bony armour

(Zangerl, 1969: 328), and generally of the reduction of the primary bony shell. This secondary bony armour is designated as epithecal, in contrast to the primary or thecal bony shell. Epithecal ossifications occur:

> "in the form of a few isolated ossicles beneath the keel points of the vertebral shields in the marine toxochelyids *Ctenochelys* and *Prionochelys* (Zangerl, 1953), or as a pavement mosaic consisting of large numbers of polygonal platelets (Dermochelyidae), or finally in the form of a pattern that simulates the thecal shell mosaic (Trionychidae)." (Zangerl, 1969: 328)

The basalmost taxa also diverge from the common pattern of the carapacial bony mosaic found in most turtles. *Proganochelys quenstedti* Baur 1887 and *Proterochersis robusta* Fraas 1913, two very basal stem turtles from the Late Triassic (Norian) of Germany, have more than eleven pairs of peripherals (Joyce, 2007: 31). It appears that several stem turtles, including *Proganochelys quenstedti*, *Kayentachelys aprix* Gaffney *et al.* 1987 and *Condorchelys antiqua* Sterli 2008, have nine costals. There are also indications that other stem taxa might have nine neurals instead of eight (Datta *et al.*, 2000; Sukhanov, 2006; Anquetin *et al.*, 2009), although this still needs to be confirmed as the difference between a neural and a suprapygal is determined by the presence or absence of an underlying vertebra, respectively.

The carapacial keratinous scales, or scutes, present a similar organisation to the underlying dermal bones (Fig. 2.1C). There is a median row of unpaired elements (from anterior to posterior): one cervical scale and five vertebral scales. Laterally to the vertebrals are found four pairs of pleural scales. Finally, the carapace is usually bordered by twelve pairs of marginal scales. This general pattern is markedly more variable than that of carapacial dermal bones. In a number of derived groups the number of scales is lower and scales are even lost in soft-shelled turtles (Trionychidae) and in *Dermochelys coriacea* (Vandelli 1761), the leatherback turtle. Additional carapacial scales are present between the marginals and pleurals in some stem turtles (e.g., *Proganochelys quenstedti* and *Proterochersis robusta*), they are called the supramarginals. These supramarginals are also found as a secondary acquisition in the Late Jurassic panpleurodire *Platychelys oberndorferi* Wagner 1853 (but see character 105 in Chapter 5) and the extant *Macrochelys temminckii* (Troost 1835). *Proganochelys quenstedti* and *Proterochersis robusta* have more than twelve pairs of marginal scales, and *P. quenstedti* is also remarkable in having four vertebral scales rather than five.

The plastron

The plastron is usually composed of nine dermal bones including four paired elements (from front to back, the epiplastra, the hyoplastra, the hypoplastra and the xiphiplastra) and one unpaired plate (the entoplastron; Fig. 2.1B). The latter is situated medially between the epiplastra anteriorly and the hyoplastra posteriorly. Epiplastra and the entoplastron are homologous to the clavicles and interclavicle of other reptiles, respectively, whereas the other plastral plates appear to be derived from the gastralia of other reptiles (Zangerl, 1939; Gilbert *et al.*, 2007). The plastron is attached to the carapace via the hyoplastron and hypoplastron, which fuse to the peripherals in cases where the bridge is osseous. Both hyoplastron and hypoplastron usually also form a buttress in order to strengthen the shell: the axillary buttress of the hyoplastron is generally sutured to the peripherals and first costal, whereas the inguinal buttress of the hypoplastron is generally sutured to the peripherals and fifth costal, sometimes also the sixth (Fig. 2.3). An additional pair of dermal bones, the mesoplastra, is found between the hyoplastra and hypoplastra in many turtles. All basal turtles have one pair of mesoplastra that fully separate the hyoplastra from the hypoplastra (Joyce, 2007: 39). Within crown-group turtles (Testudines), a pair of mesoplastra is also known in many panpleurodires, but in that case mesoplastra do not meet one another medially (i.e., they allow a partial contact between hyoplastron and hypoplastron), and in some stem cryptodires. Mesoplastra are absent in all crown-group cryptodires (Cryptodira) (ibid.).

With the exception of the epithecal ossifications of Trionychidae (see above), divergence from the aforementioned pattern is relatively rare. The entoplastron is lost in kinosternids, whereas *Proterochersis robusta* and *Odontochelys semitestacea* Li *et al.* 2008 are remarkable in having two pairs of mesoplastra.

The plastral keratinous scales are organised into six paired elements (anterior to posterior): gular, humeral, pectoral, abdominal, femoral and anal scales (Fig. 2.1D). Additionally, turtles may have a pair of axillary scales and a pair of inguinal scales respectively in the anterior and posterior region of the bridge. Between the axillary and inguinal scales often exists a row of inframarginal scales. In many taxa, including stem turtles, panpleurodires and basal pancryptodires, there is an additional pair of scales along the anterior plastral rim (Joyce, 2007: 40). These scales are usually situated posterolateral to the gulars and are called extragulars, following Hutchison & Bramble (1981). In some taxa, including the kinosternids and apparently some cheloniids, a neomorphic pair of scales, the intergulars (plastral scale set 8 of Hutchison & Bramble, 1981), is present anteriorly between the gulars. Plastral scales are lost in trionychids and in *Dermochelys coriacea*.

THE TURTLE POSTCRANIAL ANATOMY

The evolution of the peculiar turtle shell had a major impact on the postcranial skeleton of these reptiles. The most important modifications occurred in the girdles and dorsal axial skeleton.

Pectoral girdle

The pectoral girdle of turtles is a triradiate structure that is formed only by the endoskeletal elements (i.e., scapula and coracoid), whereas the dermal elements (i.e., clavicle, interclavicle, and possibly cleithrum) are parts of the plastron (see above). Morphologically, the pectoral girdle, and especially the scapula, lies inside the rib cage, which is a unique configuration among amniotes (e.g., Rieppel, 2008; Fig. 2.2A). The scapula forms a usually well developed dorsal process that is connected to the carapace by ligaments. The scapula also develops an anteroventral acromial process (Fig. 2.2D,E). The third process of the pectoral girdle is formed by the coracoid, which extends posteroventrally from the glenoid. Both the acromial process of the scapula and the coracoid are connected to the plastron by ligaments distally. Usually, both processes of the scapula are rod-like, whereas the coracoid is dorsoventrally flattened and slightly expanded distally. The glenoid cavity is formed mainly by the scapula. In basalmost turtles (e.g., *Proganochelys quenstedti*; Fig. 2.2B,C), the morphology of the scapulocoracoid differs slightly from the above description. The acromial process is considerably shorter and a ridge (the acromial ridge) extends along its ventral suface from the glenoid to the distal end of the acromion. The presence of this ridge gives a triradiate section to the acromion. In basalmost turtles, the coracoid is also shortened and its proximal base is broader than in more derived form, resulting in an extensive suture with the acromial process medial to the glenoid (Fig. 2.2C). Along this suture, a coracoid foramen is usually present.

Many early turtles (e.g., *Proganochelys quenstedti*, *Odontochelys semitestacea*, and *Kayentachelys aprix*) have paired dorsal processes on the epiplastra (i.e., the clavicles). These processes were originally interpreted as cleithra in *Proganochelys quenstedti* (Jaekel, 1915), but were later reinterpreted as mere processes of the epiplastra and renamed epiplastral processes by Gaffney (1990). However, a recent reassessment of *Kayentachelys aprix* material provides convincing evidences that these structures are ontogenetically different from the epiplastra and are best interpreted as cleithra (Joyce *et al.*, 2006). These conclusions are followed herein (see character 162 in Chapter 5 for more details), although the identity of these processes is only important when the relationships of turtles within other amniotes are considered, which is not the case in this dissertation.

Pelvic girdle

In contrast to the pectoral girdle, the pelvis of turtles is similar to that of other reptiles (Romer, 1956) and consists of three endoskeletal elements: ilium, pubis and ischium (Fig. 2.2H,I). The acetabulum is formed by these three elements. The ilim is usually a slender bone that extends posterodorsally from the acetabulum. Its distal extremity is generally slightly dilated for the attachment to the sacral ribs. The pubis extends anteroventromedially from the acetabulum and develops a usually strong lateral process. The ischium extends mainly ventromedially from the acetabulum and often possesses a moderately developed lateral process. The lateral processes of the pubis and ischium usually rest upon the visceral surface of the plastron (Romer, 1956). In all panpleurodires, but also in *Palaeochersis talampayensis* Rougier *et al.* 1995 (Sterli *et al.*, 2007) and maybe in *Proterochersis robusta*, the three elements of the pelvis are sutured to the shell: the ilium is

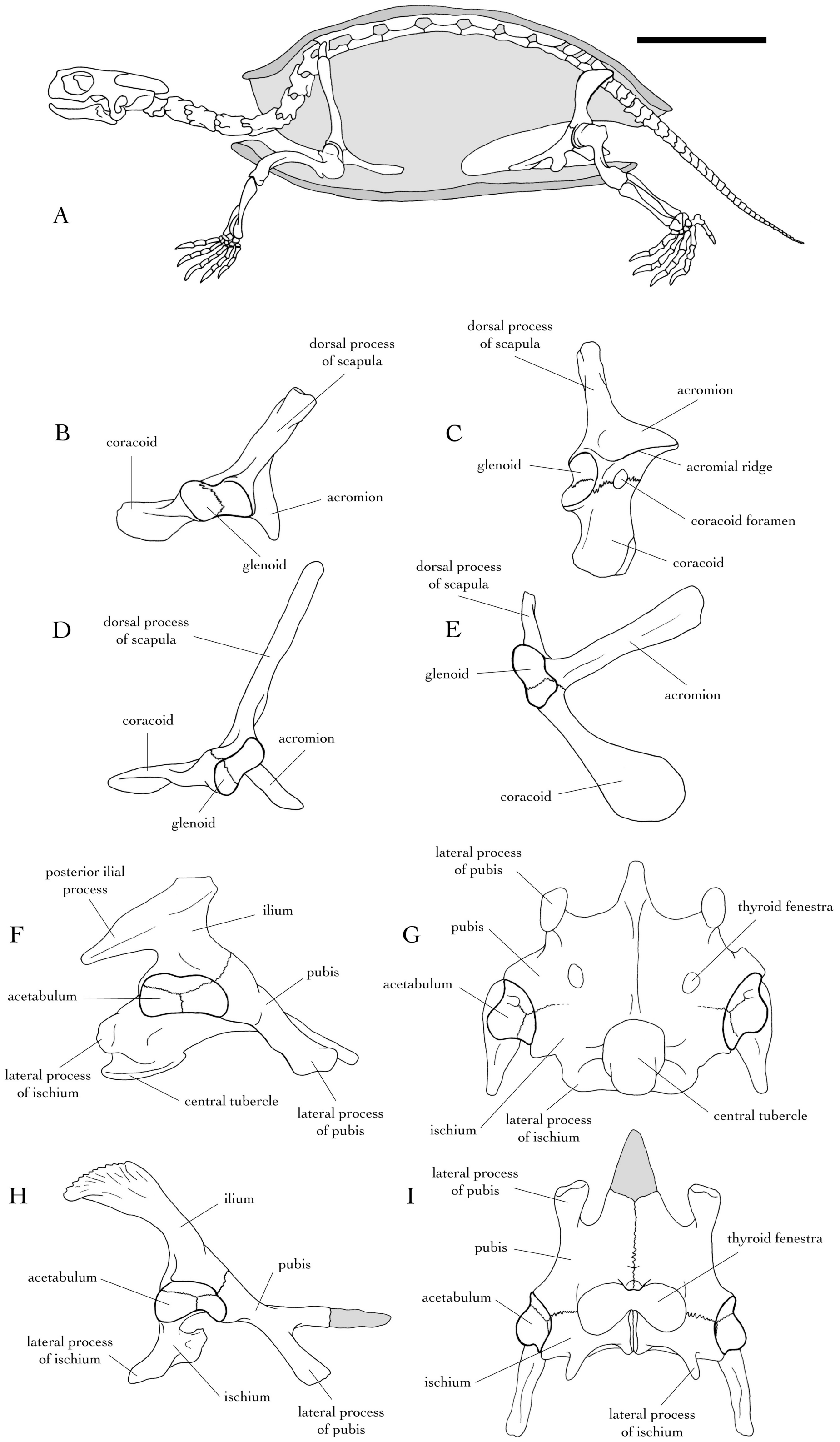

Figure 2.2—Turtle pectoral and pelvic girdles. A, parasagittal section showing the relations between the girdles and other skeletal elements in *Emys orbicularis*, the European pond turtle, scale: 50 mm; B, C, lateral and ventral view of the right scapulocoracoid of *Proganochelys quenstedti*; D, E, lateral and ventral view of the right scapulocoracoid of *Macrochelys temminckii*, the alligator snapping turtle; F, G, lateral and ventral view of the pelvis of *P. quenstedti*; H, I, lateral and ventral view of the pelvis of *M. temminckii*. Redrawn from Gaffney (1990).

distally sutured to the carapace, whereas the pubis and ischium are sutured to the plastron via their lateral processes. On each side, the pubis and ischium delimit a generally large thyroid fenestra, which may only be separated from the other fenestra by cartilage (Fig. 2.2I). In the most basal turtles (e.g., *Proganochelys quenstedti*; Fig. 2.2F,G), the pelvis is stouter and more heavily ossified than in more derived forms. The iliac neck is significantly shorter and the posterior iliac process (the distal dilatation of the ilium) is more developed. In *Proganochelys quenstedti* and *Proterochersis robusta*, the ischium contact the plastron by the way of a large central tubercle rather than via the lateral ischial processes (see character 172 in Chapter 5 for more details). *Odontochelys semitestacea*, *Proganochelys quenstedti* and *Palaeochersis talampayensis* are unique among turtles in having hypoischia: i.e., single or paired postpelvic ossifications that articulate with the ischia anteriorly.

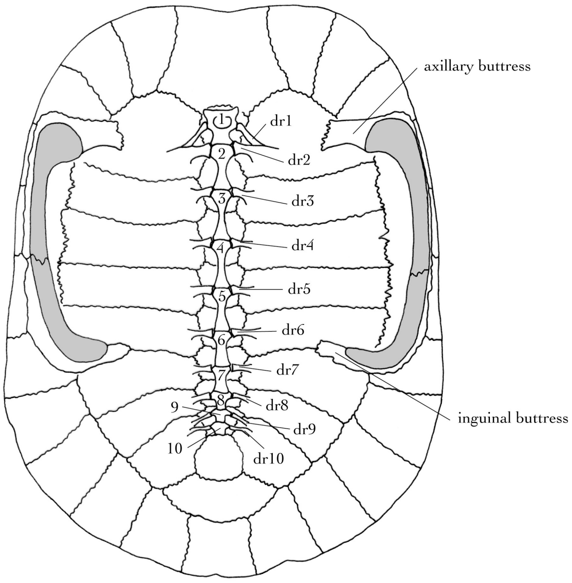

Figure 2.3—Ventral view of the carapace of *Geoclemys hamiltonii*, the spotted pond turtle, illustrating the relations between the carapace and the dorsal vertebrae and ribs. Numbers correspond to dorsal vertebrae. Redrawn from Joyce (2007). Abbreviations: dr, dorsal rib.

Dorsal axial skeleton

All turtles have 18 presacral vertebrae: 8 cervicals and 10 dorsals (Romer, 1956; Hoffstetter & Gasc, 1969; Fig. 2.3). The neural arches of dorsal vertebrae 2 to 9 are fused to the overlying neural plates of the bony carapace (see above). The first dorsal vertebra lies under the nuchal plate, but it is not fused to it. Similarly, the tenth dorsal vertebra usually lies under the first suprapygal (or last neural) without being fused to it (Romer, 1956). The centra of dorsal vertebrae 2 to 9 are cylindrical and constricted in the middle. The forward migration by half a segment of neural arches in the dorsal region of the vertebral column results in an intercentral position of at least the anterior two-thirds of neural arches and dorsal ribs (Hoffstetter & Gasc, 1969; Rieppel & Reisz, 1999: 14; and references therein). In other words, most dorsal ribs articulate with two successive centra (Fig. 2.3). This is true of all turtles, with the exception of *Odontochelys semitestacea* (Li *et al.*, 2008; see character 156 in Chapter 5). Dorsal ribs 2 to 9 are well developed and fused to the overlying costal plates. Dorsal ribs 1 and 10 are usually reduced in extant turtles, but they were as long as the other ribs in early turtles (see characters 153 and 155 in Chapter 5 for more details).

The questions of how the ribs and neural arches of dorsal vertebrae were fused to the carapace and how the pectoral girdle came to lie inside the ribcage go far beyond the subject of this dissertation. Recent developmental studies have shown that during early stages of development a thickening of the dermis on the back of the turtle embryo (the carapacial disk) was the precursor to the later carapace (e.g., Gilbert *et al.*, 2001; Cebra-Thomas *et al.*, 2005; Kuraku *et al.*, 2005; Nagashima *et al.*, 2007). In the margin of the carapacial disk, which is termed the carapacial ridge, the differentiation of epithelial cells is thought to organise carapace development in a similar fashion to tetrapod limb development (see Rieppel, 2001, 2009, for a review). It was proposed that the carapacial ridge was responsible for the deflection of rib growth within the carapacial disk, so that the ribs never penetrate the body wall and eventually include the scapula inside the ribcage (Gilbert *et al.*, 2001; Cebra-Thomas *et al.*, 2005; Kuraku *et al.*, 2005). Nagashima *et al.* (2009) partly confirmed this hypothesis and showed that a folding of the dorsal part of the lateral body wall along the carapacial ridge restricts rib growth to the horizontal plane but maintains the scapula morphologically outside the ribcage with respect to the associated musculature (see also Rieppel, 2009). These recent results show that moderate changes in developmental pathways governing rib growth explain the apparent position of the scapula 'inside' the ribcage (Nagashima *et al.*, 2009).

THE TURTLE SKULL

The turtle skull has long been considered to have a primitive morphology because of its anapsid condition. However, this is untrue and the turtle skull should be regarded as a highly modified structure (Romer, 1956: 94; see also Chapter 1). This is not only due to the changes in external shape, but also to changes in the bone arrangement itself, as well as to the formation of novel structures. The main evolutionary trends within the turtle skull are: a reduction of the number of cranial and mandibular bones (e.g., the lacrimal, nasal, supratemporal and splenial are lost in most species; Fig. 2.4A); the fusion of the basipterygoid articulation and the closing of the cranio-quadrate space (Fig. 2.4B); the development of a complex middle ear system (see below); and the formation of a trochlear mechanism for the redirection of the lower jaw musculature (see below). These trends occurred early in the evolutionary history of turtles.

Perhaps the most striking feature of the turtle skull is the absence of marginal teeth and the development of a triturating surface on the upper and lower jaw that bears a horny beak (or

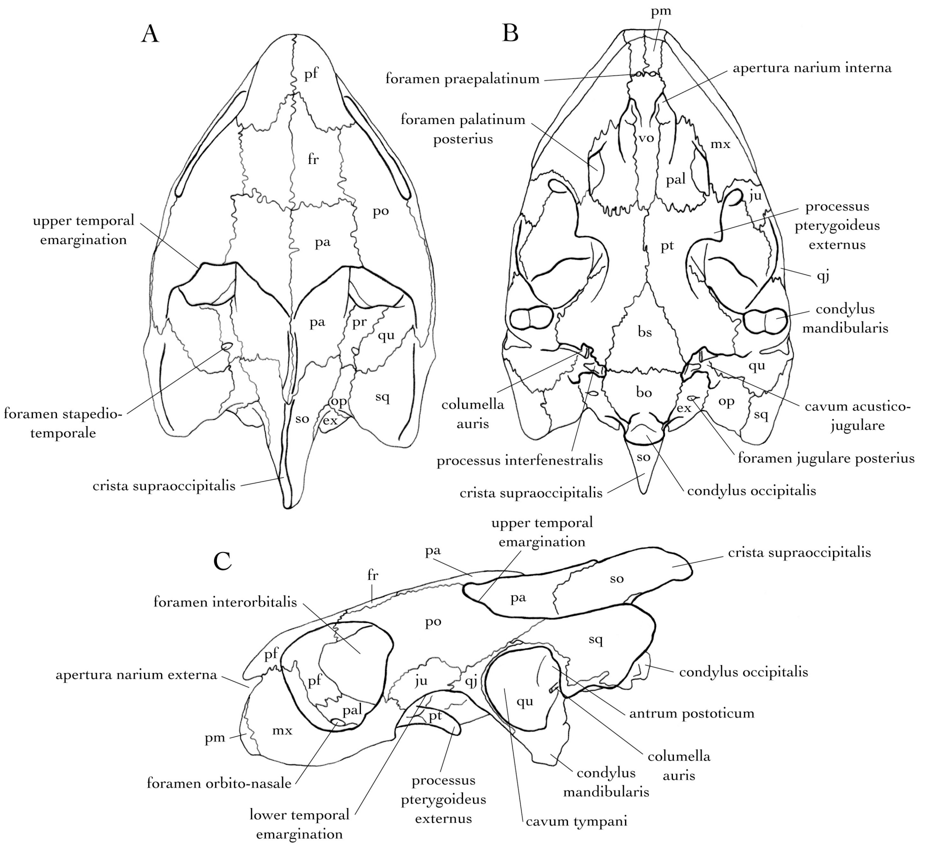

Figure 2.4—Skull of *Emys orbicularis*, the European pond turtle. A, dorsal; B, ventral; C, left. Length of the skull: 35 mm. Modified from Gaffney (1979). Abbreviations: bo, basioccipital; bs, basisphenoid; ex, exoccipital; fr, frontal; ju, jugal; mx, maxilla; op, opisthotic; pa, parietal; pal, palatine; pf, prefrontal; pm, premaxilla; po, postorbital; pr, prootic; pt, pterygoid; qj, quadratojugal; qu, quadrate; so, supraoccipital; sq, squamosal; vo, vomer.

rhamphotheca). The middle ear of turtle is highly modified compared to the condition in other reptiles. The quadrate surrounds the columella auris (i.e., the stapes) and separates the middle ear into two parts. The lateral part consists of a vast kidney-shaped cavity that is termed the cavum tympani (Fig. 2.4C). This cavum tympani is clearly visible on the lateral surface of the turtle skull and the tympanic membrane is stretched over it. In the posterodorsal part of the cavum tympani a large cavity, the antrum postoticum, is formed by the quadrate and squamosal. The medial part of the middle ear consists of a large cavity that is termed the cavum acustico-jugulare (Fig. 2.4B). The enlargement of the otic chamber in turtles led to the development of a trochlear system for the redirection of the lower jaw adductor musculature (Gaffney, 1975). Two conditions are known among extant turtles: in pleurodires the trochlea is formed on a greatly extended lateral process of the pterygoid (the processus trochlearis pterygoidei; Fig. 2.5B), whereas in cryptodires the trochlea is formed on the anterodorsal part of the otic chamber (Fig. 2.5A). In extant cryptodires, the quadrate and/or prootic are often thickened and sometimes bear a process (the processus trochlearis oticum) for the redirection of the lower jaw adductor muscle. Gaffney (1975) concluded that each of these jaw closure mechanisms was derived independently from the primitive condition found in *Proganochelys quenstedti* and hypothesised these mechanisms to be synapomorphies of pleurodires and cryptodires, respectively. In contrast, recent studies suggest that a jaw closure mechanism equivalent to that of cryptodires was probably ancestral to crown-group turtles (Joyce, 2007). Another example of the originality of the turtle skull is a descending process of the parietal, the processus inferior parietalis, which contacts palatoquadrate elements and forms an anterior extension of the braincase wall. In order to standardise the terminology associated with this derived morphology and the complex network of canals and foramina that traverses the turtle skull, Gaffney (1972, 1979) has proposed a glossary that is followed by the majority of turtle workers. This glossary is reproduced in Appendix 1 for the convenience of the reader.

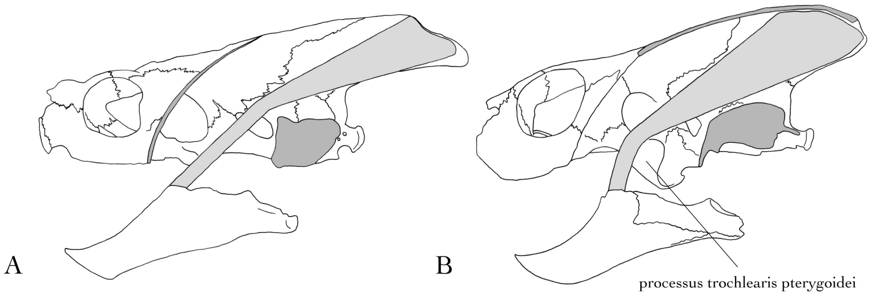

Figure 2.5—Jaw closure mechanism in crown-group turtles. A, the cryptodire *Chelydra serpentina*, the common snapping turtle, in which the main adductor musculature (light grey) is redirected by the otic chamber (dark grey); B, the pleurodire *Elseya dentata*, the northern snapping turtle, in which the jaw musculature is redirected by the processus trochlearis pterygoidei. Redrawn from Joyce (2007).

PHYLOGENETIC NOMENCLATURE OF TURTLES

Phylogenetic nomenclature names clades rather than ranked categories. In other words, names are applied to assemblages of taxa on the basis of common ancestry rather than to categories defined by an ensemble of morphological features that may correspond to synapomorphies or synplesiomorphies (i.e., by diagnosis). The advantages of phylogenetic nomenclature over the traditional ranked system include explicitness and stability: a phylogenetically defined clade name is independent from the diagnosis of the group and consequently does not depend on the conception each systematist may have of its content (e.g., Brochu & Sumrall, 2001; Lee & Skinner, 2007). Phylogenetic nomenclature is not necessarily synonymous with the PhyloCode. Although the PhyloCode (2007) is the most detailed proposal to date, it is only one of several possible sets of rules available to govern phylogenetic nomenclature and various other methodologies have been proposed (e.g., Sereno, 2005). The distinction between phylogenetic nomeclature (i.e., the fact of naming clades) and the PhyloCode (i.e., a set of governing rules) is important to make. The principles of phylogenetic nomenclature are accepted by many phylogeneticists and represent an advance over the use of the ranked Linnean system (e.g., Lee & Skinner, 2007). However, the absence of consensus in the initial definition of clade names as proposed by the PhyloCode has been criticised by several workers (e.g., Sereno, 2005).

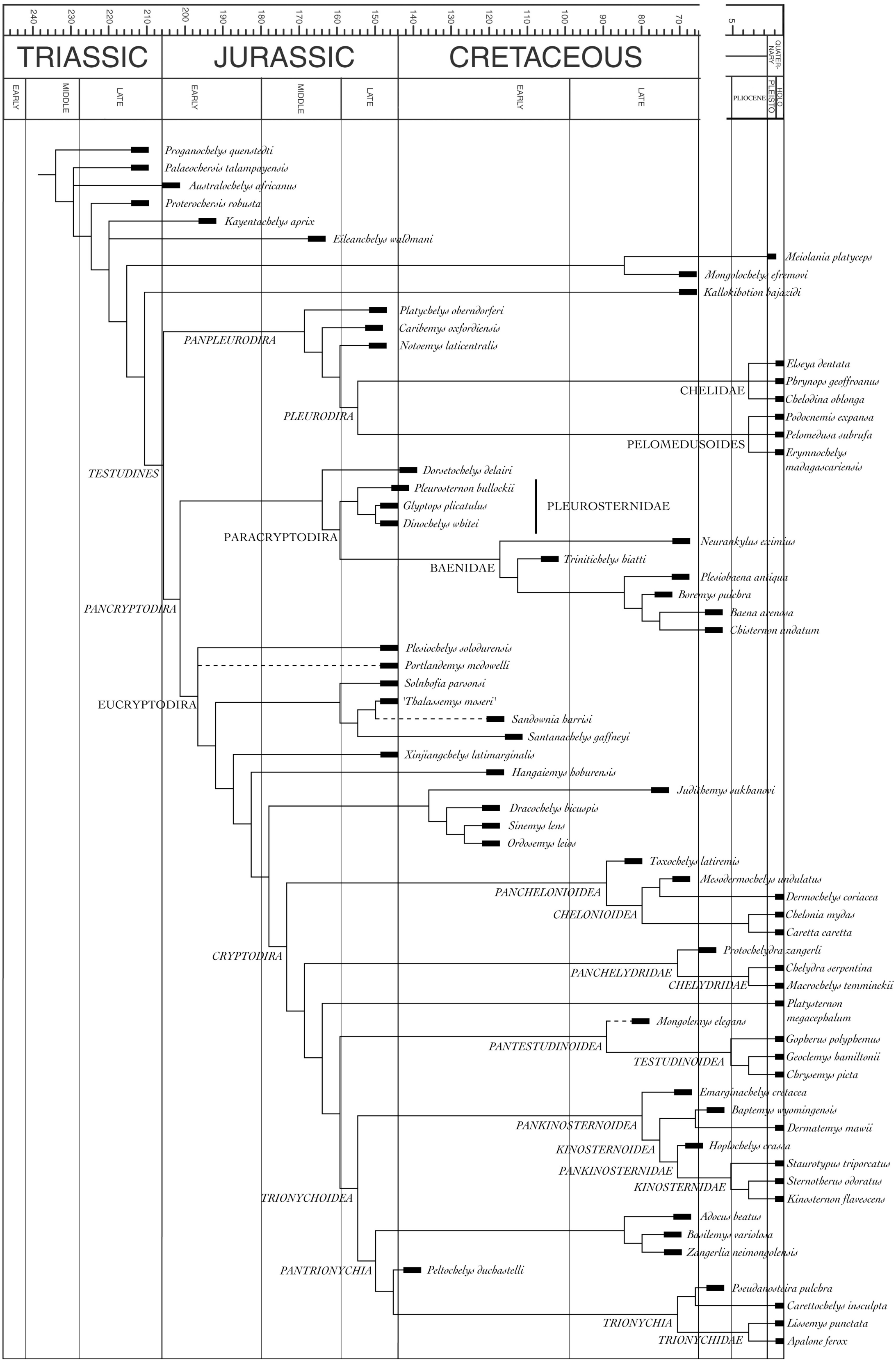

Figure 2.6—Preferred phylogenetic hypothesis of Joyce (2007), including *Eileanchelys waldmani* according to Anquetin *et al.* (2009). Dashed branches support rogue taxa added to the tree *a posteriori* (see Joyce, 2007). Clade names written in italics have been phylogenetically defined by Joyce *et al.* (2004).

Joyce *et al.* (2004) proposed phylogenetic definitions for many turtle clades (Fig. 2.6). Their methodology broadly followed the proposal of the PhyloCode and has been criticised (e.g., Sereno, 2005: 615). However, in comparison with previous nomenclature, the improvements are significant and, in the absence of a better proposal, the nomenclature of Joyce *et al.* (2004) is followed herein. This nomenclature is not complete and several names have not yet been given a phylogenetic definition. The phylogenetic definitions proposed by Joyce *et al.* (2004) refer mostly to groups that have extant relatives. Their system is relatively simple and consists of an assemblage of crown-groups and stem clades, the latter being recognised by the prefix pan-: for example, the crown-group pleurodires are the Pleurodira and the most inclusive clade that contains the crown-group pleurodires is named Panpleurodira. The only exception to this crown/stem system is Testudinata which is an apomorphy-based clade name that refers to the clade arising from the first animal with a complete turtle shell. Figure 2.6 presents the names used in the present study and phylogenetically defined clade names are italicised.

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CHAPTER 3: A NEW STEM TURTLE FROM THE MIDDLE JURASSIC OF THE ISLE OF SKYE, SCOTLAND

INTRODUCTION

Until the recent discovery of two new stem turtles from Russia (Sukhanov, 2006) and Argentina (Sterli, 2008), the majority of Middle Jurassic turtle specimens were known from eastern Asia, mainly China (e.g., Danilov & Parham, 2008; see Chapter 1). Great Britain was the only other place in the world where Middle Jurassic turtles had been discovered. I present a review of the British Bathonian localities that yielded turtles in Chapter 4, as well as a detailed reassessment of the material from Kirtlington and Stonesfield (Oxfordshire). This chapter is dedicated to a description of the most complete Middle Jurassic turtle material from the UK: the material from Cladach a'Ghlinne, Isle of Skye, Scotland.

In 1971, a geology field party from Stowe School (Buckinghamshire) led by J. B. Dobinson and M. Waldman found vertebrate bones in loose blocks that had fallen from the cliffs on the north side of Glen Scaladal (Cladach a'Ghlinne, OS grid reference NG 519 165) on the Strathaird Peninsula, Isle of Skye, Scotland. Throughout the 1970s, several workers, including M. Waldman and the late R. J. G. Savage, returned to the locality and collected further material (Waldman & Evans, 1994). The study of this material resulted in several publications (Waldman & Savage, 1972; Savage, 1984; Waldman & Evans, 1994; Evans & Waldman, 1996). In 2004, funds were granted to S. E. Evans (UCL) by the National Geographic Society to organise fieldwork at Cladach a'Ghlinne. The field party was led by S. E. Evans, P. M. Barrett (Natural History Museum) and J. Hilton (then of the National Museums of Scotland), and was further composed of researchers, technicians and students from UCL, NHM, the Universities of Cambridge and Birmingham, and the National Museums of Scotland. During four weeks in Spring 2004, a large amount of vertebrate material was collected (Barrett, 2006; Evans *et al.*, 2006;), including most of the turtle material described herein.

GEOLOGICAL SETTING

Great Estuarine Group

The Great Estuarine Group (GEG) represents a sequence of Middle Jurassic paralic deposits on the islands of the Inner Hebrides, northwestern Scotland. The GEG crops out in the isles of Skye, Raasay, Eigg and Muck and is intercalated conformably within the marine Jurassic section of the Minch Basin (Harris & Hudson, 1980; Hudson, 1983). The GEG is remarkable as it yields no marine fauna but brackish and/or freshwater assemblages; it is the only part of the Jurassic section of the Minch Basin that is not fully marine (Harris & Hudson, 1980; Hudson, 1983).

The base of the GEG rests on the Bearreraig Sandstone Formation. The uppermost part of this formation is characterised by the presence of the ammonite *Garantiana*. The *Garantiana* zone is one of the uppermost zones of the Bajocian. The GEG is overlain by the Staffin Bay Formation, which begins with the *Macrocephalites macrocephalus* zone (the first ammonite zone of the Callovian). Consequently, the GEG corresponds almost exactly to the Bathonian, plus maybe the very last part of the Bajocian (Harris & Hudson, 1980; Hudson, 1983).

The lithostratigraphy of the GEG was revised by Harris & Hudson (1980). The GEG was divided into seven formations (Fm.; from oldest to youngest): Cullaidh Shale Fm., Elgol Sandstone Fm., Lealt Shale Fm. (with two members: Kildonnan and Lonfearn), Valtos Sandstone Fm., Duntulm Fm., Kilmaluag Fm., and Skudiburgh Formation. Hudson (1983) reviewed the sedimentology and palaeontology of the GEG. The Cullaidh Shale Fm. consists of carbonaceous shales indicating the formation of a lagoonal basin with stagnation and freshening of the waters. The Elgol Sandstone Fm. represents a time of delta building in the lagoonal basin. The Kildonnan Member of the Lealt Shale Fm. is characterised by shales that indicate a marine-brackish lagoonal environment. Some beds within the Kildonnan Member are rich in fish fossils and even plesiosaur bones (see 'Hugh Miller's Bone Bed' below). The Lonfearn Member is represented by dark shales and thin layers of limestone with ooliths. In the shales, the branchiopod *Cyzicus* ('*Estheria*') is common and indicates a brackish environment (Hudson, 1963). Some horizons with desiccation cracks indicate the occurrence of emerged intervals. The Valtos Sandstone Fm. is similar to the Elgol Fm. and characterises a more energetic environment with sand deposits. The above formations, which represent the lower part of the GEG, depict a lagoonal environment with important marine influences.

The upper part of the GEG shows a growing influence from terrestrial environments (Andrews, 1985). The Duntulm Fm. is represented by limestones and shales with abundant oyster shells. However, in northern Skye there are freshwater intercalations within this formation. The Kilmaluag Fm. (see below) is characterised by the disappearance of oysters and the appearance of non-marine ostracods and *Cyzicus*. Some beds (called 'Vertebrate Beds') have yielded terrestrial vertebrate material (see below). The non-marine ostracods disappear at the base of the Skudiburgh Formation. The latter is represented by red mudstones and siltstones with some sandy channels indicating an environment of alluvial mudflats. In this formation, fossils are mainly *Unio*, fish teeth and terrestrial plant fragments. Andrews (1985: 1119) summarised the sequence of the upper part of the GEG (Duntulm, Kilmaluag and Skudiburgh Formations) as a:

> "gradual transition from near-marine salinity lagoons, through muddy

> lagoons with a low-salinity fauna, to alluvial mudflats with sandy channels."

The upper limit of the Great Estuarine Group is marked by the marine transgression of the Staffin Bay Formation.

Invertebrate and fish remains have been found in numerous horizons throughout the GEG. Tetrapod material is less common and has been recovered from two main horizons. The first horizon is known as 'Hugh Miller's Bone Bed' and has yielded plesiosaur remains among layers of fish teeth and scales (see Chapter 4). This bed is part of the Kildonnan Member of the Lealt Formation. The second horizon corresponds to the 'Vertebrate Beds' of the Kilmaluag Formation. The best exposure of this horizon is at Cladach a'Ghlinne and yields a considerably more important faunistic assemblage in term of taxonomic diversity (Savage, 1984; Evans & Milner, 1994; Evans *et al.*, 2006).

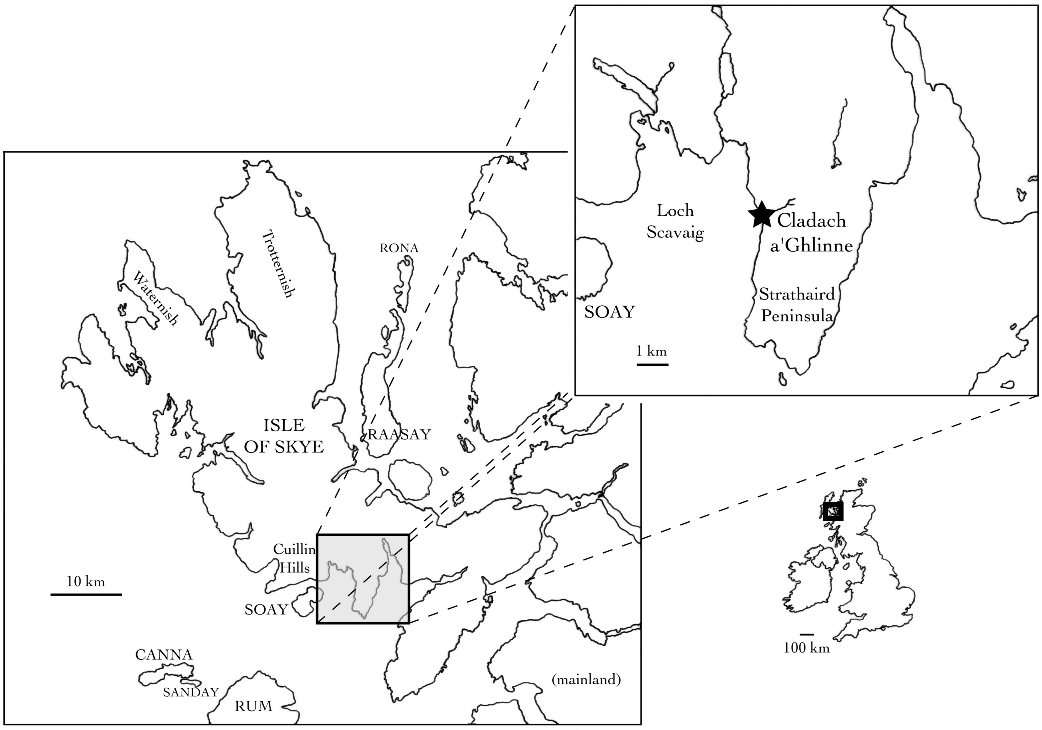

Figure 3.1—Localisation of the Cladach a'Ghlinne locality, Strathaird Peninsula, Isle of Skye, Inner Hebrides, Scotland.

Kilmaluag Formation

The Kilmaluag Fm. ('Ostracod Limestones' of previous nomenclature) crops out in northern Skye (Trotternish and Waternish Peninsulas), southern Skye (Strathaird Peninsula; Fig. 3.1), Eigg (Laig Gorge) and Muck (Camas Mor) (Harris & Hudson, 1980; Andrews, 1985). It is represented by alternations of calcareous mudstones and argillaceous calcilutites. In Trotternish, there are fine-grained sandstone intercalations within the formation (the "clastic facies" of Andrews, 1985). Desiccation cracks are common throughout the formation, as are non-marine ostracods and the brackish-water branchiopod *Cyzicus*. Among invertebrate macrofossils, the freshwater gastropod *Viviparus* is common and *Unio* occurs frequently.

The Strathaird sequences on the north side of the mouth of Cladach a'Ghlinne (OS grid reference NG 519 165; Fig. 3.1) and south of Carn Mor landslide (NG 519 154) represent the best exposure of the Kilmaluag Formation. This formation is divided into fourteen beds (Harris & Hudson, 1980: fig. 9; Andrews, 1985: fig. 4). The lower beds (1 to 9) represent an alternation between clastic and carbonate mud deposition in a low-salinity lagoon. Bed 9 corresponds to the 'Vertebrate Beds'. These layers consist of limestones with abundant *Viviparus* and bone fragments. According to Andrews (1985: 1128) who studied the chemistry of these deposits, "these beds may represent a wet climatic phase in the history of the shallow lagoons", and so a freshening phase. The upper beds (10 to 14) are characterised by a return to sublittoral lagoonal conditions.

Cladach a'Ghlinne

Harris & Hudson (1980: 247) describe the Cladach a'Ghlinne locality as the most accessible for the Kilmaluag Formation. This is to say that other outcrops of the Kilmaluag Fm. must be almost inaccessible. Indeed, Cladach a'Ghlinne itself is a difficult site to work. Access to the locality requires either a one-hour walk through the boggy terrain of Glen Scaladal or alternatively a one-hour walk along a dangerous cliff path. The locality is located on the foreshore north to the mouth of Glen Scaladal, on the west coast of the Strathaird Peninsula (Fig. 3.1). The rock is dark grey (black when wet, which occurs often in this area) and the bones are black. Early Tertiary igneous activity produced numerous sills and dikes that chemically altered and hardened the sediments (Savage, 1984). This makes fossil extraction on the field, and subsequent fossil preparation (see below), extremely difficult. In the field, collection of small specimens (e.g., isolated teeth and vertebrae) with a hammer and chisel is possible, although difficult due to the hardness of the rock, but the extraction of larger specimens requires the use of a fuel-powered circular saw (Fig. 3.2B). The cliff section at Cladach a'Ghlinne exposes the sediments of the Kilmaluag Fm. This is a protected area (Sites of Special Scientific Interest - SSSI) and collecting is consequently restricted to the fallen boulders on the beach.

The Middle Jurassic microvertebrate assemblages of England are the most diverse known for this period (Evans & Milner, 1994; Evans *et al.*, 2006). However, the remains consist mainly of disarticulated material. At Cladach a'Ghlinne, the vertebrate assemblage is as diverse as that of the contemporaneous English localities but presents some associated and articulated specimens, which make this locality extremely valuable. Waldman & Savage (1972) described a new tritylodont species of the genus *Stereognathus* (Synapsida, Therapsida) and a new genus and species of docodont (Mammalia), *Borealestes serendipitus*. In addition, Savage (1984) provided an overview of the remaining Cladach a'Ghlinne vertebrate assemblage, which includes: several fish taxa (including chondrichthyans and osteichthyans); turtles; crocodiles (Goniopholidae indet.); a large-bodied reptile (plesiosaur or archosaur); two species of supposed lizards; and a new pantothere (Mammalia). The two 'lizards' were studied by Waldman & Evans (1994) and referred to the crown-group squamate *Paramacellodus* and the stem lepidosauromorph *Marmoretta*. Evans & Waldman (1996) presented a detailed review of the small reptile and amphibian assemblage and added the following taxa to the faunal list: two salamanders (*Marmorerpeton* and an undetermined form); two or three further lizard taxa (*Parviraptor* and one or two undetermined species); and a choristodere (*Cteniogenys*). Following the 2004 fieldwork, several new taxa have been added to the faunal list (Evans *et al.*, 2006): a second crocodile (Atoposauridae indet.); two indeterminate pterosaurs; two dinosaurs; a second docodont (*Krusatodon*); and an undetermined mammal (undescribed associated mammalian material recovered by M. Waldman and R. J. G. Savage). Evans *et al.* (2006) also mention the discovery of an unusual lizard jaw that almost certainly pertains to a new genus. Rees & Underwood (2006) assessed the shark material collected in 2004 and identified two hybodonts: an indeterminate *Hybodus* species and a new species of *Acrodus*. Finally, Barrett (2006) described an isolated dinosaur tooth found in 2004 and has referred it to either a basal eusauropod or a basal titanosauriform. This is the first dinosaur tooth found in Scotland and one of the few dinosaur skeletal remains from this part of the world.

Until recently, the turtle material from Cladach a'Ghlinne had never been properly assessed (Anquetin, 2007; Anquetin *et al.*, 2009; present work). The previous referral of this material to pleurosternids (Savage, 1984; Evans & Waldman, 1996) is mostly based on the supposed presence of this group of turtles in other British Bathonian localities, especially Stonesfield and Kirtlington (Bergounioux, 1955; Romer, 1956, 1966; Gillham, 1994; see Chapter 4), rather than on a detailed morphological study.

MATERIAL AND METHODS

Material

The majority of the material described herein was collected during the 2004 fieldwork, including the holotype and paratypes (see below). The holotype and the paratype specimens were found by M. E. H. Jones (then a PhD student at UCL). The paratypes consist of an association of five or six turtles within a single large block. The extraction of this large block was extremely difficult: this was done on the last day of fieldwork in a fierce rainstorm and against a rising tide (Fig. 3.2B). The heavy blocks were then transported back to the vehicles on the backs of the field crew. Additional material was collected in the 1970s by M. Waldman and R. J. G. Savage, and later by M. Waldman and S. E. Evans (see below).

Figure 3.2—Discovery of the paratype association in 2004. A, (left to right) Ming-Mei Liang, Emily Rayfield, Susan Evans, Marc Jones and Paul Barrett posing in front of the association on the field; B, Jason Hilton and Dave Herd extracting the association with a fuel-powered circular saw; C, sketch of the association as preserved on the field; D; the same specimens as in C before the preparation work had begun in October 2005. Credits: A and B, 2004 field trip, National Geographic Society; C, Marc Jones.

The bones are black and the sediments are dark grey, although they turn to a much paler grey when weathered or abraded. Most skeletal remains are disarticulated but several articulated and associated turtle specimens are known (see below). Individual bones are often slightly crushed and the turtle shells are flattened. The major problem with these remains lies in their preparation: the sediments have been secondarily hardened by Tertiary volcanic intrusions. As a result, acid preparation is inefficient, although it facilitated mechanical preparation (see below). The preparation of the large association (paratype specimens) formed an integral part of the PhD project.

Fossil preparation

A few turtle specimens collected in the 1970s were prepared by M. Waldman or S. Finney (University of Cambridge). I was entrusted with the preparation of the large block collected in 2004 and was trained in the necessary techniques at the Palaeontology Conservation Unit (PCU) of the Natural History Museum, under the supervision of S. Moore-Fay. Due to the complexity of the paratype association, the preparation started in October 2005 and ended at the beginning of

2008. The holotype skull, which was initially incorrectly identified as a sacral vertebra, was carefully acid prepared by S. Moore-Fay.

Before the preparation — In the field, only part of the association was visible, with the rest embedded within the sediment (Fig. 3.2A). The identification as chelonian remains was evident (shell elements including a row of peripherals; Fig. 3.2C), but number of specimens and their completeness or state of articulation were unknown. The field crew accidentally cut through the specimens before extracting a much larger block. During extraction, however, the block broke into eight smaller blocks. Incidentally, this facilitated the transport of the material back to the vehicles. When I started the preparation in October 2005, the material was in the same state as when it had left the locality (Fig. 3.2D). This gave me the opportunity to observe the sections between the blocks and to try to understand the three-dimensional distribution of the skeletal remains within the sediments, which was rather complex (Fig. 3.3A).

Phase 1 (October 2005 - August 2006) — Acid preparation of the sediments from Cladach a'Ghlinne is almost ineffective. This technique works extremely slowly on these sediments and could only be used to remove the last few millimetres of rock above the skeletal remains at the end of the preparation process. Two methods of mechanical preparation were considered: to slowly remove the sediments with a pneumatic engraving pen or to try to accelerate the process by removing larger amounts of rock with a small circular saw. Indeed, the thickness of the rock covering the remains was important in some areas (Fig. 3.3A). In order to avoid deterioration of the specimens, it was decided to begin preparation with a pneumatic pen. Although slower, this technique allowed a better control of the progression of the preparation. Considering the three-dimensional distribution of the remains, it turns out to have been a sensible choice *a posteriori*. The different blocks were prepared down from the side (upper) that was exposed in the field. The aim of this first phase was to remove as much rock as possible and leave only a few millimetres of sediment on the surface of the skeletal remains (Fig. 3.3B). During the process, it appeared that four out of the eight blocks did not contain part of the turtle association. These blocks were set aside. At the end of phase 1, in August 2006, the four remaining blocks were stuck back together in their original position using an acid-resistant glue (Fig. 3.3C).

Phase 2 (September 2006 - March 2007) — The second phase involved acid preparation of the upper side of the block in order to expose the skeletal remains still embedded in the sediments. In order to protect the under side of the block from acid attack, a protective jacket was engineered using casting techniques. This jacket consisted of two layers: an internal mould of soft silicone and an external hard fibreglass shell. The PCU is equipped with a large acid preparation laboratory. The block was immersed in a large tank full of a 5% acetic acid solution buffered with calcium hydrogen orthophosphate. The process of acid preparation requires a succession of steps: firstly the immersion in the acid solution, secondly the washing of the specimens in clear water, and thirdly the drying and consolidating of the skeletal remains. Specimens were immersed in the acid for five

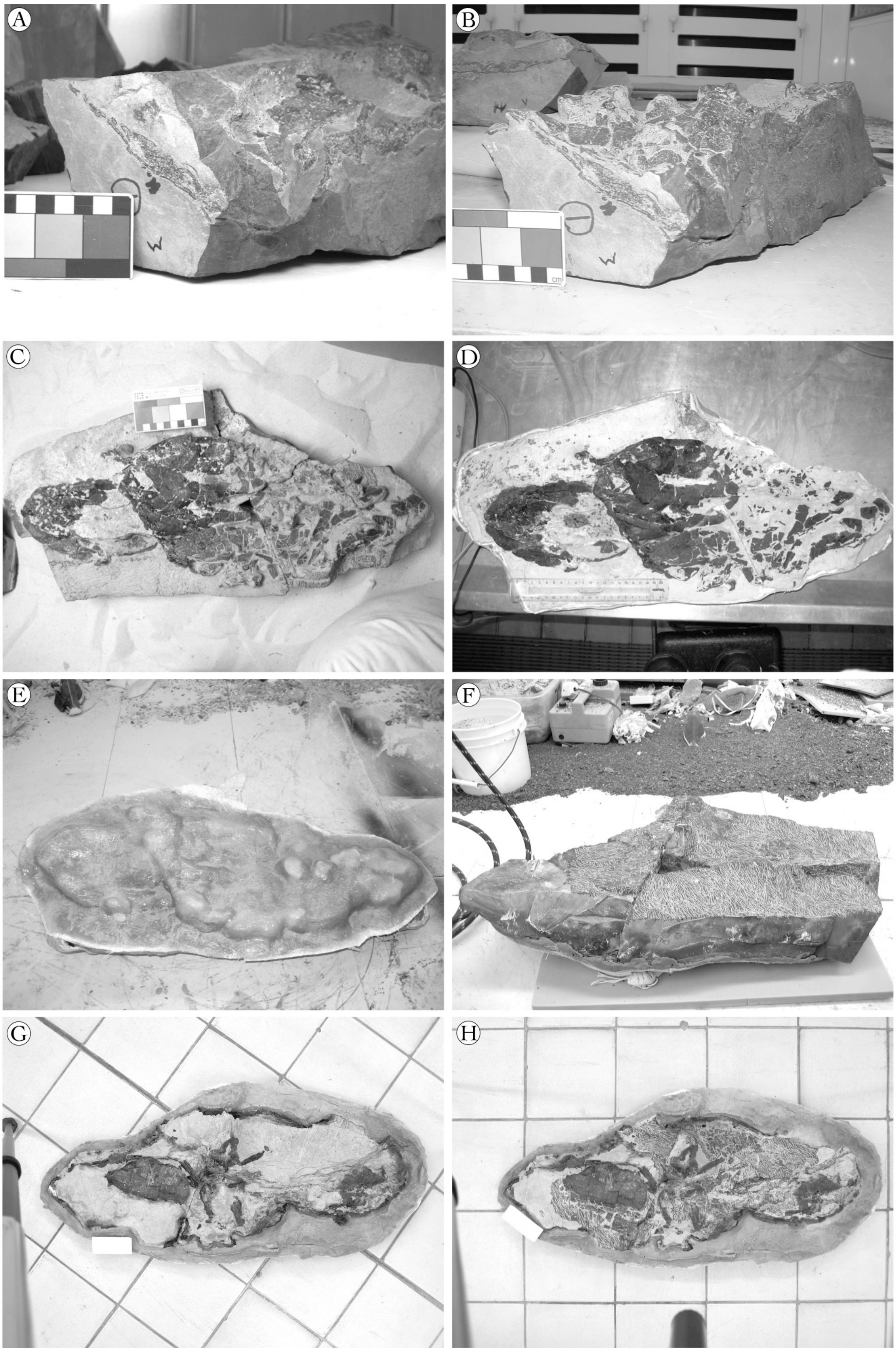

Figure 3.3—Preparation of the paratype association. A, one of the blocks before preparation (October 2005), the section on the left shows a flattened shell in transverse section; B, the same block after mechanical preparation (May 2006); C, all blocks reassembled together after mechanical preparation of the upper side (August 2006); D, acid preparation (October 2006); E, protective jacket for the upper side (April 2007); F, mechanical preparation of the under side (May 2007); G, first phase of acid preparation of the under side (June 2007); H, mechanical preparation (July 2007). See Fig 3.4 for the state of both sides after preparation.

days, then washed for two weeks (the washing period has to be three times as long as the immersion in acid). Specimens were then consolidated using an acid resistant consolidant (Synocryl 9123s). This three week process usually resulted in the removal of one or two millimetres of sediment. Consequently, the second phase consisted of a succession of rounds of acid preparation. At this stage of the preparation process, it was clear that at least two shells and maybe the fragmented remains of a third individual were present within the block (Fig. 3.3D), as well as a possible skull. Both shells were visible in ventral view, so preparation of the under side of the block was required in order to access information on the carapace.

Phase 3 (April 2007 - June 2007)—A new protective jacket for the now prepared upper side was engineered, so that the block could rest on this side during the preparation of the under side (Fig. 3.3E). This new jacket would also protect the upper side from acid attack during phase 4 (see below). As with the upper side, it was decided to start preparation of the under side with an engraving pen (Fig. 3.3F). As the three-dimensional distribution of the skeletal remains became more evident, this phase of mechanical preparation progressed more quickly than phase 1. During this phase, the carapace of a third individual was discovered, corresponding to the fragmentary remains observed on the upper side (see above). At the end of June, it was decided to accelerate the preparation by using a small circular saw to remove the remaining sediments still covering this carapace. S. Moore-Fay (PCU) carried out this delicate operation so as to prevent major damage to the specimen. Another carapace, corresponding to one of the plastra observed on the upper side, was also discovered during this phase.

Phase 4 (July 2007 - August 2007)—This fourth phase consisted of a repeated sequence of acid immersion followed by mechanical preparation (Fig. 3.3G,H). This efficient methodology resulted in the complete preparation of the aforementioned carapaces and the discovery of a fourth shell (represented by an anterior plastron) and a skull roof.

Phase 5 (September 2007 - November 2007)—The under side of the block was entirely prepared and a definitive protective jacket was designed for this surface. When the initial protective jacket of the upper side was removed, it appeared that the sediment had been further attacked by the acid solution despite the protection of the jacket. Thanks to this, the presence of a skull, suggested during phase 2 (see above), was confirmed. This skull was associated with the fourth shell discovered in phase 4. Some areas of this side needed further preparation, so acid preparation was continued until the beginning of December 2007. It appeared that only the anterior half of the aforementioned skull was visible, with the rest of it contained within the fourth shell (i.e., between the carapace and plastron, almost in life position). Skull anatomy being so important for turtle systematics, it was considered to pursue the preparation and try to reveal the posterior half of this skull by destroying part of the poorly preserved fourth shell. In order to assess whether or not the posterior part of the skull was present within the shell, the specimen was x-rayed at the NHM in mid-November, but this was unsuccessful due to the dense nature of the matrix.

Phase 6 (December 2007 - January 2008)—In December 2007, it appeared that no more skeletal material could be excavated without compromising the integrity of the association. The last phase of preparation began with the cleaning the specimens using an air abrasive tool, on both the upper and under sides. This was to remove the sediment still covering some restricted areas and also to remove the thick layer of consolidant that had protected the skeletal remains during preparation. This thick layer of consolidant prevented detailed observation of the specimens. A third skull was discovered during this operation. Finally, the skeletal remains were properly consolidated for safe manipulation and the definitive protective jacket for the upper side was designed. A last attempt to determine whether or not the skull associated with the fourth shell was complete consisted of CT-scanning the association at the Royal Veterinary College in January 2008. The scans were not clear enough to answer this particular question, however. At the end of the preparation work, this association consisted of four shells, three skulls and some additional disarticulated material (Fig. 3.4).

SYSTEMATIC PALAEONTOLOGY

TESTUDINATA Klein 1760 (*sensu* Joyce *et al.*, 2004)

***Eileanchelys* Anquetin, Barrett, Jones, Moore-Fay & Evans 2009**

Etymology—*Eilean* from the Scottish Gaelic word for island, in reference to the Isle of Skye; *chelys* from the Greek word for turtle.

Type species—*Eileanchelys waldmani* Anquetin *et al.* 2009, the only species in the genus.

Type locality—same as species.

Diagnosis—same as species.

***Eileanchelys waldmani* Anquetin, Barrett, Jones, Moore-Fay & Evans 2009**

Etymology—*waldmani* in honour of Dr Michael Waldman, discoverer of the Cladach a'Ghlinne locality and the person responsible for introducing S. E. Evans to the site.

Holotype—NMS G 2004.31.15, the posterior half of a skull (Anquetin *et al.*, 2009: fig. 1; Figs. 3.5 and 3.6).

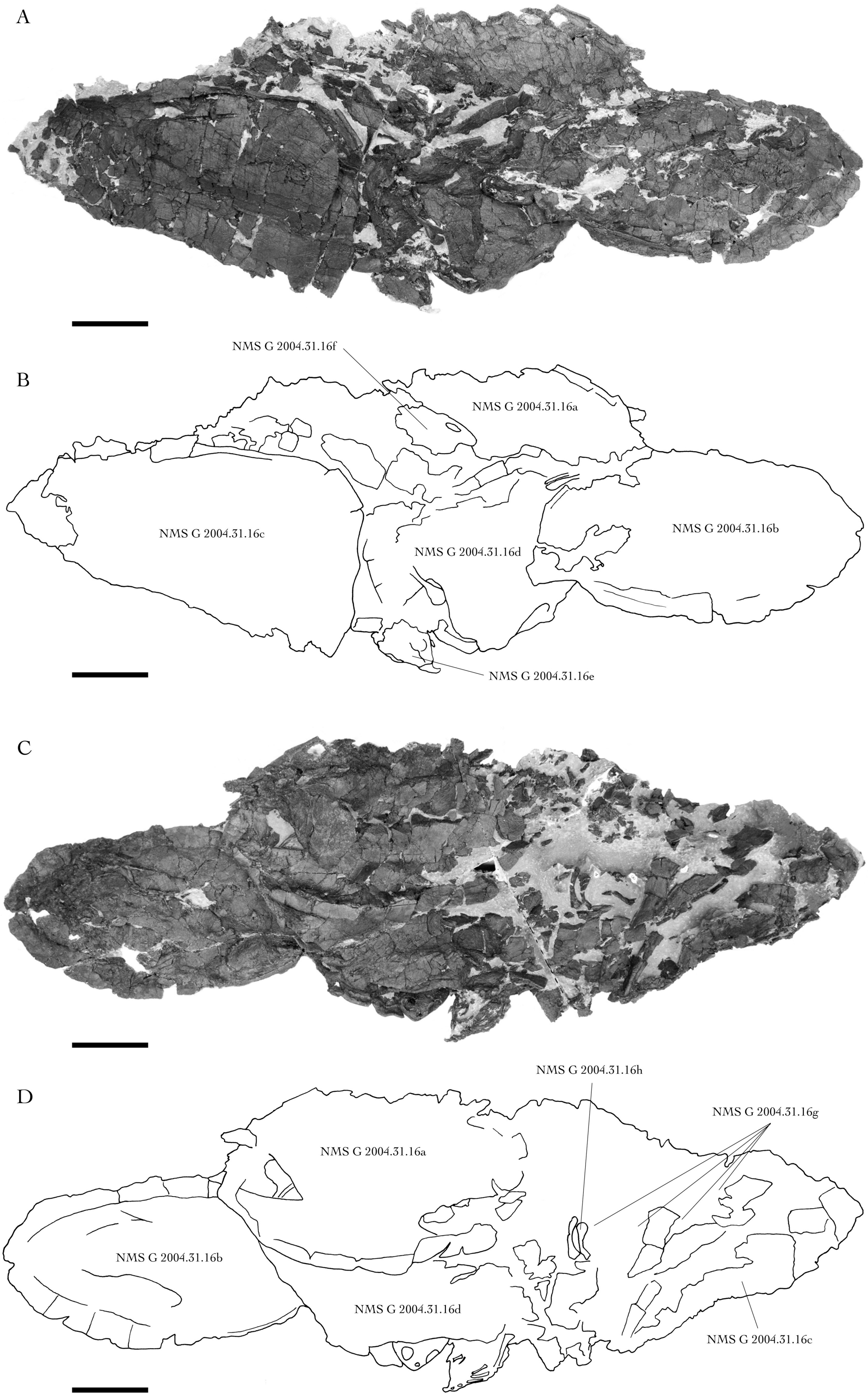

Figure 3.4—*Eileanchelys waldmani*, NMS G 2004.31.16, position of the different specimens in the association. A, upper side; B, key to photograph A; C, under side; D, key to photograph C. Scale bars: 50 mm.

Paratypes—NMS G 2004.31.16a-f, an association comprising at least five and possibly six individuals in a single block (Fig. 3.4): (a), a partial shell showing only a small part of the carapace, with the left side of the plastron missing, poorly preserved cervical vertebrae and a partial shoulder girdle; (b), a complete shell, with poorly preserved caudal vertebrae and a partial right hindlimb; (c), a nearly complete carapace missing only the posteriormost area and part of the left margin; (d), the anterior part of a shell and skull; (e), a fragmented skull consisting of the skull roof and part of the anterior palatal area (this skull may belong to the same individual as NMS G 2004.31.16c); (f), a complete crushed skull in lateral view that apparently does not belong to any individual in the association (see below).

Referred specimens—NMS G 1992.47.8 (Waldman collection), a block of matrix containing shell fragments, a partial pelvis and an incomplete hindlimb (femur, tibia and a fragment of fibula); NMS G 1992.47.37 (Evans & Waldman collection), a small bridge peripheral; NMS G 1992.47.38 (Evans & Waldman collection), an isolated fragment of costal plate; NMS G 1992.47.50 (Waldman collection), an anterior plastron with some carapace fragments; NMS G 1992.47.51 (Evans & Waldman collection), an isolated left humerus; NMS G 2004.31.16g, a series of seven more or less complete cervical vertebrae; NMS G 2004.31.16h, a partial forelimb with the ulna, radius and possibly the distal part of the humerus; NMS G 2004.31.17, an isolated left pubis; NMS G 2004.31.18, an isolated row of bridge peripherals.

Locality and horizon—Cladach a'Ghlinne, Strathaird Peninsula, Isle of Skye, Scotland. Cladach a'Ghlinne represents the best exposure of the Kilmaluag Formation, which is of late Bathonian age (Harris & Hudson, 1980; Andrews, 1985; see above).

Emended diagnosis—Relatively small turtle (carapace length of approximately 250-300 mm, although it may have been bigger; see 'Size of *Eileanchelys waldmani*', below) characterised by the following list of features: presence of nasal; elongated postorbital skull (compared to that of more basal forms); absence of flooring of the cavum acustico-jugulare; processus interfenestralis of the opisthotic more slender than that of more basal forms (e.g., *Proganochelys quenstedti*, *Kayentachelys aprix*), but more robust than that of crown-group turtles; separate openings of the canalis cavernosus and canalis stapedio-temporalis within the cavum acustico-jugulare; reduced thickness of the basicranial floor comparable with that of crown-group turtles; well-developed antrum postoticum; flat and horizontal vomer that is free of contacts for most of its length except at its extremities and along a short suture with the prefrontal; absence of processus trochlearis oticum; posteroventrally open incisura columellae auris; at least eight neurals (an additional plate between neural 8 and suprapygal 1 may be a ninth neural or a supernumerary suprapygal), two broad suprapygals, and eight costals present; contact of suprapygal 1 with peripheral laterally (probably peripheral 10); pygal region bordered by the two last pairs of peripherals (probably the tenth and eleventh); absence of carapacial or plastral fontanelles in adult individuals; one short but broad cervical scale present; vertebral scales significantly wider than pleurals; vertebral 3-4 sulcus on neural 6; reduced cleithrum present on epiplastron; arrow-shaped entoplastron that does not separate the epiplastra anteriorly; one pair of mesoplastra that meet medially; one small pair of extragulars present; and an anal scale that does not reach the hypoplastron.

DESCRIPTION

SKULL MORPHOLOGY

Dermal roofing elements

Nasal—Among extant turtles, nasals occur only in chelids (Pleurodira). However, this bone is more common in Mesozoic turtles (e.g., Gaffney, 1979). When present, the nasals roof the fossa nasalis and form the dorsal margin of the apertura narium interna. The nasal is present in *Eileanchelys waldmani* and can be observed in NMS G 2004.31.16d (Fig. 3.7). The nasal can also be observed in NMS G 2004.31.16f, but the anterior tip of this skull is severely damaged and bone sutures are extremely difficult to distinguish (Fig. 3.9). In NMS G 2004.31.16d, the nasal consists of a rectangular element that contacts the other nasal along the midline for its entire length. The nasal also contacts the maxilla laterally, the prefrontal posterolaterally and the frontal posteriorly. As in *Kayentachelys aprix* Gaffney *et al.* 1987 (Sterli & Joyce, 2007: fig. 3), the posterior contact with the frontal is slightly concave, but the frontals do not separate the nasals in the midline as it is the case in chelids and pleurosternids (Gaffney, 1979; Joyce, 2007). The nasal of *Eileanchelys waldmani* differs significantly from the large, elongate bone seen in *Proganochelys quenstedti* Baur 1887 and *Palaeochersis talampayensis* Rougier *et al.* 1995 (Gaffney, 1990; Sterli *et al.*, 2007), and more closely resembles that of *Kayentachelys aprix* and basal pancryptodires. No specimen permits a ventral view of the nasal (i.e., the roof of the fossa nasalis), so it is unknown whether or not the nasal forms part of the sulcus olfactorius as in *Proganochelys quenstedti* and *Kayentachelys aprix* (Gaffney, 1979, 1990; Sterli & Joyce, 2007).

Prefrontal—In turtles, the prefrontal usually contributes to some extent to the dorsal surface of the skull and presents a vertical descending process that forms the anterior wall of the fossa orbitalis. This descending process often contacts the palatine and vomer ventrally, although there are notable exceptions (e.g., Pleurodira and Trionychidae for the contact with the palatine: see Joyce, 2007: 9). In those species without nasal bones, the prefrontals usually form the roof of the fossa nasalis and the dorsal margin of the apertura narium interna. In *Eileanchelys waldmani*, the prefrontals have a reduced exposure on the dorsal surface of the skull and they do not meet one another medially (NMS G 2004.31.16d, NMS G 2004.31.16e and NMS G 2004.31.16f; Figs. 3.7, 3.8 and 3.9). Dorsally, the prefrontal consists of a narrow rectangular lappet that forms the

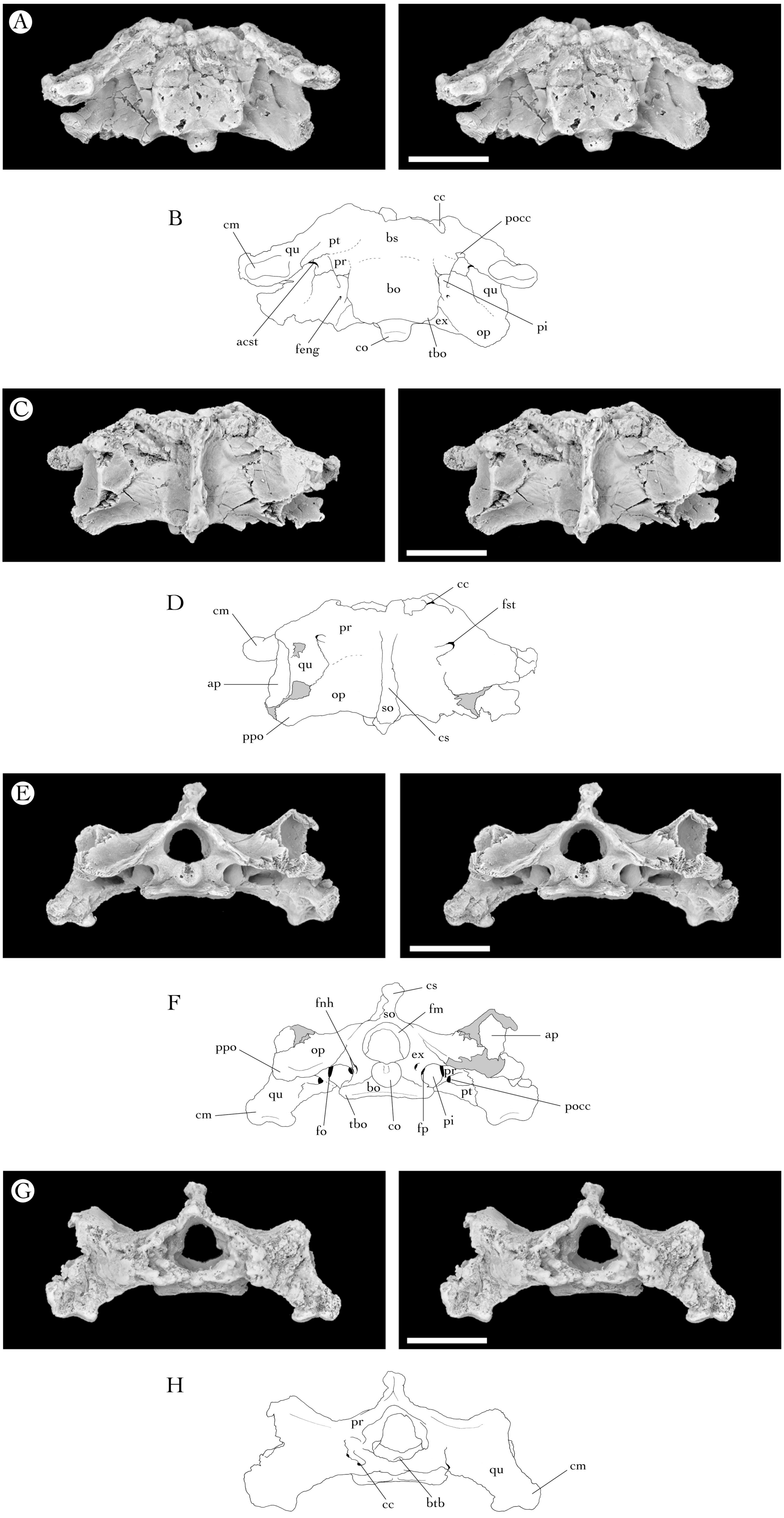
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Figure 3.5—(previous page) *Eileanchelys waldmani*, stereophotographs of the skull NMS G 2004.31.15 (holotype). A, B, ventral view; C, D, dorsal view; E, F, posterior view; G, H, anterior view. Scale bars: 10 mm. Abbreviations: acst, aditus canalis stapedio-temporalis; ap, antrum postoticum; bo, basioccipital; bs, basisphenoid; btb, basis tuberculi basalis; cc, canalis cavernosus; cm, condylus mandibularis; co, condylus occipitalis; cs, crista supraoccipitalis; ex, exoccipital; feng, foramen externum nervi glossopharyngei; fm, foramen magnum; fnh, foramen nervi hypoglossi; fo, fenestra ovalis; fp, fenestra perilymphatica; fst, foramen stapedio-temporale; op, opisthotic; pi, processus interfenestralis; pocc, posterior opening of canalis cavernosus; ppo, processus paroccipitalis of opisthotic; pr, prootic; pt, pterygoid; qu, quadrate; so, supraoccipital; tbo, tuberculum basioccipitale.

anterodorsal margin of the orbit. The prefrontal contacts the nasal anteromedially, the maxilla anteroventrally and the frontal medially and posteriorly. There is evidence that the descending process of the prefrontal contacts the vomer ventromedially (see below), but it is unknown whether or not the prefrontal contacts the palatine on the floor of the fossa orbitalis. The development of the dorsal exposure of the prefrontal is variable within Testudinata (Joyce, 2007: 10; see also Chapter 5). In the most basal turtles (i.e., *Proganochelys quenstedti* and *Palaeochersis talampayensis*), the prefrontals are large elements that form a greater part of the interorbital skull roof, although these bones do not meet one another medially. The reduced prefrontal lappets of *Eileanchelys waldmani* are also found in the stem turtle *Kayentachelys aprix*, in paracryptodires (see Chapter 4), in some stem cryptodires and in chelids. In pelomedusoids and cryptodires (crown-group), the prefrontals are extended onto the dorsal surface of the skull and usually meet one another medially. This morphology might be associated with the loss or reduction of the nasal bones.

Lacrimal— The lacrimal bone is lost very early in turtle evolution and only the basalmost taxa are known to have one (i.e., *Proganochelys quenstedti* and *Palaeochersis talampayensis*). In *Australochelys africanus* Gaffney & Kitching 1994, there is a large foramen in the anteroventral part of the orbit but the preservation of the only known specimen is not good enough to have preserved bone sutures, so that it is unknown whether or not a lacrimal bone was present (BP/1/4933; Gaffney & Kitching, 1995). In NMS G 2004.31.16d (Fig. 3.7), this area is very well preserved and there is no lacrimal bone or foramen, as in *Kayentachelys aprix* and all more derived turtles (Joyce, 2007; Sterli & Joyce, 2007).

Frontal— In *Eileanchelys waldmani*, the frontal is a large skull roof element that reaches the orbital margin laterally, preventing contact between the prefrontal and postorbital (NMS G 2004.31.16d, NMS G 2004.31.16e and NMS G 2004.31.16f; Figs. 3.7, 3.8 and 3.9). The frontal contacts the nasal anteriorly, the prefrontal anterolaterally, the postorbital posterolaterally, the parietal posteriorly and the other frontal medially. The frontal forms part of the dorsal margin of the orbit. The anterior contact with the nasal is slightly convex (see Nasal above), whereas the posterior contact with the parietal is straight and transverse. This morphology is identical to that of the vast majority of crown-group turtles and some stem turtles (i.e., *Kayentachelys aprix* and

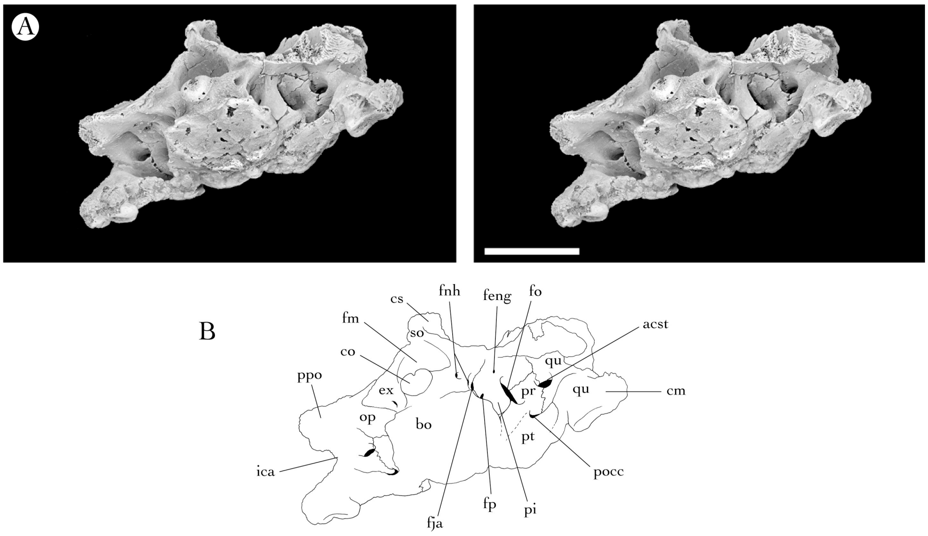

Figure 3.6—*Eileanchelys waldmani*, NMS G 2004.31.15 (holotype). A, stereophotographs of the cavum acustico-jugulare; B, key to figure A. Scale bar: 10 mm. Abbreviations: acst, aditus canalis stapedio-temporalis; bo, basioccipital; cm, condylus mandibularis; co, condylus occipitalis; cs, crista supraoccipitalis; ex, exoccipitalis; feng, foramen externum nervi glossopharyngei; fm, foramen magnum; fja, foramen jugulare anterius; fnh, foramen nervi hypoglossi; fp, fenestra perilymphatica; fo, fenestra ovalis; ica, incisura columellae auris; op, opisthotic; pi, processus interfenestralis; ppo, processus paroccipitalis of opisthotic; pocc, posterior opening of canalis cavernosus; pr, prootic; pt, pterygoid; qu, quadrate; so, supraoccipital

Kallokibotion bajazidi Nopcsa 1923), whereas in other stem turtles (e.g., *Proganochelys quenstedti*, *Palaeochersis talampayensis*, *Mongolochelys efremovi* Khosatzky 1997) the frontal is prevented from contacting the orbital margin by a prefrontal-postorbital contact (Joyce, 2007: 11). The frontal of *Eileanchelys waldmani* greatly resembles that of *Kayentachelys aprix*, except for the posterolateral contact with the postorbital that is longer in the latter (MNA V1558). The anterior process of the frontal in *Kallokibotion bajazidi* is shorter than that of *E. waldmani* and its lateral participation in the orbital margin is smaller (Gaffney & Meylan, 1992: figs. 4 and 6).

Parietal—In turtles, the parietal consists of two plates of bone: a dorsal horizontal plate forming much of the temporal skull roof and a parasagittal ventral plate that separates the anterior part of the cavum cranii from the fossa temporalis, the processus inferior parietalis (Gaffney, 1979). The parietal can be observed partly in NMS G 2004.31.16d (Fig. 3.7), NMS G 2004.31.16e (Fig. 3.8) and NMS G 2004.31.16f (Fig. 3.9), but no specimen shows the processus inferior parietalis. The parietal is a long, quadrangular element that forms at least half of the length of the skull roof. It contacts the other parietal medially for its entire length, the frontal anteriorly and the postorbital laterally. NMS G 2004.31.16f (Fig. 3.9) shows that there is a posterolateral contact between the parietal and squamosal on the skull roof, which suggests the absence or weak development of an upper temporal emargination. The posterior margin of the skull roof is not preserved in any specimens. The morphology of the parietal in *Eileanchelys waldmani* (i.e., an elongate parietal that makes up to half of the skull roof) is common in the vast majority of turtles

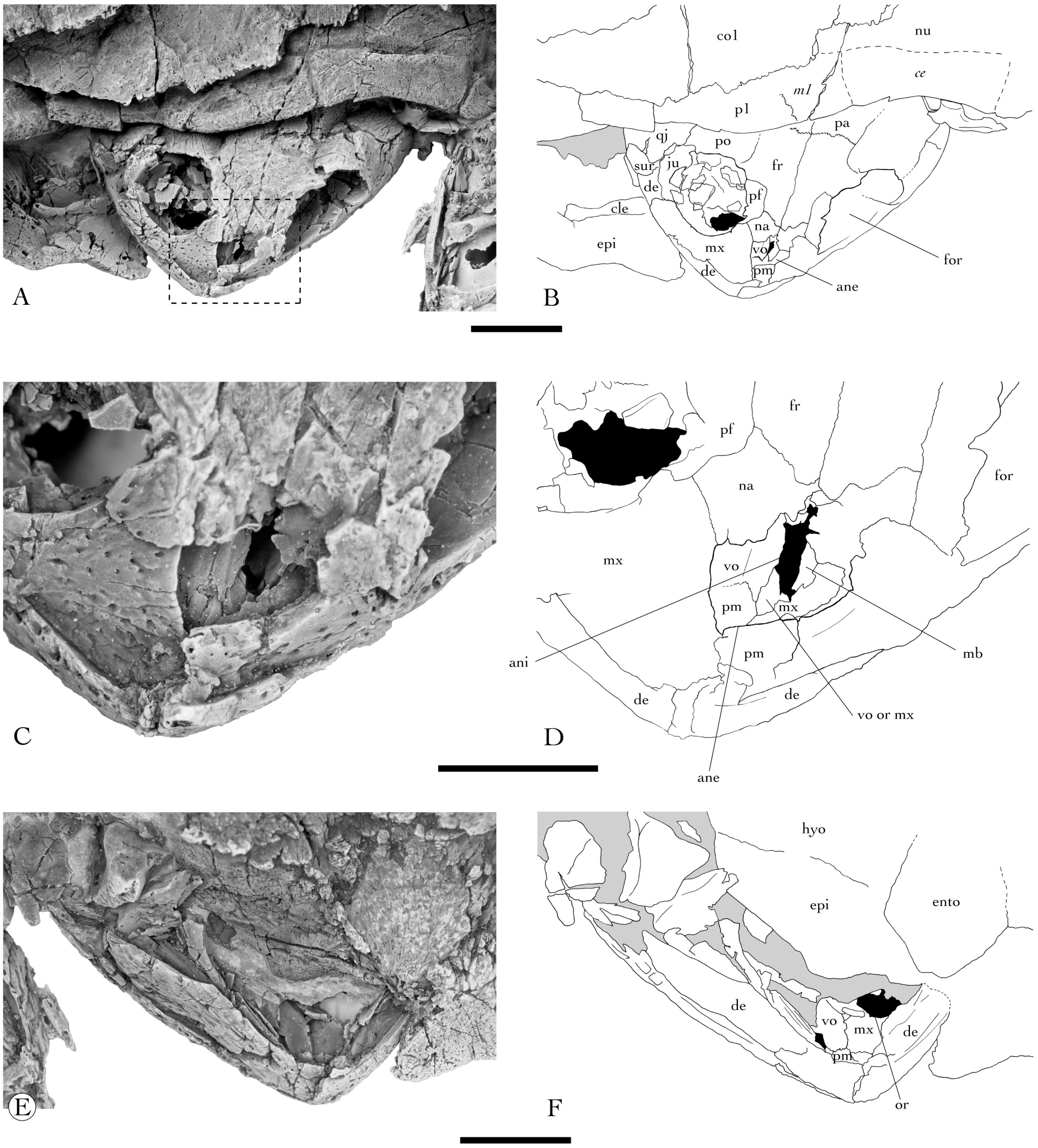

Figure 3.7—*Eileanchelys waldmani*, NMS G 2004.31.16d (skull). A, B, dorsal view; C, D, enlargement of the fossa nasalis area (shown in A); E, F, ventral view. Scale bars: A, B, and E, F, 10 mm; C, D, 5 mm. Abbreviations: ane, apertura narium externa; ani, apertura narium interna; ce, cervical scale; cle, cleithrum; co, costal plate; de, dentary; epi, epiplastron; ento, entoplastron; for, fossa orbitalis; fr, frontal; hyo, hyoplastron; ju, jugal; m, marginal scale; mb, mandible; mx, maxilla; na, nasal; nu, nuchal plate; or, orbit; p, peripheral plate; pa, parietal; pf, prefrontal; pm, premaxilla; po, postorbital; qj, quadratojugal; sur, surangular; vo, vomer.

that are more derived than *Kayentachelys aprix*, including *Mongolochelys efremovi*, *Kallokibotion bajazidi* and crown-group turtles. In the latter, the extent of the parietal on the skull roof may be secondarily reduced by the development of the upper temporal emargination, but even in these cases the parietal is still an elongate bone. In contrast, more basal turtles like *Proganochelys quenstedti* and *Palaeochersis talampayensis* have a comparatively reduced parietal that is wider than long. A similar morphology is known in *Meiolania platyceps* Owen 1886 a stem turtle from the Pleistocene of Australia (Gaffney, 1983), but in that case it is obviously a secondarily derived morphology that is probably related to the peculiar horned skull of this species. *Kayentachelys aprix* presents an intermediate morphology of the parietal (Sterli & Joyce, 2007: fig. 3): it is larger and more elongate than in the basalmost taxa, but not as much as in more derived forms like *Eileanchelys waldmani*, *Kallokibotion bajazidi*, *Mongolochelys efremovi* and crown-group turtles.

Jugal—In turtles, the jugal is one of the main elements of the cheek area. Usually, it forms part of the orbital margin and presents a medial process anteriorly that contacts the pterygoid and/or the palatine (Gaffney, 1979). The jugal can be observed in NMS G 2004.31.16f (Fig. 3.9) and also, but only partly, in NMS G 2004.31.16d (Fig. 3.7). The jugal is an elongate quadrangular element that forms a great part of the zygomatic area. It is exposed for its entire length along the ventral cheek margin, which does not present any evidence of lower temporal emargination. The jugal contacts the maxilla anteriorly below the orbit, the postorbital dorsally and the quadratojugal posteriorly. The medial process of the jugal contacts what appears to be the palatine in the floor of the left fossa orbitalis of NMS G 2004.31.16d, but no further observation of the jugal internal morphology can be made. The jugal-postorbital suture is sub-horizontal and enters the orbital margin approximately halfway up the orbit. The posterior contact with the quadratojugal (only preserved in NMS G 2004.31.16f) may have been slightly concave (Fig. 3.9). The suture between the maxilla and jugal is more or less vertical. It is remarkable that this suture is situated below the orbit, so that the jugal not only forms part of the posterior margin of the orbit as in most turtles but also part of its ventral margin. This morphology is common to all stem turtles in which this area of the skull is known, whereas it is uncommon in crown-group turtles where the jugal is entirely posterior to the orbit and only forms part of its posterior margin (with the exception of marine turtles and some pleurodires).

Quadratojugal—The quadratojugal, which forms the zygomatic arch along with the jugal, is lost or greatly reduced in those turtles with an extensive lower temporal emargination (Gaffney, 1979). In *Eileanchelys waldmani*, there is no cheek emargination and the quadratojugal is well developed (only visible in NMS G 2004.31.16f; Fig. 3.9). It is a quadrangular element that is higher than long. It contacts the jugal anteriorly, the postorbital dorsally, the squamosal posterodorsally and the quadrate posteriorly. The contact with the jugal may have been slightly convex. Posteriorly, the quadratojugal has a concave, C-shaped suture with the quadrate that is typical of most turtles. However, the quadratojugal does not appear to participate in the formation of the cavum tympani. The dorsal contact with the postorbital may have been slightly convex, although the skull NMS G 2004.31.16f is severely damaged in this area (Fig. 3.9). In the same way, the quadratojugal-squamosal suture appears to be very short but the poor preservation of the remains prevents any definitive conclusion.

Squamosal—The squamosal is usually well developed in turtles. It lies posterodorsal to the cavum tympani on each side of the skull and forms a large portion of the antrum postoticum. The morphology of the squamosal is mostly unknown in *Eileanchelys waldmani*. NMS G 2004.31.16f is the only specimen where a part of the squamosal is preserved, which consists only of a fragment of the anterior part of the bone (Fig. 3.9). It shows that the squamosal contacts the quadrate lateroventrally, the quadratojugal anteroventrally, the postorbital anteriorly and the parietal medially. Although the squamosal is missing in NMS G 2004.31.15, its sutures with the opisthotic and quadrate are partly preserved (Fig. 3.5 C,D). These sutures indicate that an antrum postoticum was present and that it was formed, at least posteriorly, by the squamosal. The exact shape and extent of the antrum postoticum is unknown in *Eileanchelys waldmani*, but it seems to be better developed than that of *Kayentachelys aprix* (MCZ 8917, TMM 43653-1 and TMM 43670-2).

***Postorbital*—**The postorbital has a great size range among turtles (Gaffney, 1979), but is generally well-developed in basal forms (i.e., stem turtles and stem cryptodires). Indeed, in *Eileanchelys waldmani*, the postorbital is a greatly elongate bone that contacts the frontal anteromedially, the jugal anteroventrally, the quadratojugal posteroventrally, the squamosal posteriorly and the parietal dorsally. The postorbital is almost entirely preserved in NMS G 2004.31.16f (Fig. 3.9), although it is severely damaged, whereas only the anteriormost part is preserved in NMS G 2004.31.16d (Fig. 3.7) and NMS G 2004.31.16e (Fig. 3.8). As in most turtles, the postorbital forms the posterodorsal margin of the orbit. There is no trace of a descending process that would contact the palatine and form a posterior wall to the orbit, in contrast to pleurodires. Compared to more basal forms, *Eileanchelys waldmani* is characterised by an expanded postorbital skull length. In accordance with this observation, the postorbital of *E. waldmani* is significantly elongated compared to that of *Proganochelys quenstedti*, *Palaeochersis talampayensis* and *Kayentachelys aprix*.

***Supratemporal*—**Currently, only the basalmost turtles *Proganochelys quenstedti*, *Palaeochersis talampayensis* and *Odontochelys semitestacea* Li *et al.* 2008 are known to possess a supratemporal, which is intercalated between the parietal and squamosal on the posterior margin of the skull roof. Due to poor preservation, it is unclear whether or not *Australochelys africanus* had a supratemporal (BP/1/4933; Gaffney & Kitching, 1995). Similarly, this area of the skull is damaged in all available specimens of *Kayentachelys aprix* (Sterli & Joyce, 2007: 680) and *Eileanchelys waldmani*, so that it is not possible to determine the presence or absence of this element in these taxa. However, all more derived taxa lack a supratemporal (Joyce, 2007). With respect to the phylogenetic position of *Kayentachelys aprix* and *Eileanchelys waldmani* (Joyce, 2007; Anquetin *et al.*, 2009; see also Chapter 5), the absence of the supratemporal in these taxa, though probable, needs to be confirmed.

Palatal elements

***Premaxilla*—**In the majority of turtles, the premaxillae are paired elements that floor the fossa nasalis and form the ventral margin of the apertura narium externa and the anterior tip of the triturating surface. The premaxilla can be observed only in NMS G 2004.31.16d (Fig. 3.7). It contacts the maxilla laterally and the vomer posteriorly on the floor of the fossa nasalis (see Vomer, below). Because of the relatively poor preservation of this area in NMS G 2004.31.16d, it is unclear whether the premaxillae are paired or fused, and whether or not foramina praepalatinum are present. The palatal surface of the premaxilla is covered by the dentaries in NMS G 2004.31.16d, so that its contribution to the triturating surface is unknown. In most tetrapods, the premaxillae send a dorsal medial process that separates the external nares into two openings. This plesiomorphic condition is present in *Proganochelys quenstedti*, *Palaeochersis talampayensis*, *Odontochelys semitestacea*, and probably also in *Australochelys africanus*. The Late Cretaceous *Kallokibotion bajazidi* and Pleistocene *Meiolania platyceps* also have an apertura narium externa divided into two openings, but the condition in these taxa does not appear to be homologous with the plesiomorphic tetrapod feature (Gaffney, 1983; Gaffney & Meylan, 1992; Joyce, 2007). All other turtles, including *Kayentachelys aprix* and *Eileanchelys waldmani*, have an undivided apertura narium externa.

Maxilla—In turtles, the maxilla usually consists of three processes (Gaffney, 1979). The alveolar process, which consists of the labial ridge, is a thin, sharp blade enclosed on both sides by the rhamphotheca (the horny beak). The palatine process is a horizontal plate that extends medially flooring the fossa orbitalis and meets the palatal bones (e.g., palatine, vomer, pterygoid). On the ventral surface of the palatine process a triturating surface is usually developed and is covered in life by the rhamphotheca. Finally, the prefrontal process is an anterodorsal extension of the maxilla that forms the lateral margin of the apertura narium externa, the lateral wall of the fossa nasalis and the anterior and ventral parts of the orbital margin and/or the anterior wall of the fossa orbitalis. *Odontochelys semitestacea* is the only turtle known to have teeth on the maxilla instead of a labial ridge (Li *et al.*, 2008). In *Eileanchelys waldmani*, all three paratype skulls show at least part of the maxilla (Figs. 3.7, 3.8 and 3.9). However, no specimen shows a ventral view of this bone, so that the triturating surface cannot be described. The maxilla contacts the jugal posteriorly, the prefrontal dorsally and medially, the nasal anterodorsally and the premaxilla anteriorly. Within the fossa orbitalis, it is apparent that the maxilla contacts the palatine medially (NMS G 2004.31.16d). A posteromedial contact with the pterygoid (found in most turtles) cannot be confirmed as this area is not preserved in any specimen. A minute but definite contact between the maxilla and vomer can be observed on the floor of the fossa nasalis lateral to the premaxilla-vomer suture (NMS G 2004.31.16d; Fig 3.7C,D; see Vomer, below). As in most turtles, the maxilla forms the lateral wall of the fossa nasalis as well as the anterior and anteroventral margins of the orbit. The foramen orbito-nasale is not preserved in any specimen.

Vomer—The contacts of the vomer with the other palatal bones are highly variable within turtles and the morphology of this bone has greatly changed between stem turtles and the crown-group. *Eileanchelys waldmani* offers a unique opportunity to understand the evolution of this feature (see Discussion, below). The vomer can be observed in NMS G 2004.31.16d (Fig. 3.7) and NMS G 2004.31.16e (Fig. 3.8). In the former, the anterior half of the vomer can be seen in ventral and

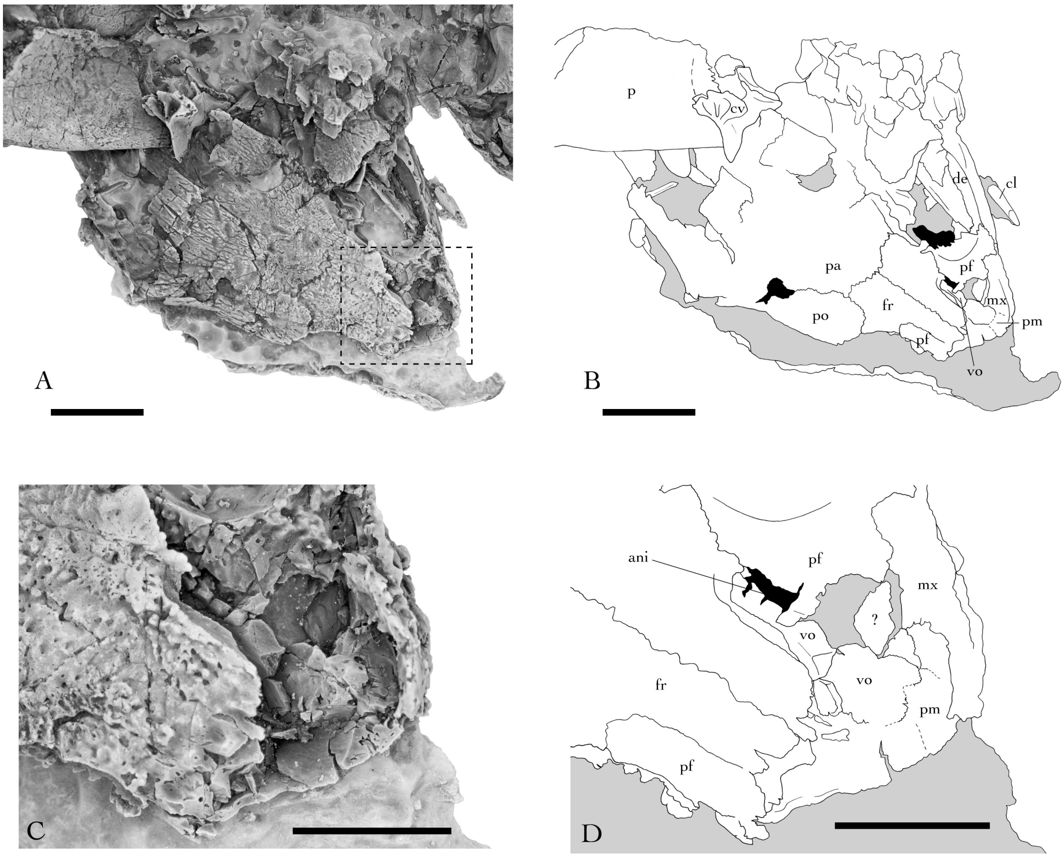

Figure 3.8—*Eileanchelys waldmani*, NMS G 2004.31.16e. A, B, dorsal view; C, D, enlargement of the snout area (shown in A). Scale bars: A, B, 10 mm; C, D, 5 mm. Abbreviations: ani, apertura narium interna; cl, claw; cv, cervical vertebra; de, dentary; fr, frontal; mx, maxilla; p, peripheral plate; pa, parietal; pf, prefrontal; pm, premaxilla; po, postorbital; vo, vomer.

dorsal (within the fossa nasalis) view, whereas in the latter specimen the vomer is only partly apparent in dorsal view. No specimen shows the posterior part of this bone. In *Eileanchelys waldmani*, the vomer is a narrow and elongate unpaired bone. The plesiomorphic condition found in most tetrapods, as well as *Proganochelys quenstedti*, *Palaeochersis talampayensis*, and also probably *Australochelys africanus* (Gaffney & Kitching, 1995; BP/1/4933), consists of paired vomers. In all more derived turtles, including *Kayentachelys aprix*, *Eileanchelys waldmani* and *Heckerochelys romani* Sukhanov 2006, the vomers are fused into a single element. In contrast to most turtles, but similar to the condition that is found in *Proganochelys quenstedti*, *Australochelys africanus*, *Palaeochersis talampayensis*, *Kayentachelys aprix* and *Heckerochelys romani*, the vomer is a flat element that lacks a medial septum dividing the apertura narium interna ventrally. However, it is planar (i.e., not curved), differing from the dorsally convex element seen in *Proganochelys quenstedti* (SMNS 16980) and *Australochelys africanus* (BP/1/4933). Sukhanov (2006: 113) described a "more or less horizontal" vomer in *Heckerochelys romani*. This might correspond to the morphology in *Eileanchelys waldmani*, but there is no illustration of the vomer of *H. romani* (Sukhanov, 2006) so that it is difficult to extend the comparison to this taxon. There is no evidence of vomerine teeth, which currently are known with confidence only in *Proganochelys quenstedti* and *Odontochelys semitestacea*

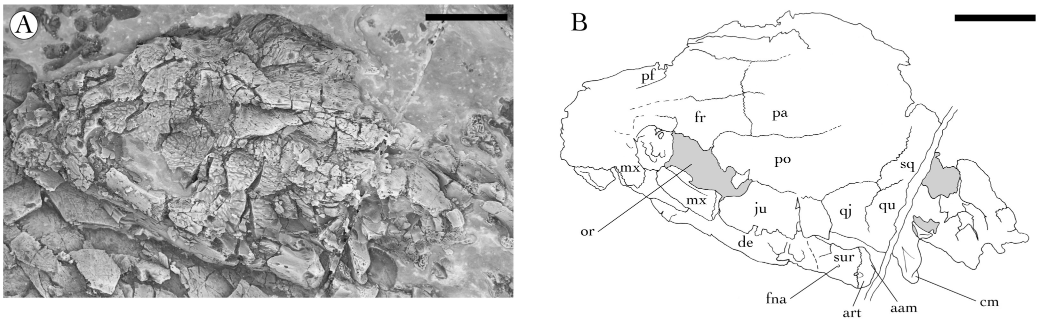

Figure 3.9—*Eileanchelys waldmani*, NMS G 2004.31.16f. A, B, dorsolateral view. Scale bars: A, B, 10 mm. Abbreviations: aam, area articularis mandibularis; art, articular; cm, condylus mandibularis; de, dentary; fna, foramen nervi auriculotemporalis; fr, frontal; ju, jugal; mx, maxilla; or, orbit; pa, parietal; pf, prefrontal; po, postorbital; qj, quadratojugal; qu, quadrate; sq, squamosal; sur, surangular.

(Gaffney, 1990; Li *et al.*, 2008). Anteriorly, the vomer contacts the premaxilla on the floor of the fossa nasalis (Figs. 3.7 and 3.8). Although the exact limits of each bone in this area are slightly uncertain, there is a definite contact between the vomer and maxilla lateral to the premaxilla-vomer suture (NMS G 2004.31.16d; Fig. 3.7C,D). The contact with the maxilla is one of the most consistent contacts of the vomer in turtles (Gaffney, 1979). Usually, the maxilla meets the vomer twice: firstly anterodorsally along the anterolateral portion of the vomer on the floor of the fossa nasalis, and secondly posteroventrally at the level of the ventral expansion of the vomer on the triturating surface, which forms an incipient secondary palate. This corresponds to the derived vomerine morphology found in most turtles (i.e., *Meiolania platyceps*, *Mongolochelys efremovi*, *Kallokibotion bajazidi*, and more derived taxa that possess a vomer): the vomer consists of an anterodorsal and a posteroventral portion expanded horizontally and connected by a sagittal septum dividing the meatus choanae (the "dumbbell shape" of Gaffney, 1979). As illustrated by *Proganochelys quenstedti* and *Eileanchelys waldmani*, in basalmost turtles the vomer is a flat element that lacks a ventral septum and that contacts the maxilla only for a short distance anterolaterally. Posterior to its anterior contacts with the premaxilla and maxilla, the vomer is exposed and forms the medial margin of the apertura narium interna (NMS G 2004.31.16d; Fig. 3.7C,D). At the level of the anterior wall of the orbit, the vomer has a small dorsal suture with the descending process of the prefrontal and they both define the ventral margin of the fissura ethmoidalis (NMS G 2004.31.16d and NMS G 2004.31.16e; see Fig. 3.8C,D). Posterior to this contact, the vomer is still exposed laterally for at least a short distance, but the posterior part of this bone is not preserved in any specimen, so that the posterior contacts of the vomer with the palatine and pterygoid are uncertain. In all turtles more derived than *Kayentachelys aprix* and *Eileanchelys waldmani*, the vomer is entirely framed laterally by the maxilla and the palatine. In contrast, *Proganochelys quenstedti*, *Palaeochersis talampayensis* and *Australochelys africanus* have a vomer that is exposed laterally for most of its length and that does not meet the descending process of the prefrontal (due to poor preservation, the latter feature is unclear for *Palaeochersis talampayensis* and *Australochelys africanus*; BP/1/4933; Sterli *et al.*, 2007). Currently, *Eileanchelys waldmani* is the most primitive turtle to show a prefrontal-vomer contact. Sterli & Joyce (2007: 680) tentatively proposed that a prefrontal-vomer contact was also present in *Kayentachelys aprix*, but this would need to be confirmed. Personal observation of MCZ 8917 and MNA V1558 (the holotype of *K. aprix*) suggests that the contact between the prefrontal and vomer is not preserved in either specimens, so that the conclusion of Sterli & Joyce (2007) may not be correct.

Palatine—The palatine is not preserved in any specimen of *Eileanchelys waldmani*, with the exception of a fragment on the floor of the left fossa orbitalis of NMS G 2004.31.16d (Fig. 3.7A,B). This fragment of palatine contacts the jugal posterolaterally and the maxilla laterally. The foramen orbito-nasale and the foramen palatinum posterius are not preserved in any specimen. Sterli & Joyce (2007: 680) state that there is no contact between the palatine and jugal in *Kayentachelys aprix*. However, as illustrated by Gaffney (1990) in *Proganochelys quenstedti*, the jugal often overlaps the maxilla dorsally and contacts the palatine in the floor of the fossa orbitalis, whereas this contact is covered ventrally by a posterior extension of the maxilla that contacts the pterygoid. A jugal-palatine contact is indeed present in the floor of the fossa orbitalis of *Kayentachelys aprix* (MCZ 8917).

Palatoquadrate elements

Quadrate—The quadrate is a major bone in the turtle skull as it participates in the formation of several important structures: the mandibular articulation, the middle ear (which is highly specialised in turtles), and the enclosed cranioquadrate space (the area between the palatoquadrate elements and the primary neurocranium). No complete quadrate is known for *Eileanchelys waldmani*, but most of this bone can be seen in NMS G 2004.31.15 (Figs. 3.5 and 3.6) and a partial quadrate is present in NMS G 2004.31.16f (Fig. 3.9). The quadrate contacts the pterygoid anteromedially, along the anterior wall of the cavum acustico-jugulare, the squamosal laterodorsally, the quadratojugal anteriorly, as well as the prootic anteromedially and the opisthotic posteromedially (both in the roof of the cavum acustico-jugulare and in the floor of the fossa temporalis superior). Laterally the quadrate forms a well-developed cavum tympani and the posterodorsal portion of the cavum indicates the presence of an antrum postoticum (NMS G 2004.31.15; Fig. 3.5E,F). However, as the squamosal is missing in NMS G 2004.31.15, the posterior development of the antrum postoticum is unknown. The incisura collumellae auris is wide open posteroventrally. The condylus mandibularis consists of two facets separated by an anteroposterior groove. The medial facet is slightly concave and appears to extends further ventrally than the lateral facet. Dorsomedial to the processus articularis, the quadrate sends a vertical pterygoid process that covers the quadrate process of the pterygoid anteriorly. As in all turtles, these two processes form the anterior wall of the cavum acustico-jugulare and the posterior wall of the fossa temporalis inferior. Due to poor preservation of the relevant area, the medial extent of the pterygoid process of the quadrate is unclear. In the floor of the fossa temporalis superior (i.e., on the dorsal part of what could be called the otic chamber), the quadrate forms the lateral half of the foramen stapedio-temporale, the medial half being formed by the prootic. There is no trace of a processus trochlearis oticum on the anterodorsal slope of the otic chamber. The aditus canalis stapedio-temporalis and the posterior opening of the canalis cavernovus open along the quadrate-prootic suture in the roof of the cavum acustico-jugulare, so that the quadrate forms their lateral half. It is noteworthy that in *Eileanchelys waldmani* these openings are situated far apart within the cavum acustico-jugulare, with the aditus canalis stapedio-temporalis opening at the level of the anterior wall of the fenestra ovalis, whereas they are often closer or even associated (the aditus canalis stapedio-temporalis opening in the roof of the canalis cavernosus) in more derived species, with the aditus canalis stapedio-temporalis opening anterior to the fenestra ovalis. A similar morphology occurs in *Kayentachelys aprix* (MCZ 8917) and maybe also in *Australochelys africanus* (BP/1/4933; see Discussion, below).

***Pterygoid*—**The pterygoid plays an important role in the early evolution of the turtle skull and in the differentiation of pleurodires and cryptodires, although this last point is not completely elucidated. In turtles, the pterygoid can be described as a triradiate plate of bone with an anterior palatine process, a lateral transverse process and a posterolateral quadrate ramus (Gaffney, 1990). Only the posterior part of the pterygoid is preserved in the available material of *Eileanchelys waldmani*. Ancestrally, the tetrapod skull is kinetic, with two movable joints between the braincase and palatoquadrate elements. *Proganochelys quenstedti* and *Odontochelys semitestacea* retain one of these kinetic joints (Gaffney, 1990; Li *et al.*, 2008): the basipterygoid articulation (the cranioquadrate space is open and the pterygoid articulates with the basisphenoid). All other turtles possess an akinetic skull: the cranioquadrate space is closed by a sutural contact between the pterygoid and basisphenoid. The closing of the cranioquadrate space in turtles implies the formation of specific structures for the passage of nerves and arteries. For example, the lateral head vein (vena capitis lateralis), which passes through the cranioquadrate space in other reptiles, lies on the dorsal surface of the pterygoid in a trough, the sulcus cavernosus. This sulcus may be roofed posteriorly, notably by the quadrate and prootic, forming the canalis cavernosus. The posterior extent of the pterygoid is highly variable among turtles. In stem turtles and in panpleurodires, the posterior extent of the pterygoid is usually limited. In contrast, the pterygoid extends posteriorly between the basisphenoid and quadrate for an extensive length and even contacts the basioccipital in numerous pancryptodires. In this case, the pterygoid floors the cavum acustico-jugulare and even forms a great part of the canalis caroticus internus in eucryptodires. The pterygoid of *Eileanchelys waldmani* can only be observed in NMS G 2004.31.15 (Fig. 3.5A,B). The pterygoid of this specimen is broken approximately at the hypothetical level of the basipterygoid processes, which are small lateral processes of the basisphenoid that contributed to the former basipterygoid articulation and that are found in *Kayentachelys aprix*, *Heckerochelys romani* and *Condorchelys antiqua* Sterli 2008, despite the fusion of the basipterygoid articulation. Consequently, the presence of these basipterygoid processes, of pterygoid teeth (found in *K. aprix*) and of an interpterygoid vacuity (found in *K. aprix*, *H. romani* and *C. antiqua*) remain conjectural in *Eileanchelys waldmani*. As preserved in NMS G 2004.31.15, the pterygoid contacts the quadrate posterolaterally, the prootic posteriorly and the basisphenoid medially. Posteriorly, the pterygoid does not reach the basioccipital. A canalis cavernosus is present and is entirely floored by the pterygoid. However, the posterior extent of the pterygoid is relatively short and there is no flooring of the cavum acustico-jugulare, neither by the pterygoid as in pancryptodires nor by the quadrate and/or prootic as in most panpleurodires. A similar morphology (i.e., a pterygoid that floors a canalis cavernosus but does not floor the cavum acustico-jugulare) is known in *Kayentachelys aprix*, *Heckerochelys romani* and *Condorchelys antiqua* (Sukhanov, 2006; Sterli & Joyce, 2007; Sterli, 2008). The posterior extent of the pterygoid (or the location of the posterior opening of the canalis cavernosus) is similar in *Eileanchelys waldmani* and in *Heckerochelys romani*. This posterior extent is less pronounced in *Kayentachelys aprix*, but more pronounced in *Condorchelys antiqua*, which could suggest a transformation series. More evidence is needed to test this hypothesis. As a result of the posterior extent of the pterygoid in *Eileanchelys waldmani*, the posterior opening of the canalis nervi facialis is located in the roof of the canalis cavernosus, whereas in *Kayentachelys aprix* it is located outside of the canalis cavernosus in the roof of the cavum acustico-jugulare (Sterli & Joyce, 2007: fig. 5D).

Braincase elements

Supraoccipital**—** In turtles, the supraoccipital forms posterior part of the cavum cranii and is characterised by the development of a dorsal, vertical crest, the crista supraoccipitalis, which separates the posterior portion of the fossae temporalis superior medially. The crista supraoccipitalis is very poorly developed in *Proganochelys quenstedti*, whereas it is fully developed in more derived forms and sometimes extends posteriorly far beyond the occipital region, creating an additional attachment site for the jaw musculature (Gaffney, 1979; Joyce, 2007). Concerning *Eileanchelys waldmani*, the supraoccipital can only be observed in NMS G 2004.31.15 (Fig. 3.5), but its contacts are difficult to establish. As in most turtles (Gaffney, 1979), the supraoccipital seems to contact the exoccipital posteroventrally, the opisthotic posterolaterally, the prootic anterolaterally and the parietal anteriorly. In both dorsolateral margins of the foramen magnum, the suture between the supraoccipital and the exoccipital is clearly visible. The sutures of the supraoccipital with the opisthotic and prootic are either fused or not preserved in NMS G 2004.31.15. In dorsal view, the supraoccipital-opisthotic contact might be represented by a light wrinkle that curves medially from the point where the supraoccipital-exoccipital suture meets the opisthotic to the area located just posteromedial to the groove marking the passage of the stapedial artery. As in most turtles, the supraoccipital forms the dorsal margin of the foramen magnum. Internally, the supraoccipital also forms the dorsal margin of the hiatus acusticus, the opening between the cavum cranii and the cavum labyrinthicum. There is a well-developed crista supraoccipitalis, but the total height of this structure is unknown as the temporal skull roof is missing. The part of the crista supraoccipitalis positioned just above the foramen magnum shows a sub-vertical margin that faces posteriorly, which could indicate that the crista supraoccipitalis did not extend posteriorly much beyond the level of the foramen magnum.

***Exoccipital*—** In turtles, the exoccipitals lie lateral to the foramen magnum and usually form part of the condylus occipitalis, although this is variable. The exoccipital can only be seen in NMS G 2004.31.15 (Figs. 3.5E,F and 3.6). It contacts the supraoccipital dorsally, the opisthotic laterally and anteriorly, and the basioccipital ventrally. There is no medial contact of the exoccipitals, either dorsal or ventral to the foramen magnum. The basioccipital-exoccipital suture can be followed up to the base of the condylus occipitalis then it appears to be fused, hence the exoccipital probably forms part of the condyle but it is unclear how much it contributes. Posteroventrally, the exoccipital also participates in the formation of the tuberculum basioccipitale (see Basioccipital, below). As in *Proganochelys quenstedti*, *Palaeochersis talampayensis*, *Australochelys africanus*, *Heckerochelys romani* and *Condorchelys antiqua*, there is no foramen jugulare posterius, and consequently no proper recessus scalae tympani, but a foramen jugulare intermedium (*sensu* Sterli & Joyce, 2007: 685). The exoccipital forms the posteromedial and ventral margins of the foramen jugulare intermedium, as well as the posterior half of the foramen jugulare anterius and the ventromedial margin of the fenestra perilymphatica (see Opisthotic, below). In NMS G 2004.31.15, each exoccipital is pierced by two foramina nervi hypoglossi, the anterior one opening in the margin of the foramen jugulare intermedium. The exoccipital forms the lateral and ventrolateral margins of the foramen magnum, which is approximately circular in outline.

***Basioccipital*—** The basioccipital floors the posterior part of the cavum cranii and usually forms part of the condylus occipitalis. The morphology of the ventral surface of the basioccipital is somewhat variable among turtles. Most turtles possess variably developed paired tubercula basioccipitales, some may also develop a series of rugosities and depressions for muscular attachment (Gaffney, 1979). In *Eileanchelys waldmani*, the basioccipital can only be observed in NMS G 2004.31.15 (Figs. 3.5 and 3.6). It contacts the basisphenoid anteriorly, the processus interfenestralis of the opisthotic anterodorsally and the exoccipital dorsally. The basioccipital-basisphenoid suture is either fused or not preserved in the specimen, but it can be approximately located (Fig. 3.5A,B). There is no contact between the basioccipital and pterygoid, which differs from what can be found in most pancryptodires (Joyce, 2007; see Pterygoid, above). In contrast to *Proganochelys quenstedti*, *Palaeochersis talampayensis* and *Australochelys africanus*, the thickness of the basicranial floor (formed by the basioccipital and basisphenoid) is reduced in *Eileanchelys waldmani*. This reduction is characteristic of all more derived turtles, whereas the condition in *Kayentachelys aprix* is intermediate between the aforementioned species and other turtles (Sterli & Joyce, 2007). The ventral surface of the basioccipital is flat and proportionally wider than that of *Kayentachelys aprix*, *Heckerochelys romani* and *Condorchelys antiqua*. Posterolaterally, the basioccipital, along with the exoccipitals, develops a pair of dorsoventrally flattened tubercula basioccipitales. These structures are thicker and oriented more ventrally in *Kayentachelys aprix*, whereas their development in *Heckerochelys romani* and *Condorchelys antiqua* is difficult to estimate from published illustrations (Sukhanov, 2006; Sterli, 2008). On the dorsal surface of the basioccipital (i.e., on the floor of the cavum cranii), the basis tuberculi basalis (Fig. 3.5G,H) is preserved near the basisphenoid-basioccipital suture, but posteriorly there is no trace of the crista dorsalis basioccipitalis. It cannot be determined if the crista is genuinely absent or if this is merely a consequence of poor preservation, but in place of the crista there is a rounded concavity on this part of the braincase floor. As in other turtles, the basioccipital forms the posteroventral margin of the hiatus acusticus dorsoanterolaterally. Posteriorly the basioccipital forms at least part of the condylus occipitalis. It seems that the remainder of the condyle is formed by the exoccipitals, but their sutures with the basioccipital are closed (see Exoccipital, above). In contrast to the majority of turtles where it is a rounded triangular or oval structure, the condylus occipitalis of *Eileanchelys waldmani* is circular in posterior view (Fig. 3.5E,F). In *E. waldmani*, the basioccipital does not participate in the formation of either the fenestra perilymphatica (see Opisthotic, below) or the foramen jugulare anterius. This differs from *Kayentachelys aprix* where the basioccipital participates in both openings (Sterli & Joyce, 2007). In turtles, the fenestra perilymphatica is usually either formed by the opisthotic alone or by the opisthotic and a small ventromedial contribution from the basioccipital (Gaffney, 1979). The foramen jugulare anterius is usually formed by the opisthotic anteriorly and exoccipital posteriorly, but the basioccipital often enters its ventral margin and forms a small part of the medial wall of the recessus scalae tympani (Gaffney, 1979). Consequently, the formation of these two openings by the opisthotic and exoccipital to the exclusion of the basisphenoid in *Eileanchelys waldman*i is rather uncommon among turtles. However, the detailed anatomy of this region of the skull is rarely available in fossil turtles, so that comparisons are difficult.

Prootic**—**The prootic forms most of the anterior part of the otic chamber and is involved in the formation of numerous structures of the inner ear. In the turtle skull, the prootic has two main exposures: the first within the cavum acustico-jugulare where the prootic participates in the formation of the inner ear, and the second on the dorsal surface of the otic chamber where the prootic participates in the formation of diverse structures related to the temporosphenoidal area. In *Eileanchelys waldmani*, the prootic is exposed in ventral view (NMS G 2004.31.15; Figs. 3.5A,B and 3.6). This plesiomorphic condition is also present in *Proganochelys quenstedti*, *Palaeochersis talampayensis*, *Odontochelys semitestacea*, *Kayentachelys aprix*, *Heckerochelys romani*, *Condorchelys antiqua* and most panpleurodires, but not in *Meiolania platyceps*, *Mongolochelys efremovi* or *Kallokibotion bajazidi* in which the pterygoid extends posteriorly and covers the prootic as it does in pancryptodires (Joyce, 2007). In NMS G 2004.31.15, the prootic contacts the opisthotic posteriorly, the supraoccipital dorsomedially, the basisphenoid ventromedially, the pterygoid anteroventrally and the quadrate laterally. The prootic forms the anterior half of the large fenestra ovalis as well as the anterior wall of the cavum labyrinthicum (Fig. 3.6). Ventrally, the prootic contacts the anteroventral margin of the processus interfenestralis of the opisthotic. This contact is sutural for its anterior half, but it may have been cartilaginous posteriorly as a small space is present between these bones in NMS G 2004.31.15. Because of the sutural contact between the prootic and the processus interfenestralis of the opisthotic, the fenestra ovalis and cavum labyrinthicum are entirely floored. This feature is present in most stem turtles, but not in more derived turtles, or at least not in a homologous fashion: the cavum labyrinthicum of most pancryptodires is floored due to the posterior extent of the pterygoid. The recessus labyrinthicus prooticus of the cavum labyrinthicum is very large in *Eileanchelys waldmani*. Again, comparison is limited by the fact that this region is rarely available in fossils. In the anterior part of the cavum acustico-jugulare, the prootic forms the medial part of the canalis cavernosus. The canalis nervi facialis, which is formed by the prootic, opens in the dorsal roof of the canalis cavernosus just anterior to the posterior opening of the latter. The fact that the canalis nervi facialis opens within the canalis cavernosus, as in most turtles, is an indication of the posterior extent of the latter (see Pterygoid, above). Laterally, the prootic also forms the medial half of the aditus stapedio-temporalis, which is located approximately at the level of the anterior margin of the fenestra ovalis as in *Kayentachelys aprix* (Sterli & Joyce, 2007: 686). As in most turtles, the prootic forms the anterior margin of the hiatus acusticus, the fossa acustico-facialis and the anterolateral wall of the braincase (all of this is visible within the cavum cranii of NMS G 2004.31.15). On the dorsal surface of the otic chamber most of the sutures are either fused or not preserved, so that the relationships between the prootic, supraoccipital, parietal, quadrate and opisthotic remain conjectural. This part of the prootic is severely damaged in NMS G 2004.31.15 and corresponds to where the specimen was eroded prior to collection (Fig. 3.5G,H). The prootic apparently forms the medial half of the foramen stapedio-temporale, the lateral half being formed by the quadrate. A trough curving anteromedially from the foramen stapedio-temporale marks the passage of the stapedial artery on the dorsal surface of the supposed prootic (Fig. 3.5C,D). Although this area is damaged, there is no evidence of a processus trochlearis oticum on the quadrate and prootic. The anteromedial part of the prootic is missing in NMS G 2004.31.15, so that the presence of a prootic foramen (resulting from an ossification of the pila prootica between the processus clinoideus and the prootic, which is found in *Proganochelys quenstedti* and *Kayentachelys aprix*) and the development of the foramen nervi trigemini cannot be assessed.

Opisthotic**—**The opisthotic forms the posterior part of the otic chamber and the posterolateral wall of the braincase. It roofs the posterior part of the cavum acustico-jugulare and possesses a lateral process, the processus paroccipitalis, that has a broad sutural contact with the squamosal and quadrate (the location of a former kinetic joint in the ancestral tetrapod skull; see Romer, 1956 and Gaffney, 1990). Finally, the opisthotic is characterised by a ventromedial process, the processus interfenestralis, which plays an important role in various structures of the inner ear (see below). NMS G 2004.31.15 is the only specimen in which the opisthotic can be observed (Figs. 3.5 and 3.6). It contacts the supraoccipital dorsomedially, the prootic anteriorly, the basioccipital ventrally, the quadrate laterally, the squamosal posterolaterally and the exoccipital posteromedially. On the dorsal surface of the otic chamber, the sutures of the opisthotic with the prootic and supraoccipital are either fused or not preserved, so that it is unclear whether or not the opisthotic is involved in the formation of the foramen stapedio-temporale. The processus paroccipitalis is flattened dorsoventrally and extends posteriorly beyond the level of the condylus occipitalis (left side of NMS G 2004.31.15). The lateral extent of the processus paroccipitalis is somewhat variable among turtles, being for example short in *Chelonia mydas* (the green turtle) and long in podocnemids (Gaffney, 1979: 136). In *Eileanchelys waldmani*, the processus paroccipitalis of the opisthotic reaches the level of the condylus mandibularis laterally, which is similar to the extent present in most turtles. As described above (see Prootic), the processus interfenestralis of the opisthotic has a sutural contact with the prootic and this contact floors the fenestra ovalis and cavum labyrinthicum. The processus interfenestralis also has a broad sutural contact with the basioccipital ventrally, so that there is no hiatus postlagenum. The development of the processus interfenestralis of the opisthotic in *Eileanchelys waldmani* is intermediate between the robust, thick structure seen in the most basal turtles (i.e., *Proganochelys quenstedti*, *Palaeochersis talampayensis*, *Australochelys africanus* and *Kayentachelys aprix*) and the slender, flattened sheet of bone seen in most crown-group turtles. The processus interfenestralis of *Eileanchelys waldmani* is still a relatively large element with respect to the rest of the skull, but it is considerably flattened and reaches the basicranium floor ventrally, which is not the case in more basal taxa. However, it is not the transverse sheet of bone that forms a proper anterior wall to the recessus scalae tympani as seen in more derived turtles. It is difficult to assess the morphology of the processus interfenestralis in *Heckerochelys romani* and *Condorchelys antiqua* based on the published illustrations (Sukhanov, 2006; Sterli, 2008), but it appears to be more robust in these taxa than in *Eileanchelys waldmani*. As in all turtles, the base of the processus interfenestralis is pierced by the foramen externum nervi glossopharyngei. The processus interfenestralis of the opisthotic forms the posterior and posteroventral margins of the fenestra ovalis, as well as the posterior half of the cavum labyrinthicum (Fig. 3.6). The processus interfenestralis forms most of the fenestra perilymphatica, but a ventromedial contribution from the exoccipital is uncommon among turtles. Usually, when the fenestra perilymphatica is not entirely contained within the opisthotic, it is the basioccipital that forms the ventromedial part of it. The processus interfenestralis of the opisthotic also forms the posterior margin of the hiatus acusticus, the anterodorsal margin of the foramen jugulare anterius and the anterolateral margin of the foramen jugulare intermedium. The fenestra ovalis of *Eileanchelys waldmani* is a relatively large triangular opening that faces laterally. The fenestra ovalis of more derived turtles appears to be proportionally smaller, but there is currently no detailed survey of this character among turtles. Finally, several foramina and canals associated with the membranous inner ear (semicircular canals) are preserved in the roof of the cavum labyrinthicum (formed by the prootic and opisthotic). However, these are not readily observable and their description would require further investigation (e.g., following CT-scanning).

***Basisphenoid*—**The basisphenoid forms the anteroventral floor of the cavum cranii. In turtles, the basisphenoid is actually composed of the fused basisphenoid and parasphenoid of other reptiles (Romer, 1956; Gaffney, 1979). The morphology of the basisphenoid is relatively important for turtle systematics (e.g., Gaffney, 1979; Gaffney & Meylan, 1988; Joyce, 2007). Unfortunately, most of the basisphenoid is unknown in *Eileanchelys waldmani*. The posteriormost part of the basisphenoid is preserved in NMS G 2004.31.15 (Fig. 3.5A,B) and some internal parts of the basisphenoid seems to be observable in NMS G 2004.31.16e, but the latter are extremely difficult to interpret. In NMS G 2004.31.15, the basisphenoid is broken anteriorly at the level of the basipterygoid process (if present; see Pterygoid, above). The basisphenoid contacts the pterygoid laterally, the prootic posterolaterally and the basioccipital posteriorly. Most of the sutures of the basisphenoid with neighbouring bones are all either closed or not preserved in the specimen. Posteriorly, at the level of the supposed basisphenoid-basioccipital suture, the basisphenoid seems to have two small ventral protuberances, but these may be preservational artefacts. In contrast to *Kayentachelys aprix* and *Condorchelys antiqua* (Sterli & Joyce, 2007; Sterli 2008), there is no evidence of paired pits on the ventral surface of the basisphenoid. However, this area is severely damaged in NMS G 2004.31.15 and a definitive conclusion is impossible to reach. Dorsally (i.e., on the floor of the cavum cranii), the basisphenoid forms the anteroventral margin of the hiatus acusticus but it does not seems to participate in the floor of the cavum labyrinthicum, in contrast to *Kayentachelys aprix* (Sterli & Joyce, 2007). Anteriorly, the basisphenoid is broken just posterior to the dorsum sellae so not much can be said about the dorsal morphology of this bone (e.g., sella turcica, processus clinoideus, foramen anterius canalis carotici interni, rostrum basisphenoidale). The carotid arterial system has been a major source of information for systematists (e.g., Gaffney, 1979; Gaffney & Meylan, 1988; Meylan & Gaffney, 1989; Gaffney *et al.*, 1991; Gaffney, 1996; Shaffer *et al.*, 1997; Brinkman & Wu, 1999; Hirayama *et al.*, 2000; Jamniczky *et al.*, 2006; Jamniczky & Russell, 2007; Joyce, 2007; Jamniczky, 2008). This is mainly because the location of the foramen posterius canalis carotici interni (fpcci), the foramen through which the carotid artery enters the bony skull, is notably variable within the major turtle clades. The fpcci opens medially in the ventral surface of the basisphenoid in most stem turtles, which represents the plesiomorphic reptilian condition (Romer, 1956). In panpleurodires, the fpcci is formed by the prootic and/or the basisphenoid (laterally) with sometimes a small contribution by the quadrate. Two morphologies occur in pancryptodires: in paracryptodires, the fpcci is formed by the pterygoid and basisphenoid halfway along the suture between two bones, whereas in eucryptodires, the fpcci is formed mostly or fully by the pterygoid and located near the posterior end of the basisphenoid or even further posteriorly (for more details see Chapters 4 and 5). In *Proganochelys quenstedti*, *Kayentachelys aprix*, *Heckerochelys romani*, *Condorchelys antiqua*, *Mongolochelys efremovi* and *Kallokibotion bajazidi* (i.e., in all stem turtles, with the exception of *Meiolania platyceps*), the fpcci opens fully within the basisphenoid. However, the fpcci is not preserved in any specimen of *Eileanchelys waldmani*.

Mandibular elements

Mandibular elements are associated with two of the paratype skulls (NMS G 2004.31.16d and NMS G 2004.31.16f), but their state of preservation prevents any useful comparisons. In NMS G 2004.31.16d (Fig. 3.7), the mandible is closely appressed to the skull so that only some parts of the lateral and ventral portion of the lower jaw can be observed. The dentary is the only mandibular bone identifiable in the latter specimen. It is apparently fused to the other dentary anteromedially at the symphysis. Its lateral surface is perforated by multiple small foramina, presumably serving as nutrient canals for the rhamphotheca (Gaffney, 1979). Medial to the left dentary in NMS G 2004.31.16d, there are several splinters of bone that might represent the angular and/or the splenial, but their identity cannot be determined. In NMS G 2004.31.16f (Fig. 3.9), only the lateral surface of the left mandibular ramus is visible. In this specimen the mandible is also appressed to the skull. The left ramus can be followed from a point close to the symphysis to the area articularis mandibularis posteriorly. The dentary appears to be a very elongate bone in lateral view. Posteriorly, the left ramus is damaged at the level of the processus coronoideus and of the dentary-surangular suture, so that this suture is impossible to follow. Most of the surangular is preserved and the foramen nervi auriculotemporalis is clearly apparent on its lateral surface. Two smaller foramina are present close to the foramen nervi auriculotemporalis: one slightly anterior and one slightly posteroventral. These smaller foramina may be subdivisions of the foramen nervi auriculotemporalis (Gaffney, 1979). Posteriorly, the surangular has a broad subvertical contact (in lateral view) with the articular. Halfway along the lateral suture between the surangular and the articular there is a relatively large foramen or circular depression that cannot be identified, but that is probably an artefact of preparation. Posteriorly, the articular is damaged and the area articularis mandibularis is not preserved. The posterior process of the dentary does not appear to reach the articular. Because the mandible is appressed to the skull in both NMS G 2004.31.16d and NMS G 2004.31.16f, no information on the mandibular triturating surface is available. In *Eileanchelys waldmani* the mandible is an elongate and relatively thin structure that differs significantly from the high, robust mandible of *Kayentachelys aprix* (Sterli & Joyce, 2007).

SHELL MORPHOLOGY

Carapace

Nuchal—The nuchal, the single anteromedial plate of the carapace, is at least partly preserved on NMS G 2004.31.16a (Fig. 3.10), NMS G 2004.31.16b (Fig. 3.11), NMS G 2004.31.16d (Fig. 3.13) and NMS G 2004.31.16c (Fig. 3.12), but it is best seen on the latter specimen. The nuchal consists of a large trapezoidal element that is wider than long. It contacts the first neural posteromedially, the first costal posterolaterally (on both sides) and at least the first

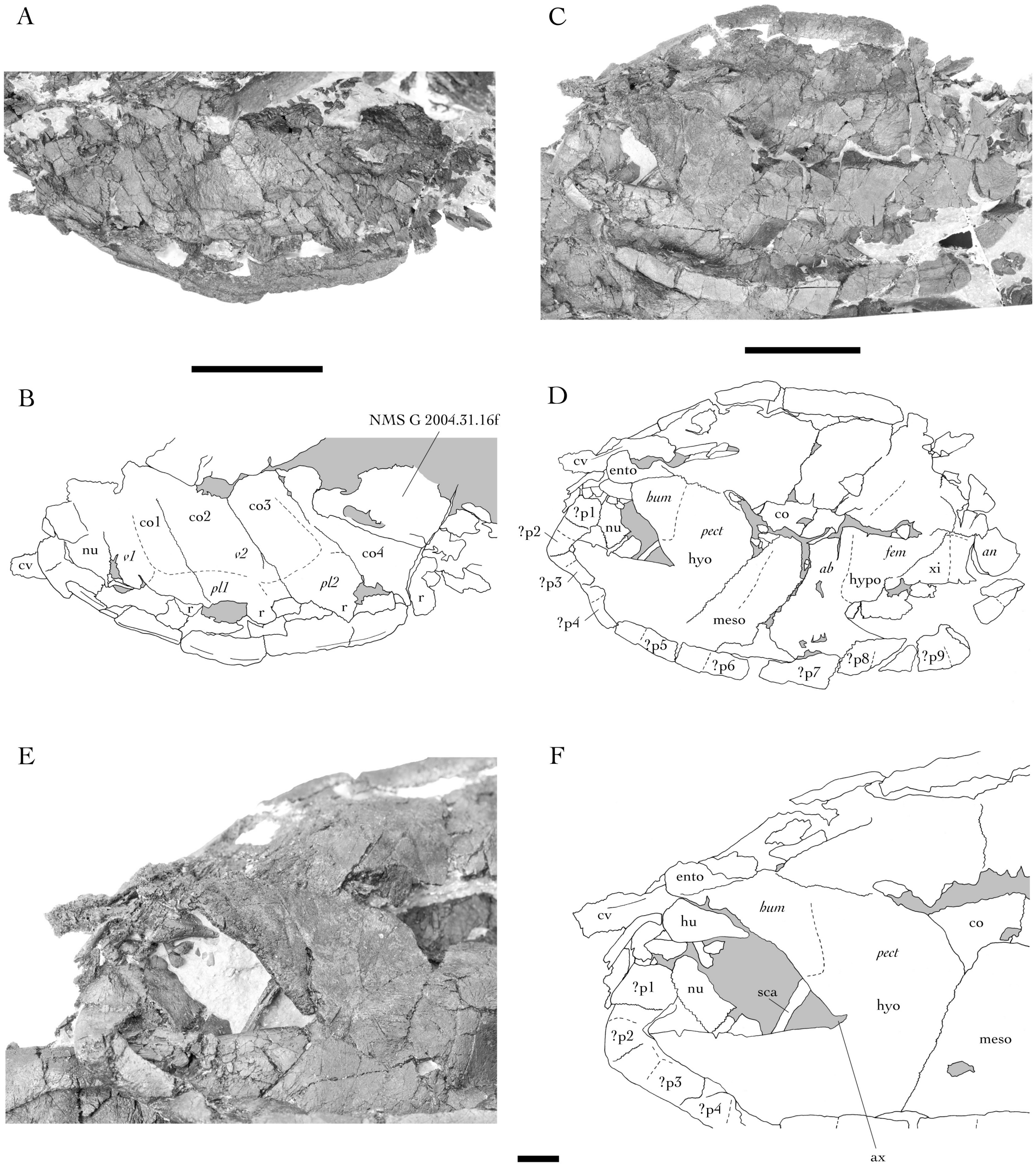

Figure 3.10—*Eileanchelys waldmani*, NMS G 2004.31.16a. A, B, carapace (anterior to the left); C, D, plastron (anterior to the left); E, F, enlargement of the anterior plastral area. Epidermal scales are in italics. Scale bars: A-D, 50 mm; E, F, 10 mm. Abbreviations: ab, abdominal scale; an, anal scale; ax, axillary notch; co, costal plate; cv, cervical vertebra; ento, entoplastron; fem, femoral scale; hu, humerus; hum, humeral scale; hyo, hyoplastron; hypo, hypoplastron; meso, mesoplastron; nu, nuchal; p, peripheral plate; pect, pectoral scale; pl, pleural scale; r, dorsal rib; sca, scapula; v, vertebral scale; xi, xiphiplastron.

peripheral laterally. The number of peripherals contacted by the nuchal is unclear as no specimen has a complete nuchal. However, as in most turtles, it is probable that the nuchal only contacted peripheral 1 laterally (NMS G 2004.31.16b and NMS G 2004.31.16c; see Figs. 3.11 and 3.12). The contact with peripheral 1 is straight and faces anterolaterally. The posterolateral contact with costal 1 is also straight and may have faced slightly anteromedially. This morphology is very common among turtles from both the stem- and the crown-group. The nuchal of *Eileanchelys waldmani* closely resembles that of *Kayentachelys aprix* and *Heckerochelys romani*. The nuchal emargination (the

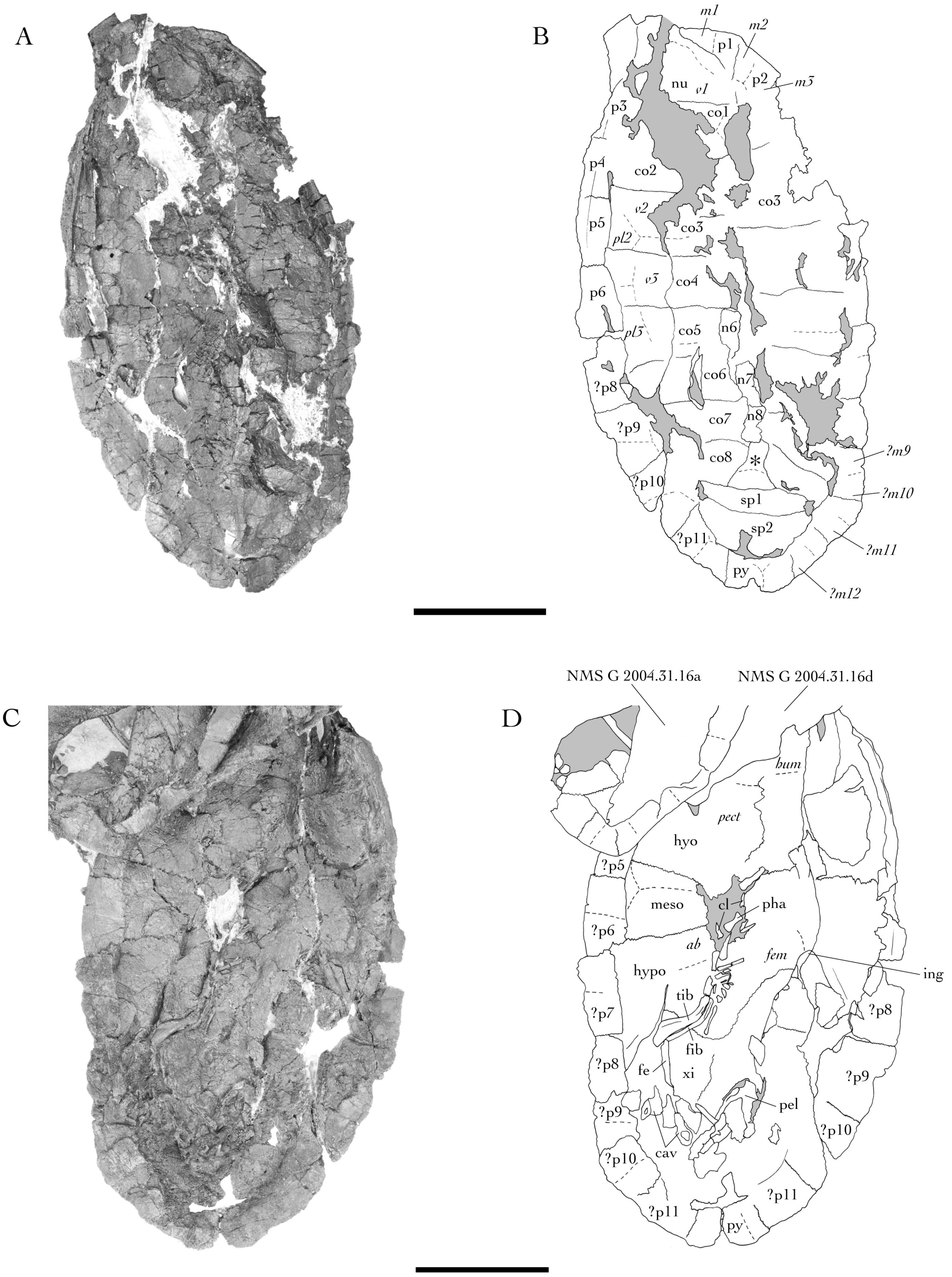

Figure 3.11—*Eileanchelys waldmani*, NMS G 2004.31.16b. A, B, carapace; C, D, plastron. Epidermal scales are in italics. Scale bars: 50 mm. Abbreviations: ab, abdominal scale; cav, caudal vertebra; cl, claw; co, costal plate; fe, femur; fem, femoral scale; fib, fibula; hum, humeral scale; hyo, hyoplastron; hypo, hypoplastron; ing, inguinal notch; m, marginal scale; meso, mesoplastron; n, neural plate; nu, nuchal plate; p, peripheral plate; pect, pectoral scale; pel, pelvis; pha, phalange; pl, pleural scale; py, pygal plate; sp, suprapygal plate; tib, tibia; v, vertebral scale; xi, xiphiplastron; *, supernumerary plate.

anteromedian emargination of the carapace formed by the nuchal plate) is very shallow (NMS G 2004.31.16c and NMS G 2004.31.16d). This is also very common in turtles and among stem turtles it is known at least in *Kayentachelys aprix* and *Heckerochelys romani*.

Neurals — The neural plates form a median row of unpaired elements in the carapace. Their number can be somewhat variable, but it is usually eight (Zangerl, 1969). Ventrally, the neural plates are fused with the neural arch of the dorsal vertebrae (see Chapter 2). The neurals can be observed in NMS G 2004.31.16b (Fig. 3.11), NMS G 2004.31.16c (Fig. 3.12) and NMS G 2004.31.16d (Fig. 3.13). In NMS G 2004.31.16c, eight well-developed, elongate neurals are present. In NMS G 2004.31.16b, the anterior neurals are missing, but geometrical relationships allow identification of the seventh and eighth neurals. Posterior to the eighth neural of NMS G 2004.31.16b is an additional plate. Its shape (elongate and trapezoidal) differs from that of the first eight neurals and from that of the two posterior suprapygals (see below). As no visceral view of the carapace is available, it is impossible to state whether this plate is a ninth neural (which would be fused to the neural arch of an underlying vertebra) or a supernumerary suprapygal (which would not have a ventral relation to the axial skeleton). The presence of nine neurals has been suggested or discussed for several stem turtles. Gaffney *et al.* (1987) recorded nine neurals in their original description of *Kayentachelys aprix*, but according to Joyce & Sterli (pers. comm., 2007) this is impossible to confirm based on the available material. The number of neurals is uncertain in *Heckerochelys romani*, but it may have been nine (Sukhanov, 2006). According to Sukhanov (2000), *Mongolochelys efremovi* has nine neurals. Nine neurals are also described in *Indochelys spatulata* Datta *et al.* 2000. In all of these species, as in *Eileanchelys waldmani*, the presence of nine neurals remains conjectural as no visceral view of the carapace confirms the relationship between this supposed ninth neural and the axial skeleton. All neurals in *Eileanchelys waldmani* consist of rectangular elements that are approximately twice as long as they are wide. Neural 1 is the only neural for which the exact outline is known (NMS G 2004.31.16c; Fig. 3.12); all other neurals are partly damaged. Neural 1 has a slightly convex anterior margin for the contact with the nuchal, concave lateral margins contacting the first costals, a concave posterior margin which contacts neural 2, and straight and short posterolateral margins contacting the second costals. This gives neural 1 a stretched hexagonal outline with short posterior sides. In turtles, neurals often have the shape of stretched hexagon with short anterior sides. Neural 1 also appears to be the largest neural. In *Eileanchelys waldmani*, neural 1 greatly resembles that of *Kayentachelys aprix*, and to a lesser extent that of *Heckerochelys romani*, although in the latter neural 1 is much more elongate than in the aforementioned species. In addition to the first and third neurals, neural 2 contacts costal 2 for most of its length as well as the anteromedial part of costal 3 posterolaterally. The contacts of costals 3 and 4 are unclear and costal 4 is poorly preserved in all specimens. The contacts of neural 5 with neighbouring costals are not preserved in any specimen, but from the contacts of neural 6 it can be concluded that neural 5 contacts costal 4 and probably also costal 5. Neurals 6, 7 and 8 are proportionally shorter than the anterior neurals, but they are still longer than wide. Neural 6 contacts mostly costal 5 and a posterolateral contact with costal 6 is absent or very reduced. Similarly, neural 7 mostly contacts costal 6 and might have a short contact with costal 7 posterolaterally. Neural 8 only contacts costal 7 laterally and may be the smallest plate of the series. The additional median plate (possible ninth neural or supernumerary suprapygal) has a remarkable

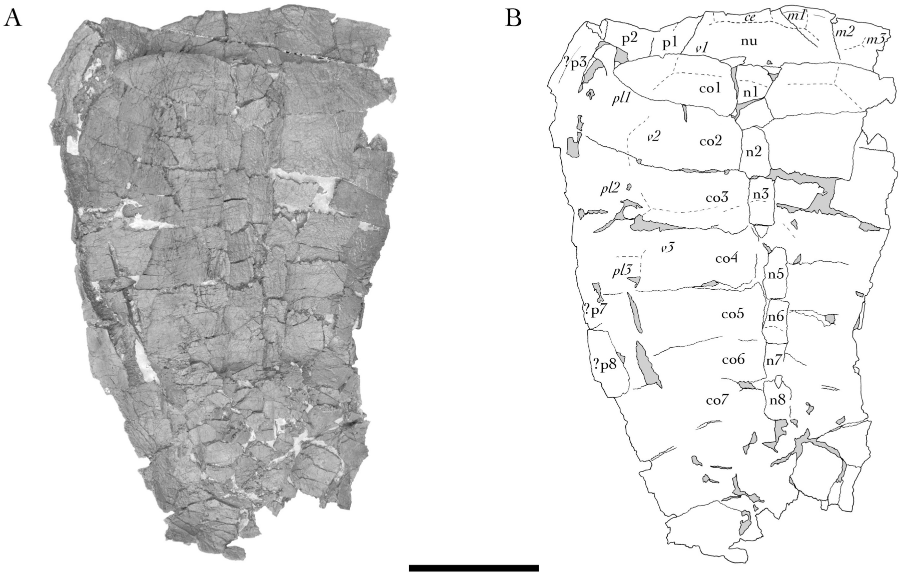

Figure 3.12—*Eileanchelys waldmani*, NMS G 2004.31.16c. A, B, carapace. Epidermal scales are in italics. Scale bar: 50 mm. Abbreviations: ce, cervical scale; co, costal plate; m, marginal scale; n, neural plate; nu, nuchal plate; p, peripheral plate; pl, pleural scale; v, vertebral scale.

shape: it consists of an elongate trapezoid with the anterior margin significantly shorter than the posterior margin and with somewhat concave lateral margins. It contacts the eighth neural anteriorly, the first suprapygal posteriorly and the eighth costal laterally. This shape differs markedly from that of the neurals and suprapygals of the same species and this additional plate does not appear to result from the splitting of either a neural or a suprapygal as may occur in some turtles with additional plates. Moreover, this plate resembles the possible ninth neural of *Heckerochelys romani* as reconstructed by Sukhanov (2006: fig. 3).

Suprapygals—The suprapygals are unpaired elements that are located posterior to the neural row. There are usually two suprapygals. Their development and shape are extremely variable among turtles (the first usually being the smaller of the two), which makes them valuable for systematic purposes. Suprapygals, in contrast to neurals, do not have sutural relationships with the underlying axial skeleton. In *Eileanchelys waldmani*, there are at least two suprapygals easily identifiable by their shape: they are very wide crescent-shaped elements with the concavity facing anteriorly (NMS G 2004.31.16b; Fig. 3.11). Due to deformation, suprapygal 1 may have had a lens-shape with slightly convex anterior and posterior margins. Suprapygal 1 is very narrow anteroposteriorly and it is remarkable that it reaches the peripheral row laterally. In most turtles, suprapygal 2 has an anterolateral contact with the last costal that prevent suprapygal 1 from contacting the peripherals. In *Eileanchelys waldmani*, the first suprapygal contacts what is putatively (see Peripherals, below) the tenth peripheral laterally, preventing a contact between costal 8 and suprapygal 2. To date, among stem turtles, only *Kallokibotion bajazidi* is known to have a contact between the first suprapygal and a peripheral (the eleventh), but aside from this the morphology of the pygal region in *K. bajazidi* is radically different from that of *Eileanchelys waldmani* (see Gaffney &

Meylan, 1992: fig. 17). In *E. waldmani*, suprapygal 1 contacts the additional plate (see above) anteromedially, the eighth costal anterolaterally, the putative peripheral 10 laterally and the second suprapygal posteriorly. On the dorsal surface of both suprapygals, there is a low medial keel that continues posteriorly on the pygal (see below). Suprapygal 2 is a broad crescent-shaped plate that is longer than suprapygal 1, but that is still broader than long (actually, almost three time wider than long). Its anterior margin, which only contacts suprapygal 1, is slightly concave. Laterally, suprapygal 2 contacts the putative peripherals 10 and 11 (see Peripherals, below). Posteriorly, it has a broad convex contact with the pygal. A comparable morphology of the second suprapygal may be found in *Indochelys spatulata* in which suprapygal 2 is a boomerang-shaped element that contacts the tenth and eleventh peripherals laterally. However, the morphology of suprapygal 1 in *Indochelys spatulata* is different from that of *Eileanchelys waldmani*. In *Heckerochelys romani* and *Mongolochelys efremovi*, the second suprapygal is also a broad element, but it is rather trapezoidal in shape, whereas the first suprapygal is significantly reduced compared to that of *Eileanchelys waldmani*. In *Condorchelys antiqua*, both suprapygals are markedly reduced compare to that of the Skye species.

Pygal—The pygal is a single element that forms the posteromedial portion of the rim of the carapace. Its shape and development is variable among turtles, depending for example on the posterior outline of the carapace (i.e., the presence or absence of a caudal emargination). In *Eileanchelys waldmani*, the pygal is a simple rectangle about the size of the neighbouring peripherals (NMS G 2004.31.16b; Fig. 3.11). It is slightly arched along the posterior margin of the second suprapygal and contacts the putative eleventh peripherals on both sides. The slight medial keel that is observed on the suprapygal is also present on the pygal. There is no evidence of a caudal emargination along the posterior rim of the carapace. The morphology of the pygal in *Eileanchelys waldmani* corresponds to that found in most turtles. For example, within stem turtles, this morphology is also found in *Heckerochelys romani*, *Condorchelys antiqua* and *Mongolochelys efremovi*.

Costals—The costals are paired, band-like elements that form most of the lateral part of the carapace. Each costal plate is fused to an underlying rib, which may stick out at the lateral end of the costal and insert into the peripherals in some turtles (Zangerl, 1969). On its visceral side, each costal has a rib head that protrudes ventromedially and that articulates with the dorsal vertebra. Most turtles have eight pairs of costals, but nine pairs have been recorded in *Proganochelys quenstedti*, *Condorchelys antiqua* and *Mongolochelys efremovi* (Gaffney, 1990; Khosatzky, 1997; Sukhanov, 2000; Sterli, 2008). Gaffney *et al.* (1987) also described nine costals in *Kayentachelys aprix*, but a recent review of the original material as well as newly discovered specimens was unable to reproduce this observation (Joyce & Sterli, pers. comm., 2007). Costals can be observed in all four carapaces from the paratype association, but they are best seen in NMS G 2004.31.16b (Fig. 3.11) and NMS G 2004.31.16c (Fig. 3.12). The posterior part of the carapace is damaged in NMS G 2004.31.16c, but it is possible to see the first seven costal plates. In NMS G 2004.31.16b, the anterior part of the carapace is severely damaged, but the comparison with NMS G 2004.31.16c enables the identification of most carapacial plates and it appears that *Eileanchelys waldmani* has eight costals. As described for *Kayentachelys aprix* (Joyce & Sterli, pers. comm., 2007), there is a slight curving of the first two costals toward the anterior end of the carapace in *Eileanchelys waldmani*. This anterior curving is also present in *Indochelys spatulata* and *Mongolochelys efremovi*. In contrast, costal 3 appears to be perpendicular to the neural row and, as in most turtles, the posterior costals (4-8) seem to bend increasingly toward the posterior end of the carapace, although this is not obvious due to the preservation of the specimens. If a count of eleven pairs of peripherals is considered (see Peripherals, below), then the contacts are as follows: costal 1 contacts peripherals 2 and 3 and maybe also peripheral 1; costal 2 contacts peripherals 3 and 4; costal 3 contacts peripherals 4 and 5; costal 4 contacts peripherals 5 and 6; costal 5 contacts peripherals 6 and 7; costal 6 contacts peripherals 7 and 8; costal 7 contacts peripherals 8 and 9; and costal 8 contacts peripherals 9 and 10. This is the general pattern found in most turtles. Small costal fontanelles (i.e., incomplete ossification of the distal end of the costal plates that fail, completely or partly, to contact the peripherals, except for the distal end of the ribs) are present in NMS G 2004.31.16a (Fig. 3.10A,B), but are absent in all other individuals. This suggests that NMS G 2004.31.16a is a slightly younger individual, because its morphology is otherwise congruent with that of associated specimens. Due to intensive deformation, the exact size of these specimens is difficult to assess, so that this hypothesis could not be confirmed by specimen measurements.

Peripherals — The peripherals are the bony plates that form the rim of the carapace, with the exception of the anteromedial- and posteromedialmost portions, which are formed by the nuchal and pygal respectively. Peripherals are usually flat, wedge-shaped elements, except in the bridge region where they are sutured to the plastron, which gives them a 'V'-shaped cross-section. No complete row of peripherals is known in any specimen of *Eileanchelys waldmani*, so that the number of peripherals is unclear. According to the different counts on each specimen (mostly on NMS G 2004.31.16b and NMS G 2004.31.16a; see Figs. 3.10 and 3.11) and the correlation between them, it appears that *E. waldmani* would have eleven pairs of peripherals, as it is usual for turtles (Zangerl, 1969). *Proganochelys quenstedti* and *Proterochersis robusta* Fraas 1913 have more than eleven pairs of peripherals, but *Kayentachelys aprix*, *Heckerochelys romani*, *Mongolochelys efremovi*, *Meiolania platyceps*, panpleurodires and most pancryptodires have eleven pairs of peripherals (Joyce, 2007: 31). Following from the two previous statements, it is reasonable to considere that *Eileanchelys waldmani* has eleven pairs of peripherals. Peripheral 1 differs from the others in its triangular shape: it tapers medially along the lateral margin of the nuchal plate. All other peripherals have a quadrangular shape and are more elongate than they are wide. The contacts between peripherals and costals are described above (see Costals). In contrast to most turtles, in which only peripheral 11 contacts the suprapygals and pygal, peripherals 10 and 11 border the pygal region in *Eileanchelys waldmani*. Peripheral 11 contacts the pygal posteromedially and the second suprapygal anteromedially.

Medially and from posterior to anterior, peripheral 10 contacts suprapygal 2, suprapygal 1 and costal 8. Among stem turtles, *Indochelys spatulata* and perhaps also *Mongolochelys efremovi* are the only species in which peripheral 10 contacts suprapygal 2, although in these species suprapygal 1 does not contact the peripherals laterally (see Suprapygals, above). Specimens NMS G 2004.31.16a and NMS G 2004.31.16b show that the bridge in *Eileanchelys waldmani* is extensive and that peripherals 2 to 8 are the bridge peripherals. This corresponds to the morphology in *Kayentachelys aprix* (Joyce & Sterli, pers. comm., 2007). In most other turtles, the bridge extends from peripherals 3 or 4 to peripherals 7 or 8. This is only a tentative observation as no comprehensive review of this feature is available in the literature. In contrast to *Heckerochelys romani* in particular, the bridge of *Eileanchelys waldmani* is osseous. Fossil turtle shells are often flattened during fossilisation, so that the original doming of the shell remains unsuspected. For example, all known shells of *Kayentachelys aprix* are flat, leading Gaffney *et al.* (1987: 290) to describe the shell of this species as being "moderately low-domed". However, a recent review of the material proved this assertion to be incorrect (Joyce & Sterli, pers. comm., 2007). Indeed, some three dimensional bridge peripherals of *Kayentachelys aprix* present a distinct gutter on the dorsal surface and a steep angle between the ventral and dorsal branches of the 'V'-shaped plates. This indicates an important doming of the shell. Similarly, all available shells of *Eileanchelys waldmani* are more or less flattened, but bridge peripherals of several specimens have a morphology similar to that described for *Kayentachelys aprix* by Joyce & Sterli (pers. comm., 2007). Specimens NMS G 2004.31.16b and NMS G 2004.31.16c show that peripherals 3 to 7 have a deep longitudinal gutter dorsally as well as a steeply ascending medial margin where they meet the costals (Figs. 3.11 and 3.12). NMS G 2004.31.18, an isolated row of bridge peripherals preserved in three dimensions, shows an angle of approximately 90 degrees between the ventral and dorsal branches of the V-shaped peripherals. These specimens demonstrate that *Eileanchelys waldmani* had a domed shell. Based on the highly domed shell of most extant terrestrial forms (e.g., *Chelonoidis nigra*, the Galápagos giant tortoise) and the flattened shell of many extant aquatic species (e.g., *Chelodina expansa*, *Chelonia mydas*, *Trachemys scripta*), it would be tempting to assume a direct link between possession of a domed shell and terrestriality and, conversely, between a flattened shell and aquatic habits. However, this link does not exist among extant turtles, as demonstrated by the highly domed shell of some aquatic forms: e.g., *Cuora amboinensis*, *Pelusios carinatus* and several *Kinosternon* species, including *K. subrubrum*. Similarly, several extant terrestrial taxa possess a flattened shell: e.g., *Malacochersus tornieri* (the pancake tortoise), *Geoemyda spengleri*, and all five *Homopus* species (Bonin *et al.*, 2006). Moreover, jumping to conclusions about the habitat preference of stem turtles, which have no close relationships with extant clades, based only on the shell shape of extant species would be hazardous. In other words, the domed shells of *Kayentachelys aprix* and *Eileanchelys waldmani* should probably not be used as an indication of their habitat preferences (see Palaeoecology, below). Peripherals 8 to 11 are larger than the anterior ones, mostly because they taper laterally for a greater extent. A sharp tapering of the posterolateral margin of the carapace is common among turtles.

Cervical scale—The cervical scale can be seen as the epidermal equivalent of the dermal nuchal plate, although the cervical scale is always greatly reduced compared to the size of the nuchal. The cervical scale usually contacts the first marginal scale laterally and the first vertebral scale posteriorly, and forms the anteromedial part of the carapace rim. This holds true for *Eileanchelys waldmani* (NMS G 2004.31.16b, NMS G 2004.31.16c and NMS G 2004.31.16d; Figs. 3.11, 3.12 and 3.13). In this species, the cervical scale is a broad but short rectangular element lying entirely on the nuchal plate. It appears less wide in NMS G 2004.31.16d than in the other two aforementioned specimens, but this may be an intraspecific variation. This morphology is relatively common among chelonians and, concerning stem turtles only, it is found in *Proganochelys quenstedti*, *Proterochersis robusta*, *Kayentachelys aprix*, *Heckerochelys romani* and *Meiolania platyceps*.

Vertebral scales—The vertebral scales are unpaired elements that form the median row of the epidermal layer of the carapace. *Proganochelys quenstedti* is unique among turtles in having only four vertebral scales. All other turtles with epidermal scales have at least five vertebrals (some have six). The combination of observations from NMS G 2004.31.16a (Fig. 3.10), NMS G 2004.31.16b (Fig. 3.11), NMS G 2004.31.16c (Fig. 3.12) and NMS G 2004.31.16d (Fig. 3.13) indicates that *Eileanchelys waldmani* had five vertebral scales, but little information can be gathered on their outlines. The vertebral scales are notably wide (about 2.5 times wider than long), a plesiomorphic characteristic that is usual in the basalmost turtles (i.e., *Proganochelys quenstedti*, *Proterochersis robusta*, *Kayentachelys aprix*, *Indochelys spatulata*, *Heckerochelys romani* and *Condorchelys antiqua*). Vertebrals 2 and 3 appear to be the widest vertebral scales. Vertebral 1 contacts the cervical scale anteromedially, marginals 1 and 2 anterolaterally, the first pleural posterolaterally and the second vertebral posteriorly. The vertebral 1-2 sulcus is mostly straight and transverse, except for a slight protrusion on the midline. This sulcus passes through the anterior half of neural 1. Vertebral 2 has two oblique lateral margins, the anterior of which may have been slightly longer than the posterior. The vertebral 2-3 sulcus is on the posterior part of the third costal and passes through the middle of neural 3. Vertebral 3 has two lateral margins that are oblique, but less so than those of vertebral 2, and equal in length. The vertebral 3-4 sulcus is on the posterior part of costal 5 and passes through the posterior half of neural 6. The vertebral 4-5 sulcus is only partially apparent on NMS G 2004.31.16b (Fig. 3.11A,B) and it passes through the posterior half of the additional medial plate (ninth neural or supernumerary suprapygal).

Pleural scales—The pleural scales cover the lateral side of the carapace between the vertebrals and the marginals. Most turtles have four pairs of pleural scales. In relation to the broadened vertebral scales (see above), the pleurals of many basal turtles, including *Eileanchelys waldmani*, are reduced in width compared to those of more derived turtles. In *E. waldmani*, the pleurals are notably more elongate than they are wide. This arrangement of the pleural and vertebral scales is similar to that found in *Proganochelys quenstedti*, *Proterochersis robusta*, *Kayentachelys aprix*, *Heckerochelys romani* and *Condorchelys antiqua*. Pleurals 1 and 2 are partly visible on NMS G

2004.31.16c (Fig. 3.12), whereas only pleurals 2 and 3 are observable on NMS G 2004.31.16b (Fig. 3.11). The pleural 1-2 sulcus is probably mostly on costal 2 and the pleural 2-3 sulcus is on costal 4.

Marginal scales — The marginal scales are the epidermal equivalent of the dermal peripheral plates. Most turtles usually have twelve pairs of marginals, although some of the basalmost forms (i.e., *Proganochelys quenstedti* and *Proterochersis robusta*) have more than twelve pairs. As for the peripherals (see above), no complete row of marginals is known for *Eileanchelys waldmani*. The marginal sulci are poorly preserved in the available specimens, but because a close correlation exists among turtles between the number of peripherals and that of marginals (Joyce, 2007: 31) it is probable that *E. waldmani* had twelve pairs of marginals. Marginals 1 and 2 are apparent in NMS G 2004.31.16c (Fig. 3.12). The first marginal is smaller than the second and overlaps both the nuchal and the first peripheral. Marginal 2 lies on peripherals 1 and 2, and does not overlap the nuchal or the first costal. Posterior marginals (probably marginals 8 to 12) are visible on NMS G 2004.31.16b (Fig. 3.11). It is unknown whether or not some of these overlapped the costals medially. The last pair of marginals (probably the twelfth) meet each other along the midline, as it is usual in turtles. In contrast to *Proganochelys quenstedti*, *Palaeochersis talampayensis* and *Proterochersis robusta*, there is no evidence of supramarginal scales in *Eileanchelys waldmani*.

Plastron

Epiplastron — The epiplastron is a paired element that forms most, if not all, of the anterior tip of the plastron. It is generally understood that the epiplastra are homologous to the clavicles of other reptiles (e.g., Romer, 1956; Zangerl, 1969). In *Eileanchelys waldmani*, the epiplastron is a relatively small element that contacts the hyoplastron posteriorly, the entoplastron posteromedially and the other epiplastron medially (NMS G 2004.31.16d and NMS G 1992.47.50; Figs. 3.13 and 3.14). The outer contour of each epiplastron presents two low, rounded protrusions: a first one anterolaterally at the level of the extragular (see Extragular scales, below), and a second one anteromedially that may be shared between the two epiplastra. These low protrusions are also present in *Kayentachelys aprix* and may be the remnants of the well-developed epiplastral tuberosities found in more basal taxa (i.e., *Odontochelys semitestacea*, *Proganochelys quenstedti*, *Palaeochersis talampayensis* and *Proterochersis robusta*). The posterior contact of the epiplastron with the hyoplastron is transverse and mostly straight. The posteromedial contact with the entoplastron is oblique and straight. The medial contact of the epiplastra prevents the entoplastron from entering the anterior plastral margin, in contrast to basalmost turtles (i.e., *Proganochelys quenstedti*, *Proterochersis robusta*, *Palaeochersis talampayensis*, *Kayentachelys aprix* and *Indochelys spatulata*). The morphology of the epiplastron in *Eileanchelys waldmani* does not resemble that of any other stem turtle, especially not that of *Heckerochelys romani* in which the epiplastron is an oblique element that

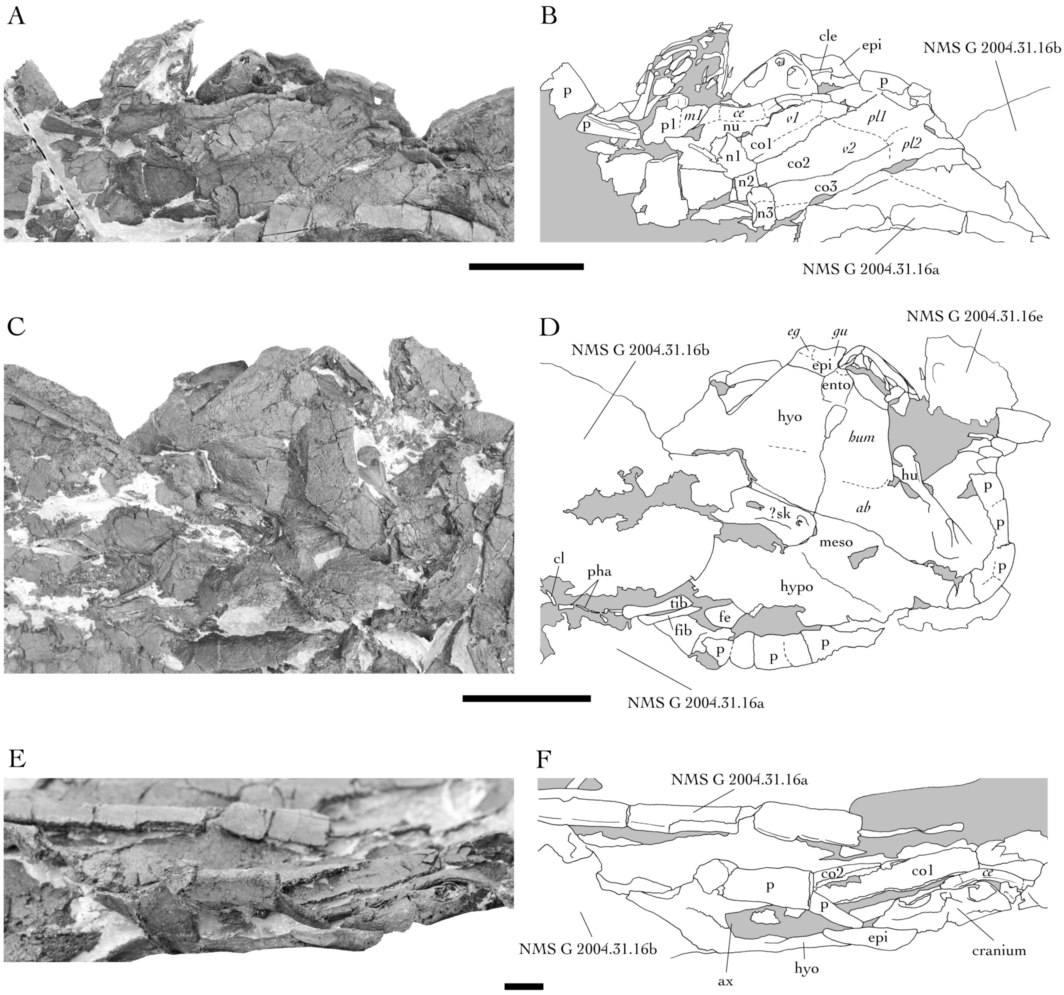

Figure 3.13—*Eileanchelys waldmani*, NMS G 2004.31.16d (shell). A, B, carapace; C, D, plastron; E, F, anterior view. Epidermal scales are in italics. Scale bars: A-D, 50 mm; E, F, 10 mm. Abbreviations: ab, abdominal scale; ax, axillary notch; ce, cervical scale; cl, claw; cle, cleithrum; co, costal plate; eg, extragular scale; ento, entoplastron; epi, epiplastron; fe, femur; fib, fibula; gu, gular scale; hu, humerus; hum, humeral scale; hyo, hyoplastron; hypo, hypoplastron; m, marginal scale; meso, mesoplastron; n, neural plate; nu, nuchal plate; p, peripheral plate; pha, phalange; pl, pleural scale; ?sk, possible skull; tib, tibia; v, vertebral scale.

tapers posteriorly along the anterolateral margin of the plastron, as also occurs in *Mongolochelys efremovi* and *Meiolania platyceps*. On the dorsal surface of the right epiplastron of NMS G 2004.31.16d lies a small rod-like bone (Figs. 3.7 and 3.13). Basal turtles (i.e., *Proganochelys quenstedti, Palaeochersis talampayensis, Odontochelys semitestacea, Proterochersis robusta, Kayentachelys aprix, Heckerochelys romani, Meiolania platyceps, Mongolochelys efremovi* and *Kallokibotion bajazidi*) and at least some crown-group turtles (e.g., some pleurosternids and *Xinjiangchelys latimarginalis* Young & Chow 1953) have a dorsal process on the epiplastron. The nature of this process, often referred as the epiplastal process, has been discussed recently. This structure is interpreted by some (e.g., Gaffney, 1990) as a simple dorsal extension of the epiplastron. Indeed, a well-developed ascending process of the clavicle occurs in many primitive tetrapods (Romer, 1956). In contrast, Joyce *et al.* (2006) reinterpreted this structure as a cleithrum based on newly discovered specimens of *Kayentachelys aprix* that show a sutural contact between this structure and the epiplastron. Indeed, when disarticulated, this structure leaves a scar on the dorsal surface of the epiplastron that is more similar to a sutural contact than to the broken base of a process (e.g., NHM R3727 and NHM R4317 for *Pleurosternon bullockii*). The interpretation of Joyce *et al.* (2006), which is based on morphological evidence, is probably correct, but has recently been questioned because the presence of a cleithrum in turtles would be incongruent with their hypothesised saurian relationships (Rieppel, 2008). No matter which interpretation is correct, the presence of cleithra, or epiplastral processes, in *Eileanchelys waldmani* is a primitive feature. However, this element appears to be disarticulated from the epiplastron at its base suggesting a possible sutural contact with the epiplastron (NMS G 2004.31.16d; Fig. 3.7). This observation is more in agreement with Joyce *et al.*'s (2006) interpretation of this structure as a cleithrum.

Entoplastron**—**The entoplastron, which corresponds to the interclavicle of other tetrapods, is the only unpaired element within the plastron. The entoplastron is preserved in NMS G 2004.31.16d (Fig. 3.13) and NMS G 1992.47.50 (Fig. 3.14). It is a diamond-shaped element that is stretched posteriorly. It is elongate, apparently more so in NMS G 2004.31.16d than in NMS G 1992.47.50, but this may be a misleading impression due to the incompleteness of the latter specimen. The entoplastron contacts the epiplastron anterolaterally and the hyoplastron posterolaterally. *Proganochelys quenstedti*, *Palaeochersis talampayensis*, *Proterochersis robusta*, *Kayentachelys aprix* and *Indochelys spatulata* each have a distinct, well-developed anterior entoplastral process that reaches the anterior plastral border and that prevents the medial contact of epiplastra. This anterior process is absent in more derived turtles, including *Eileanchelys waldmani*. Among basal turtles, the entoplastron of *E. waldmani* is more similar to that of *Heckerochelys romani*, although the latter is significantly sleeker. The visceral development of the entoplastron is important in turtles: usually the dorsal exposure of the entoplastron is larger than its ventral exposure, and the entoplastron also develops a posterior entoplastral process that extends a variable distance along the visceral surface of the plastron. None of these features is preserved in available specimens of *Eileanchelys waldmani*.

Hyoplastron**—**The hyoplastron is a large paired element that forms most of the anterior plastral lobe (with the exception of the anteriormost part which is formed by the epiplastra and entoplastron) and the anterior part of the lateral extension of the plastron that connects with the peripherals laterodorsally to form the bridge. The hyoplastron contacts the epiplastron anteriorly, the entoplastron anteromedially, the peripherals laterodorsally and the mesoplastron posteriorly (NMS G 2004.31.16a, NMS G 2004.31.16b, NMS G 2004.31.16d and NMS G 1992.47.50; Figs. 3.10, 3.11, 3.13 and 3.14). Posterior to the contact with the entoplastron, the hyoplastra meet one another along the midline. In NMS G 2004.31.16a, a young individual with incomplete ossification, the hyoplastra may have been separated posteriorly along the midline due to the development of a central plastral fontanelle. However, the presence of such a fontanelle in this specimen is ambiguous because this area is damaged (see Mesoplastron, below). The lateral part of the

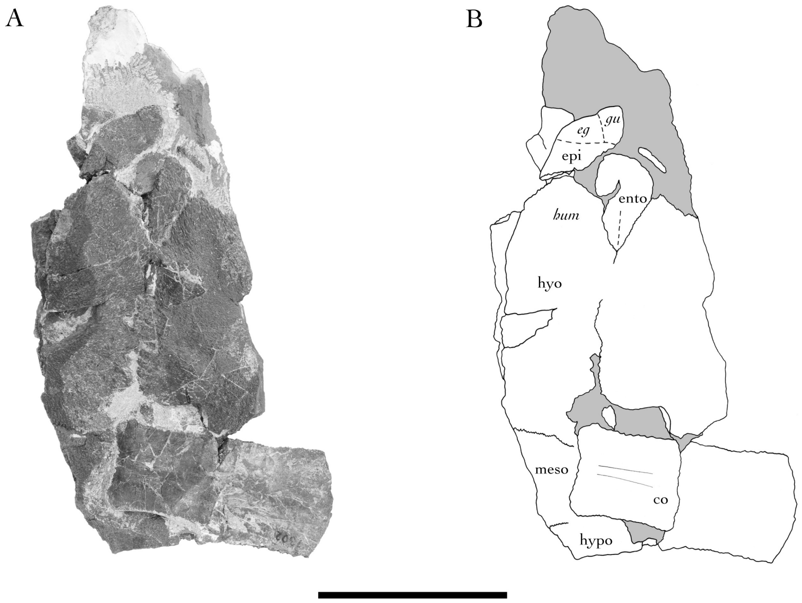

Figure 3.14—*Eileanchelys waldmani*, NMS G 1992.47.50. A, B, partial plastron. Epidermal scales are in italics. Scale bar: A, B, 50 mm. Abbreviations: co, costal plate; eg, extragular scale; ento, entoplastron; epi, epiplastron; gu, gular scale; hum, humeral scale; hyo, hyoplastron; hypo, hypoplastron; meso, mesoplastron.

hyoplastron greatly extends anterodorsally to meet peripheral 2, thus defining a deep axillary notch (Fig. 3.10E,F). As no specimen show a visceral view of this part of the plastron or of the carapace, the development of the axillary buttress is unknown in *Eileanchelys waldmani*. Laterally, the hyoplastron contacts peripherals 2, 3, 4 and most of perpiheral 5 (NMS G 2004.31.16a and NMS G 2004.31.16b; Figs. 3.10 and 3.11).

Mesoplastron**—**The mesoplastron is a dermal, paired element that ossifies between the hyoplastron and the hypoplastron in some turtles. In Eucryptodira and Chelidae, the mesoplastra are lost. In contrast, most stem turtles and paracryptodires have a fully developed mesoplastron that prevents any contact between the hyoplastron and hypoplastron and that usually meets the other mesoplastron medially, unless a central plastral fontanelle is present (e.g., *Mongolochelys efremovi*). In *Kallokibotion bajazidi* and most panpleurodires (to the exception of chelids), the mesoplastron is present but reduced, so that partial contact between the hyoplastron and hypoplastron is possible. Finally, *Proterochersis robusta* and *Odontochelys semitestacea* are unique among turtles in having two pairs of mesoplastra. *Eileanchelys waldmani*, like the majority of stem turtles (with the exception of the two aforementioned species and *Kallokibotion bajazidi*), has one fully developed pair of mesoplastra that prevents contact between the hyoplastra and hypoplastra (NMS G 2004.31.16a, NMS G 2004.31.16b and NMS G 2004.31.16d; Figs. 3.10, 3.11 and 3.13). The mesoplastron contacts the hyoplastron anteriorly, the fifth and sixth peripherals laterally and the hypoplastron posteriorly. The anteroposterior length of the mesoplastron is greatest laterally where it contacts the peripherals, but it tapers slightly toward the midline. In NMS G 2004.31.16a, a central plastral fontanelle, which prevents the midline contact of the mesoplastra, appears to be present, but because the concerned area is damaged the presence/absence of this feature is ambiguous (Fig. 3.10C,D). Moreover, if a central plastral fontanelle (i.e., the absence of ossification of the central area of the plastron) was present, this would not lead to a revision of the present description as such fontanelles occur very commonly in young individuals of many turtle species, including *Kayentachelys aprix* (Joyce & Sterli, pers. comm., 2007): NMS G 2004.31.16a is indeed interpreted as a younger individual (see Costals, above). In NMS G 2004.31.16b (Fig. 3.11C,D) and NMS G 2004.31.16d (Fig. 3.13C,D), there is no evidence for a central plastral fontanelle and the mesoplastra appear to meet one another along the midline. As so many turtle species retain fontanelles during ontogeny, they are only phylogenetically informative if present in adult individuals. Fossil material rarely offers the opportunity to investigate ontogenetic issues adequately.

Hypoplastron — The hypoplastron can be seen as the posterior equivalent of the hyoplastron: it is a paired element that forms the posterior part of the bridge and approximately half of the posterior plastral lobe. In *Eileanchelys waldmani*, the hypoplastron contacts the mesoplastron anteriorly, peripherals 6, 7 and 8 laterally, the xiphiplastron posteriorly and the other hypoplastron medially (NMS G 2004.31.16a and NMS G 2004.31.16b; Figs. 3.10 and 3.11). The lateral part of the hypoplastron supports a posterodorsal process that meets peripheral 8, thus defining the inguinal notch. As no specimen shows a visceral view of this part of the plastron or of the carapace, the development of the inguinal buttress is unknown in *Eileanchelys waldmani*. The hypoplastra-xiphiplastra suture is poorly preserved in all specimens. Laterally, this suture is transverse for a short distance, but becomes arched posteriorly to form a broad 'U'-shape.

Xiphiplastron — The xiphiplastron is a paired element that forms the posterior half of the posterior plastral lobe. In all turtles, including *Eileanchelys waldmani*, the only contacts of the xiphiplastron are with the hypoplastron anteriorly (see Hypoplastron, above) and the other xiphiplastron medially. In *E. waldmani*, the xiphiplastron is triangular in shape. Although, the posterior rim of the plastron is not well-preserved in any specimen (NMS G 2004.31.16a and NMS G 2004.31.16b; Fig. 3.10 and 3.11), there is no evidence for the presence of an anal notch.

Gular scales — The gulars (plastral scale set 1 of Hutchison & Bramble, 1981) are usually paired, but some turtles have only one median gular (e.g., *Pleurosternon bullockii* and all known panpleurodires; see Joyce, 2007). No specimen of *Eileanchelys waldmani* has a complete anterior plastral rim, so it is uncertain whether there were one or two gular scales. Observation of NMS G 2004.31.16d (Fig. 3.13C,D) suggests that there were paired gulars, but the midline sulcus between the two scales is not preserved. In all specimens of *Eileanchelys waldmani*, most plastral scale sulci are poorly preserved. Because paired gulars are present in all stem turtles for which this area of the plastron is known, the following description assumes that two gular scales were present in *Eileanchelys waldmani*. The gulars were small quadrangular elements that were slightly broader than long and that lay mostly on the epiplastra. Anteriorly, the gulars covered most of the anterior tip of the plastron. The gular scale contacted the extragular laterally, the humeral posteriorly and the other gular medially. The gular-extragular sulcus is slightly convex laterally. The gular-humeral sulcus is mostly straight and oblique, facing posterolaterally. Posteromedially, the gular-humeral sulcus runs over the anteriormost part of the entoplastron.

Extragular scales—The extragulars (plastral scale set 2 of Hutchison & Bramble, 1981) are paired scales that are usually located lateral to the gulars. Extragulars are found in all turtles with the exception of most crown-group cryptodires (Joyce, 2007). In *Eileanchelys waldmani*, extragulars are very small scales that lay in the anterolateral corner of the epiplastron (NMS G 2004.31.16d and NMS G 1992.47.50; Figs. 3.13 and 3.14). They consisted of roughly triangular elements that contacted the gular laterally and the humeral posteriorly. The extragular scale bordered the anterior plastral rim and corresponds exactly to the anterolateral low protrusion of the epiplastron (see Epiplastron, above). The sulci of the extragular with the gular and with the humeral are of similar length. The contact with the gular may have been slightly concave.

Humeral scales—The humerals (plastral scale set 3 of Hutchison & Bramble, 1981) are paired scales that cover most of the anterior plastral lobe. In *Eileanchelys waldmani*, as in most turtles, the humeral contacted the extragular anteriorly, the gular anteromedially, the pectoral posteriorly and the other humeral medially (NMS G 2004.31.16a, NMS G 2004.31.16b and NMS G 2004.31.16d; Figs. 3.10, 3.11 and 3.13). The anterior contact with the extragular and gular is almost straight and it faces slightly anteromedially. The posterior sulcus with the pectoral is not preserved entirely in any available specimen, but it appears to be mostly transverse, may be slightly convex anteriorly, and it lies entirely on the hyoplastron. Laterally, before reaching the plastral rim, the humeral-pectoral sulcus turns sharply toward the anterior and runs anterolaterally for a short distance. The humeral scale lay on the hyoplastron, the entoplastron and the posterior part of the epiplastron.

Pectoral scales—Pectorals (plastral scale set 4 of Hutchison & Bramble, 1981) are paired scales that usually cover the hyoplastron-mesoplastron suture, when the mesoplastron is present. In *Eileanchelys waldmani*, the pectoral was present (NMS G 2004.31.16a and NMS G 2004.31.16b; Figs. 3.10 and 3.11) but the pectoral-abdominal sulcus is not preserved in any specimen.

Abdominal scales—Abdominals (plastral scale set 5 of Hutchison & Bramble, 1981) are paired scales that usually cover the mesoplastron-hypoplastron suture, when the mesoplastron is present. As stated above (see Pectoral scales), the pectoral-abdominal sulcus is not preserved in any available specimen of *Eileanchelys waldmani*. The abdominal-femoral sulcus is located at the same level as the inguinal notch. Starting at the inguinal notch, the sulcus runs anteromedially for a short distance, then curves posteriorly to resume a sub-transverse course. Rather than strictly transverse, the sulcus appears to be slightly convex anteriorly reaching its maximum anterior extent in the midline (Figs. 3.10 and 3.11). This pattern is found commonly among turtles.

***Femoral scales*—**Femorals (plastral scale set 6 of Hutchison & Bramble, 1981) are paired scales that cover at least half, but often more, of the posterior plastral lobe. They also usually cover part, if not all, of the hypoplastron-xiphiplastron suture. The femoral sulci are best seen in NMS G 2004.31.16a (Fig. 3.10C,D). It consisted of a relatively large quadrangular scale covering two thirds of the posterior plastral lobe. As in all turtles, the femoral contacted the abdominal anteriorly, the anal posteriorly and the other femoral medially. The abdominal-femoral sulcus is described above (see Abdominal scales). The femoral-anal sulcus appears to have been more or less transverse and lies entirely on the xiphiplastron, although the sulcus and the hypoplastron-xiphiplastron suture become very close in the midline. In this configuration, the femoral entirely covered the hypoplastron-xiphiplastron suture.

***Anal scales*—**Anals (plastral scale set 7 of Hutchison & Bramble, 1981) are paired scales that cover the posteriormost portion of the plastron. As in all turtles, the anal of *Eileanchelys waldmani* contacted the femoral anteriorly and the other anal medially (NMS G 2004.31.16a; Fig. 3.10C,D). The femoral-anal sulcus is described above (see Femoral scales). The anal scale lay entirely on the xiphiplastron and did not overlap the hypoplastron medially.

***Inframarginal scales*—**Inframarginals are paired scales located in the bridge portion of the plastron. Their number is variable among turtles. Stem turtles and most pancryptodires have a complete row of inframarginals that fully separate the marginals from the plastral scales. Testudinoids are characterised by the presence of only two pairs of inframarginal scales: the anterior axillaries and the posterior inguinals. Inframarginals are lost in all known panpleurodires (Joyce, 2007). Although NMS G 2004.31.16a and NMS G 2004.31.16b present a relatively well-preserved bridge area, no inframarginal sulci preserved are in any specimen, so that the number and morphology of inframarginal scales in *Eileanchelys waldmani* remain unknown.

POSTCRANIAL MORPHOLOGY

***Material*—**Postcranial turtle material (other than shell) is rare at Cladach a'Ghlinne, which prevents a comprehensive description. However, several specimens preserve limb bones or vertebrae that merit mention. NMS G 2004.31.16a possesses a few articulated cervical vertebrae, but these are so poorly preserved that nothing can be said about their morphology (see Fig. 3.10). Ventral to the cervical vertebrae, the distal head of either a radius or ulna, as well as some smaller elements that probably pertain to the autopodium, are present. At the level of the right axilla, this specimen also possesses a long, thin columnar bone that undoubtedly corresponds to the dorsal process of the scapula (Fig. 3.10E,F). In NMS G 2004.31.16b, the left hindlimb is folded onto the plastron so that the zeugopodium and a partial autopodium are visible (Fig. 3.11C,D). In the posterior part of the shell cavity of this specimen, some poorly preserved caudal vertebrae are

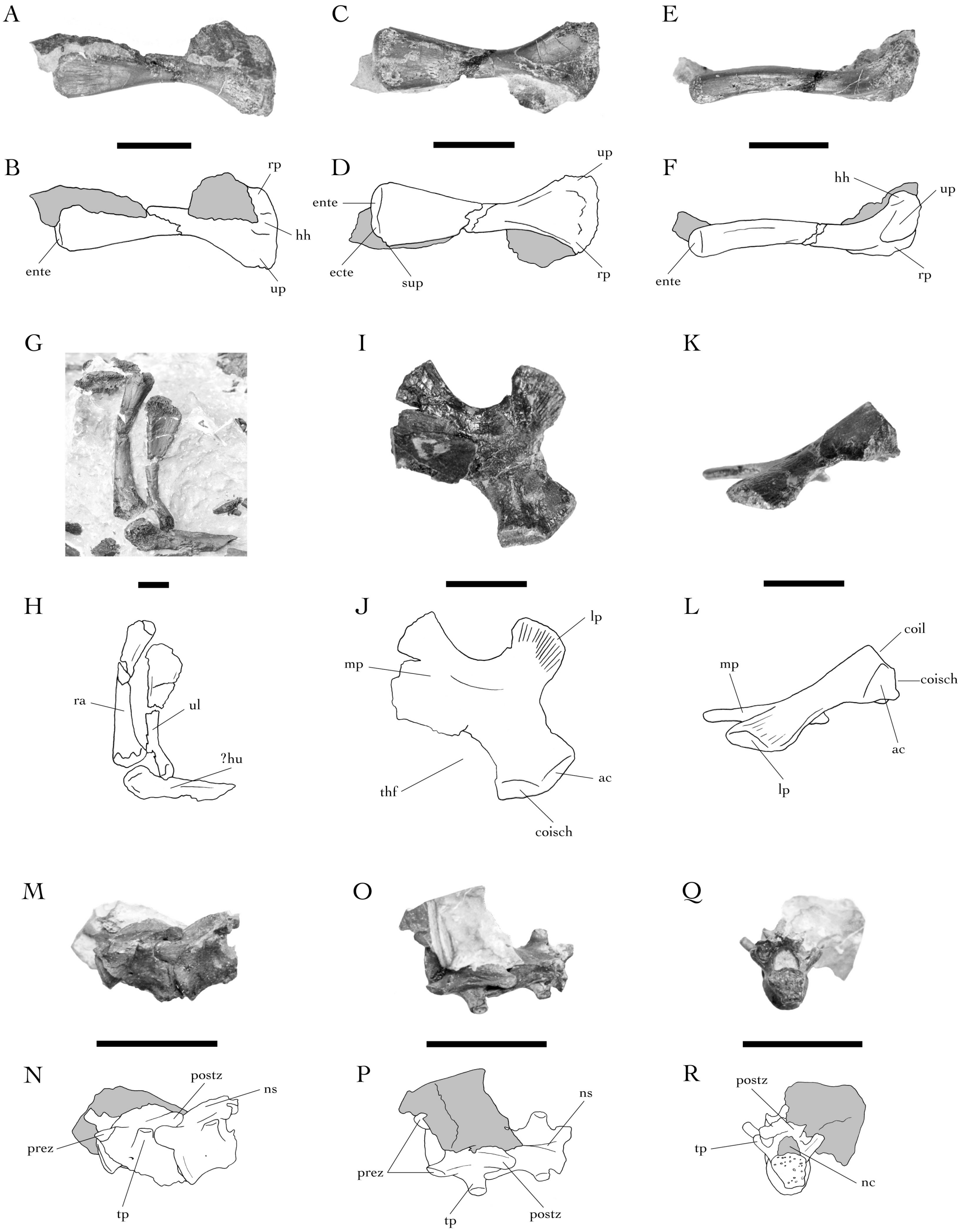

Figure 3.15—*Eileanchelys waldmani*, postcranial material. A-F, NMS G 1992.47.51, left humerus in dorsal (A, B), ventral (C, D) and posterior (E, F) view; G, H, NMS G 2004.31.16h, radius and ulna; I-L, NMS G 2004.31.17, left pubis in ventral (I, J) and lateral (K, L) view; M-R, NMS G 2004.31.16g, cervical vertebrae (specimen A) in lateral (M, N), dorsal (O, P) and posterior (Q, R) view. Scale bars: 10 mm. Abbreviations: ac, acetabulum; coil, contact with ilium; coisch, contact with ischium; ecte, ectepicondyle; ente, entepicondyle; hh, humeral head; hu, humerus; lp, lateral process; mp, medial process; nc, neural canal; ns, neural spine; postz, postzygapophysis; prez, prezygapophysis; ra, radius; rp, radial process; sup, supinator process; thf, thyroid fenestra; tp, transverse process; ul, ulnar; up, ulnar process.

present, but these are very poorly preserved. Slightly anterior to the anterior carapacial rim of NMS G 2004.31.16c, the incomplete remains of two or three cervical vertebrae are present. It is not clear if these pertain to NMS G 2004.31.16c or to the partial skull NMS G 2004.31.16e (if this skull represents a different individual; see above). In NMS G 2004.31.16d, the left humerus and part of the left hindlimb (distal part of the femur, zeugopodium and fragmentary autopodium) are preserved (Fig. 3.13C,D). A very poorly preserved partial limb (probably a forelimb zeugopodium and autopodium) is present ventral to NMS G 2004.31.16e. This may pertain to either NMS G 2004.31.16c or NMS G 2004.31.16d. NMS G 2004.31.16g consists of a series of a series of cervical vertebrae. NMS G 2004.31.16h represents a partial forelimb: the zeugopodium and possibly the distal part of the humerus. NMS G 2004.31.17 is an isolated left pubis. Finally, NMS G 1992.47.8 is a block of matrix containing shell fragments, a partial ilium and an incomplete hindlimb (femur, tibia and a fragment of fibula).

***Description*—**In NMS G 2004.31.16d (Fig. 3.13C,D), the humerus is preserved approximately in anatomical position. It appears to be an elongate element relatively to the dimensions of the shell, but this may due to deformation and this is consequently hard to quantify. As preserved, the humerus is straight and exposed in ventral view. The proximal head is greatly eroded, whereas the distal half of the bone is crushed. The morphology of this bone can be best seen in NMS G 1992.47.51, a small isolated left humerus (Fig. 3.15A-F). The bone is only slightly arched. The proximal head is eroded, but the ulnar process appears to be more developed than the radial process. The distal head is better preserved and the two condyles for the radius and ulna are visible in ventral view (Fig. 3.15C,D). Sediment covers the area where the ectepicondylar foramen would be, but a supinator (or supracondylar) process is visible in ventral view. NMS G 2004.31.16h consists of an ulna and radius that may be associated with the distal part of the humerus (Fig. 3.15G,H). However, the relations of these bones with other specimens in the association are unclear. The ulna and radius have similar dimensions. The ulna is a flattened element, whereas the radius is more rod-like. Both extremities of the ulna are expanded and flattened. The olecranon and sigmoid notch are embedded in the matrix. The proximal head of the radius expands slightly, whereas the distal head is slightly flattened. The femur is best seen in NMS G 1992.47.8, although the proximal head is broken (Fig. 3.16). As preserved, the femur is flattened, but this is probably due to deformation. The diaphysis of the femur is relatively broad. The distal head expands slightly, but the state of preservation of both epiphyses does not permit further description. The hindlimb zeugopodium is preserved in NMS G 2004.31.16b (Fig. 3.11C,D), NMS G 2004.31.16d (Fig. 3.13C,D) and NMS G 1992.47.8 (Fig. 3.16). The tibia has a greatly expanded, triangular proximal head. The distal head of the tibia is only slightly expanded. The fibula is a thin, rod-like bone that expands slightly distally. Parts of the hindlimb autopodium are preserved in NMS G 2004.31.16b and NMS G 2004.31.16d, but are difficult to exploit because the connexions between the remaining elements are lost. These remains consist mostly of an assemblage of moderately elongate phalanges and claws (Figs. 3.11C,D and 3.13C,D). NMS G 1992.47.8 shows a partial ilium (Fig. 3.16). This bone resembles that of *Proganochelys quenstedti* and *Palaeochersis talampayensis*, although it is slightly higher (i.e., the iliac neck is slightly more developed). As in *Proganochelys quenstedti* and *Palaeochersis talampayensis*, the posterior iliac process is

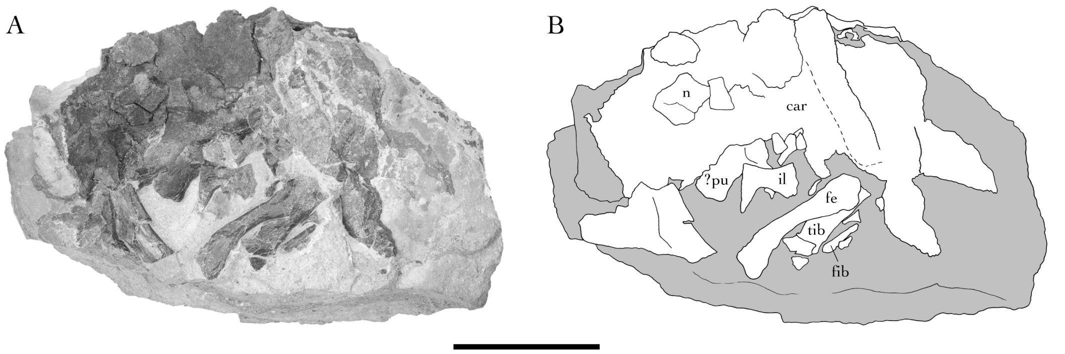

Figure 3.16—*Eileanchelys waldmani*, NMS G 1992.47.8. A, carapace fragments, partial pelvis and partial hindlimb; B, key to photograph A. Scale bar: 50 mm. Abbreviations: car, carapace fragments; fe, femur; fib, fibula; il, ilium; n, neural plate; pu, pubis; tib, tibia.

elongate (Gaffney, 1990; Sterli *et al.*, 2007). The morphology of the ilium in *Eileanchelys waldmani* appears to be intermediate between the primitive morphology seen in *Proganochelys quenstedti* and *Palaeochersis talampayensis* and the rather derived morphology seen in *Kayentachelys aprix* (MCZ 8988). NMS G 2004.31.17 is an isolated left pubis (Fig. 3.15I-L). It is a triradiate element, with a well-developed medial process. However, the morphology of the thyroid fenestra is unknown. The lateral process is strong and flattened. It is striated at its extremity. The posterior extremity of the posterior process shows three surfaces: the lateral surface corresponds to the acetabulum, the dorsomedial surface to the contact with the ilium, and the ventromedial surface to the contact with the ischium.

NMS G 2004.31.16g consists of a series of seven cervical vertebrae in different states of preservation. They cannot be associated with any of the other specimens in the association and it is unclear whether or not they pertain to the same individual. Two of the vertebrae are in articulation (Fig. 3.15M-R). No atlas or axis can be confidently identified within this assemblage. Apart from one that is very fragmentary, all of the vertebrae are similar in morphology. They are distinctly platycoelous, by contrast with the cervical vertebrae found in other stem turtles. In *Proganochelys quenstedti*, *Palaeochersis talampayensis*, *Kayentachelys aprix* and *Kallokibotion bajazidi*, the cervical centra are amphicoelous, which represents the plesiomorphic condition for Reptilia (e.g., Romer, 1956; Hoffstetter & Gasc, 1969). The cervical vertebrae of *Meiolania platyceps* and *Mongolochelys efremovi* have formed articular surfaces (Joyce, 2007). In the available cervical vertebrae, the articular surface of the centrum in *Eileanchelys waldmani* is variable in shape from a higher than wide oval to a triangle. As in other turtles, the centrum is laterally hollowed to form a sagittal keel on the ventral surface of the cervical vertebra, but this sagittal keel is only incipient and the vertebral centrum has a concave ventral margin in lateral view. The cervical vertebrae are approximately as long as high. The transverse process is located in the middle of the centrum and is directed laterodorsally. There is no other rib process on the cervical vertebra. The neural spine is incipient. The articular surface of the prezygapophyses faces mostly medially with a small dorsal component, but this area can be observed in only one cervical vertebra. The articular surface of the postzygapophyses is oriented at an angle of approximately 45 degrees and faces ventrolaterally, but again, this cannot be determined in all of the preserved vertebrae.

Size of *Eileanchelys waldmani*

Due to the fact that most specimens are either crushed or fragmented, it is difficult to accurately appraise their size. However, it is apparent that a rather broad size range characterises the available specimens of *Eileanchelys waldmani*. Of the four shells found within the association NMS G 2004.31.16 two are smaller in size: NMS G 2004.31.16a and NMS G 2004.31.16b. Because of the presence of shell fenestrations, it has already been suggested that NMS G 2004.31.16a represents a juvenile individual (see Costals, above). All other known specimens, including NMS G 2004.31.16b, have a completely ossified shell. However, NMS G 2004.31.16b appears to be significantly smaller than NMS G 2004.31.16c and NMS G 2004.31.16d. This is especially obvious when comparing limb bone sizes between NMS G 2004.31.16b and NMS G 2004.31.16d. A broad size range in the available specimens of *Eileanchelys waldmani* is also indicated by the thickness of the shell bone in NMS G 2004.31.18 and by the size of the hindlimb bones in NMS G 1992.47.8. All these observations suggest that the carapace length of *Eileanchelys waldmani* (250-300 mm; see Emended diagnosis, above) may have been slightly underestimated. This also indicates that both adult and juvenile individuals lived in the lagoonal palaeoenvironment.

DISCUSSION

Anatomy

Eileanchelys waldmani bridges the temporal and morphological gap between the most basal turtles (e.g., *Proganochelys quenstedti* and *Kayentachelys aprix*) and the crown-group turtles that appear in the fossil record during the Middle Jurassic (e.g., Danilov & Parham, 2008; Scheyer & Anquetin, 2008; see Chapter 4). *Eileanchelys waldmani* presents an intermediate morphology that is characterised by a mosaic of derived and plesiomorphic characters. Derived characters include: an elongate postorbital skull; a basicranial floor that is reduced in thickness; a well-developed antrum postoticum; and a slender, flatter processus interfenestralis of the opisthotic. In *Eileanchelys waldmani*, the development of the processus interfenestralis of the opisthotic is structurally intermediate between the robust structure seen in *Proganochelys quenstedti* and *Kayentachelys aprix* and the thin vertical sheet of bone found in most crown-group turtles. The orientation of the processus interfenestralis is also different in *Eileanchelys waldmani*. In crown-group turtles, the processus interfenestralis is flattened anteroposteriorly and forms a vertical wall between the cavum labyrinthicum and the recessus scalae tympani. In contrast, the recessus scalae tympani *sensu stricto* is not developed in *Eileanchelys waldmani*, with the result that the processus interfenestralis merely forms the posterolateral margin of the cavum labyrinthicum and has a more oblique orientation. Plesiomorphic characters of *Eileanchelys waldmani* include: a slender, diamond-shaped entoplastron; a reduced posterior extension of the pterygoid; an unfloored cavum acustico-jugulare; separate posterior openings of the canalis cavernosus and canalis stapedio-temporalis in the cavum acustico-jugulare; and a flat vomer that is free of contact for most of its length and which forms the medial margin of the apertura narium interna. The last two characters represent intermediate states and document the evolution from the primitive morphology of *Proganochelys quenstedti* to the derived morphology that is characteristic of most turtles. These characters are detailed below.

Evolution of the vomer

The vomer in *Proganochelys quenstedti*, *Palaeochersis talampayensis* and *Australochelys africanus* is very different from that found in crown-group turtles (see below). In contrast, the most derived stem turtles known to date (i.e., *Meiolania platyceps*, *Mongolochelys efremovi* and *Kallokibotion bajazidi*) possess a vomer with a modern morphology. In other words, the evolution of the modern chelonian vomer occurred along the phylogenetic stem of Testudines. In *Kayentachelys aprix*, *Heckerochelys romani* and *Condorchelys antiqua*, the vomer is severely damaged, poorly described and not preserved, respectively. Therefore, *Eileanchelys waldmani* offers a unique opportunity to understand the evolution of the vomer in basal turtles. In the plesiomorphic condition, illustrated by *Proganochelys quenstedti* (SMNS 15759 and SMNS 16980) and *Australochelys africanus* (BP/1/4933), the vomer consists of a large sheet of bone that curves dorsally well above the level of the palatine and pterygoid. It is free of contact for most of its length and it does not meet the descending process of the prefrontal (Fig. 3.17A,D). In the next step of its evolution, as documented by *Eileanchelys waldmani* and also partly by *Kayentachelys aprix* (MNA V1558 and MCZ 8917; see also Sterli & Joyce, 2007), the vomer becomes a more horizontal sheet of bone in the same plane as the palatine and pterygoid (Fig. 3.17B,E). At this stage, the vomer is still free of contact for most of its length with the exception of anterior contacts with the premaxillae and maxillae, and posterior contacts with the palatines and pterygoids (at least in *Kayentachelys aprix*). In *Eileanchelys waldmani*, the descending process of the prefrontal now has a sutural contact with the vomer (Fig. 3.17B). Sterli & Joyce (2007) tentatively proposed that this contact was also present in *Kayentachelys aprix*, but reasonable doubts exist on this point (see Vomer, above). In all more derived turtles (i.e., *Meiolania platyceps*, *Mongolochelys efremovi*, *Kallokibotion bajazidi* and crown-group turtles), the vomer progressively develops a three-dimensional morphology with the formation of a ventral sagittal septum that separates the meatus choanae (i.e., the internal narial canals; Fig. 3.17C,F). Hence, the vomer progressively acquires the dumbell-shaped cross section that is typical of the majority of

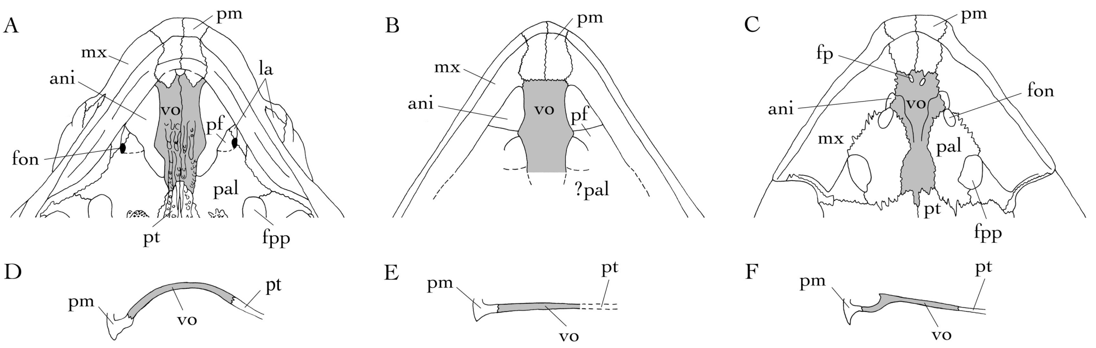

Figure 3.17—Evolution of the vomer in basal turtles. A, D, *Proganochelys quenstedti* in ventral view (A) and sagittal section (D); B, E, *Eileanchelys waldmani* in ventral view (B) and sagittal section (E); C, F, *Chelydra serpentina* in ventral view (C) and sagittal section (F). A, redrawn from Gaffney (1990); C, redrawn from Gaffney (1979). Abbreviations: ani, apertura narium interna; fon, foramen orbito-nasale; fp, foramen praepalatinum; fpp, foramen palatinum posterius; la, lacrimal; mx, maxilla; pal, palatine; pf, prefrontal; pm, premaxilla; pt, pterygoid; vo, vomer.

turtles, with the ventralmost part of the bone forming a horizontal plate that contributes to the formation of an incipient secondary palate and that floors the meatus choanae. In these forms, the contacts of the vomer with the maxilla and especially the palatine become extensive and the vomer is surrounded by bone (Fig. 3.17C). This sequence shows that the evolution of the vomer in basal turtles is linked to the development of the internal narial canals (meatus choanae). In most stem turtles (i.e., *Proganochelys quenstedti*, *Palaeochersis talampayensis*, *Australochelys africanus*, *Kayentachelys aprix*, *Eileanchelys waldmani* and *Heckerochelys romani*), these canals do not exist and the apertura narium interna is confluent with the opening in the floor of the fossa nasalis. By developing a ventral septum that meets the premaxillae and maxillae ventrally, the vomer forms the incipient meatus choanae and the apertura narium interna becomes differentiated from the opening in the floor of the fossa nasalis. Although they are only incipient in most turtles (e.g., *Chelydra serpentina*), the meatus choanae are greatly developed in those turtles with an extensive secondary palate (e.g., chelonioids).

Aditus canalis stapedio-temporalis and canalis cavernosus

The well-preserved cavum acustico-jugulare of NMS G 2004.31.15 (Fig. 3.6), the holotype of *Eileanchelys waldmani*, documents a further step in the evolution of this area toward the modern morphology seen in crown-group turtles. The cavum acustico-jugulare is a structure found only in turtles and corresponds to a subdivision of the middle ear (the anatomical region between the tympanum and the fenestra ovalis). In turtles, the middle ear region in divided into two parts by a constriction of the quadrate around the columella auris (i.e., the stapes). This is achieved in all turtles with the exception of *Proganochelys quenstedti*, *Palaeochersis talampayensis* and *Australochelys africanus* (Joyce, 2007). *Proganochelys quenstedti* is unique among turtles in having an open cranioquadrate space (plesiomorphic amniote condition; see Gaffney, 1990), which allows the passage of nerves and arteries, such as the vena capitis lateralis (the lateral head vein).

Proganochelys quenstedti is also unique in having a passage for the stapedial artery (there is no proper canal) that is formed by the processus paroccipitalis of the opisthotic and quadrate, rather than by the prootic and quadrate as in other turtles, and that is located posterior to the fenestra ovalis (ancestral amniote condition; see Gaffney, 1990; Joyce, 2007). In *Palaeochersis talampayensis* and *Australochelys africanus*, the basipterygoid articulation is fused and the pterygoid encloses the vena capitis lateralis forming a short canalis cavernosus that is located approximately at the level of the former articulation. The location of the passage of the stapedial artery is unclear in these taxa (Gaffney & Kitching, 1995; Sterli *et al.*, 2007), but in any case there is no opening between the processus paroccipitalis of the opistothic and the quadrate unlike the condition present in *Proganochelys quenstedti*. Moreover, several holes in the roof of the middle ear cavity of BP/1/4933, the holotype and only specimen of *Australochelys africanus*, may correspond to the passage of the stapedial artery (pers. obs.). If this is the case, then the passage would be located approximately at the level of the fenestra ovalis in this species. In all more derived turtles, including *Kayentachelys aprix* and *Eileanchelys waldmani*, there is a well-developed canal for the stapedial artery that is formed by the quadrate and prootic, the canalis stapedio-temporalis. Ventrally, this canal opens into the roof of the cavum acustico-jugulare via the aditus canalis stapedio-temporalis. In *Kayentachelys aprix* (MCZ 8917) and *Eileanchelys waldmani* (NMS G 2004.31.15; Fig. 3.6), the aditus canalis stapedio-temporalis is situated at the level of the anterior wall of the fenestra ovalis, whereas in all more derived turtles it is positioned anterior to the fenestra ovalis. In comparison with *Palaeochersis talampayensis* and *Australochelys africanus*, the length of the canalis cavernosus increases in *Kayentachelys aprix*, *Eileanchelys waldmani*, *Heckerochelys romani* and *Condorchelys antiqua* with the progressive posterior development of the pterygoid along the basisphenoid, so that the location of the posterior opening of this canal is variable among these species. The posterior opening of the canalis cavernosus is located slightly more anteriorly in *Kayentachelys aprix* and more posteriorly in *Condorchelys antiqua*, whereas it is intermediate in *Eileanchelys waldmani* and probably also in *Heckerochelys romani*. This suggests that this character is continuous. In more derived turtles, the posterior opening of the canalis cavernosus is located further posteriorly and is actually very close to the aditus canalis stapedio-temporalis. In *Kayentachelys aprix* and *Eileanchelys waldmani* (to a lesser extent), these two openings are widely separated from one another documenting an intermediate stage between the configuration seen in basalmost turtles like *Proganochelys quenstedti* and the modern morphology found in crown-group turtles. Hence, the recent reassessment of the cranial material of *Kayentachelys aprix* (Sterli & Joyce, 2007) and the description of *Eileanchelys waldmani* (Anquetin *et al.*, 2009; present work) allow a better understanding of the evolution of the middle ear region in basal turtles, especially by documenting the progressive migration of the aditus canalis stapedio-temporalis forward and posterior opening of the canalis cavernosus backward.

Palaeoecology

The palaeoecology of stem turtles has been debated intensively over the past two decades (see Joyce & Gauthier, 2004), as the purported ancestral ecology of the turtle lineage has been used as circumstantial evidence in discussions on the origin of turtles. In other words, if turtles were ancestrally terrestrial then this would favour hypotheses placing the origin of this group within basal 'anapsid' reptiles (e.g., Reisz & Laurin, 1991; Laurin & Reisz, 1995; Lee, 1995, 1996, 1997; Joyce *et al.*, 2009), whereas if turtles were ancestrally aquatic this would be more congruent with hypotheses relating turtles to sauropterygians (e.g., deBraga & Rieppel, 1997). Although it is generally accepted that crown-group turtles are primitively aquatic, the habitat preference of stem turtles has remained controversial. Two recent studies, based on independent methods, have reinvigorated this debate (Joyce & Gauthier, 2004; Scheyer & Sander, 2007). Forelimb proportions and extensive comparisons with extant taxa of known ecology led Joyce & Gauthier (2004) to conclude that *Proganochelys quenstedti* and *Palaeochersis talampayensis* were terrestrial animals and were not competent swimmers. This conclusion was supported by Scheyer & Sander (2007) who reported that the shell bone histology of *Proganochelys quenstedti*, *Proterochersis robusta*, *Kayentachelys aprix* and an indeterminate meiolaniid was more similar to that of terrestrial turtles than to that of aquatic forms. Both of these studies imply that the aquatic habitat preference, optimised to be basal for the crown-group, must have appeared along the turtle stem-lineage. Inferring the palaeoecology of fossil turtles based solely on their obvious morphological traits has proved problematic (Joyce & Gauthier, 2004; see also Peripherals, above, and the discussion about *Heckerochelys romani*, below). With the exception of fully marine species (presence of paddles, greatly reduced ossification of the shell, presence of a broad interorbital opening accommodating a large salt gland), the distinction between aquatic and terrestrial turtles may be difficult to identify on the basis of fossil material. Indeed, the boundary between terrestriality and aquatic habits is often blurred and many extant species actually live partly on land and partly underwater (Bonin *et al.*, 2006). This explains why discussions on the ecology of fossil turtles, especially the more basal ones, rarely reach a consensus.

Based on the presence of shell fontanelles and an inferred ligamentous shell bridge, it has been proposed that *Heckerochelys romani* was an aquatic form (Danilov, 2005: 350). Alternatively, however, the presence of reduced plastral and carapacial fontanelles may indicate that known specimens of *H. romani* are juveniles, as it is the case for one specimen of *Eileanchelys waldmani* (NMS G 2004.31.16a). Moreover, the ligamentous nature of the shell bridge in *Heckerochelys romani*, a feature usually absent in basal species, is impossible to confirm on the basis of published illustrations (Sukhanov, 2006). From a more global point of view, there is no logical reason, nor factual evidence, that a ligamentous bridge should be associated with an aquatic habitat preference. For instance, all extant terrestrial box turtles (i.e., *Terrapene* spp. and *Cuora* spp.) have a ligamentous bridge, whereas many aquatic turtles (e.g., all Deirochelyinae, most batagurids, and all pleurodires) have an osseous bridge (W. G. Joyce, pers. comm., 2008). Similarly, several extant

Figure 3.18—Reconstruction of the Kilmaluag Formation fauna (late Bathonian, Isle of Skye, Scotland) representing *Eileanchelys waldmani* in its natural habitat. For a complete faunal list of the Kilmaluag Formation see Evans *et al.* (2006). Credit: Robert F. Laws, 2008.

terrestrial turtles (e.g., *Manouria* spp. and *Malacochersis* tornieri) have many fontanelles, whereas many aquatic forms have a fully ossified shell (ibid.). Clearly, neither the ligamentous nature of the shell bridge nor the presence of shell fontanelles is diagnostic of habitat preference. Consequently, no positive evidence is currently available to conclude that *Heckerochelys romani* was aquatic and further investigations are needed. *Condorchelys antiqua* was discovered in a series of lacustrine mudstones and limestones at Queso Rallado (Argentina) alongside terrestrial and aquatic vertebrates (Rauhut *et al.*, 2002; Sterli, 2008), and turtles are among the most common vertebrates at this locality (O. W. M. Rauhut, pers. comm., 2008). This taphonomic information might indicate that *Condorchelys antiqua* was an aquatic form, but the habitat preferences of this taxon have yet to be assessed.

In this context, Anquetin *et al.* (2009) argued that *Eileanchelys waldmani* may be interpreted as the earliest known aquatic turtle. As stated above (see Geological settings), the Kilmaluag Formation at Cladach a'Ghlinne consists of alternations of calcareous mudstones, shales and occasional limestone horizons, which were formed in closed water systems that represent cycles of alternating low-salinity lagoons and freshwater floodplain lakes and pools (Harris & Hudson, 1980; Andrews, 1985). Although the Cladach a'Ghlinne locality yields some articulated specimens

(Evans *et al.*, 2006), most of the material recovered from this site is scattered, fragmentary and has obviously suffered transport and/or other forms of disarticulation process. By contrast, many of the turtle specimens consist of articulated skulls, shells, limbs and vertebrae, indicating the absence or near absence of transport for them. Moreover, turtle remains represent some of the most abundant elements at the locality along with those of sharks and salamanders (i.e., aquatic forms), whereas remains of terrestrial vertebrates (e.g., lizards, dinosaurs, synapsids) are exceptionally rare. This taphonomic evidence (i.e., the abundance of the turtle remains, the numerical dominance of other aquatic taxa and the absence of transportation) suggests that *Eileanchelys waldmani* was a denizen of these lagoons and lakes, rather than a terrestrial taxon that inhabited the inland areas adjacent to the lagoons and that was subsequently fossilised in the aquatic facies.

Anquetin *et al.* (2009) was published just one week before the announcement of the discovery of the astonishing *Odontochelys semitestacea* (Li *et al.*, 2008). *Odontochelys semitestacea* is the oldest and probably the most basal turtle known to date (Li *et al.*, 2008; see also Chapters 1 and 5). It is characterised, among other features, by the virtual absence of an ossified carapace and has been interpreted as having marine habits (Li *et al.*, 2008). This discovery challenges our view of the early stages of turtle evolution and reactivates the discussion on the origin of turtles (Reisz & Head, 2008). Li *et al.* (2008) consider that *Odontochelys semitestacea* represents the primitive ecology for turtles, whereas Reisz & Head (2008) think that the shell morphology of *O. semitestacea* is probably secondarily derived and that this species represents the earliest turtle radiation from terrestrial environments into marine habitats. With the discovery of this new Triassic turtle, *Eileanchelys waldmani* cannot be considered as the earliest aquatic turtle anymore. However, *E. waldmani* is still interpreted to be an aquatic taxon, whereas most other stem turtles are interpreted to be terrestrial. Because no direct relationship appears to exist between *O. semitestacea* and *E. waldmani*, the adaptation of the latter species to aquatic habitats must have evolved independently. The discoveries of the two aforementioned species demonstrate that stem turtles were morphologically and ecologically more diverse than previously suspected. This is perhaps unsurprising as only about ten species of stem turtles are known representing a time span of approximately 60 million years.

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CHAPTER 4: A REASSESSMENT OF MIDDLE JURASSIC TURTLES FROM THE UK

As stated above (see Chapter 1), Middle Jurassic turtle remains were, until recently, rare and poorly studied worldwide. However, turtles have long been known from British Middle Jurassic microvertebrate localities (e.g., Evans & Milner, 1994; Benton & Spencer, 1995). Most of these remains are fragmentary and difficult to interpret, yet, within the context of the present work, their reassessment (especially that of the remains from Kirtlington and Stonesfield) was necessary in order to evaluate the new material from Skye and to place them within a more recent taxonomic and phylogenetic contexts.

A REVIEW OF BRITISH MIDDLE JURASSIC TURTLES

Kirtlington Quarry, Oxfordshire, England

The Mammal Bed (Forest Marble Formation, upper Bathonian, *Oppelia aspidoides* zone; Evans & Milner, 1994) at Kirtlington is the most productive British Middle Jurassic locality for terrestrial vertebrates (Benton & Spencer, 1995). At least 30 different species of tetrapods have been recovered, representing frogs, salamanders, turtles, stem lepidosauromorphs, lizards, choristoderes, crocodiles, pterosaurs, ornithischian and saurischian dinosaurs, tritylodonts, morganucodonts, docodonts, multituberculates, symmetrodonts and eupantotheres (Evans & Milner, 1994: 306). Turtles are represented by shell and cranial fragments as well as some vertebrae. Gillham (1994) tentatively assigned these fragments to a pleurosternid turtle. In order to test this identification, this material was reassessed during this study (see below).

Forest Marble Formation of Dorset, Gloucestershire and Whiltshire

The following upper Bathonian exposures of the Forest Marble Formation have yielded similar faunas to Kirtlington, including some fragmentary turtle material: Tarlton Clay Pit, near Cirencester; Watton Cliff, Dorset; Swyre, Dorset; and Leigh Delamere, Wiltshire (Evans & Milner, 1994: 308-310). This material is undetermined.

Stonesfield Slate, Oxfordshire, England

The Stonesfield Slate is a recurrent lithofacies of the Taynton Limestone Formation (early middle Bathonian, *Procerites progracilis* zone; Boneham & Wyatt, 1993). The locality consists of a series of mines and quarries around the village of Stonesfield. After Kirtlington, this is the richest British Middle Jurassic site for terrestrial vertebrates (Benton & Spencer, 1995). It is also the type locality of the famous *Megalosaurus bucklandii* Mantell 1827, the first dinosaur to have been described. The Stonesfield Slate has yielded some very interesting turtle material, which was first described during the 1860s and early 1870s (Blake, 1863; Mackie, 1863; Phillips, 1871; see below). However, this material has been mostly overlooked by subsequent authors (Benton & Spencer, 1995: 144). A reassessment of this material is provided herein (see below for additional details).

Huntsman's Quarry, Naunton, Gloucestershire, England

Benton & Spencer (1995: 148) mention the presence of an indeterminate turtle carapace from Huntsman's Quarry (Cotswold Slate = Eyford Member, middle Bathonian, *Procerites progracilis* zone; Evans & Milner, 1994; Benton & Spencer, 1995) and state that this specimen is housed at the Natural History Museum, London with the registration number NHM R2634. According to the NHM catalogue, this number refers to a "turtle scute" (so probably a shell fragment) but the specimen is apparently lost.

Hornsleasow Quarry, Snowshill, Oxfordshire, England

Hornsleasow Quarry is an exposure of the Chipping Norton Member (Chipping Norton Formation, lower Bathonian, *Zigzagiceras zigzag* zone; Evans & Milner, 1994). A clay lens containing vertebrate remains was discovered at this locality in 1987. "Turtle plates" have been mentioned within an assemblage composed of dinosaur teeth and bones, crocodilian teeth, *Lepidotes* scales, pterosaurian teeth, lizards, stem lepidosauromorphs, tritylodont teeth, mammals and amphibians (ibid.). The turtle material, like most of the material from this locality, is broken and rolled (S. E. Evans, pers. comm., 2009).

Shipton-on-Cherwell Quarry, Oxfordshire, England

The Shipton-on-Cherwell Quarry provides exposure of the White Limestone (*fimbriata-waltoni* clay), Forest Marble and Cornbrash Formations (middle to upper Bathonian; Evans & Milner, 1994; Benton & Spencer, 1995). A single "turtle scute" has been mentioned from this locality (OXFUM J17567), but "little can be said" about it according to Benton & Spencer (1995: 154).

Hugh Miller's Bone Bed, island of Eigg, Scotland

In addition to the Vertebrate Beds of the Kilmaluag Formation (see Chapter 3), a second horizon from the Great Estuarine Group of the Inner Hebrides, referred to as 'Hugh Miller's Bone Bed', has yielded vertebrate material. This horizon is part of the Kildonnan Member of the Lealt

Formation (lower Bathonian; see Chapter 3) and is found at two localities, Kildonnan and Eilean Thuilm (Benton & Spencer, 1995: 131):

> "Hugh Miller visited Eigg in the Free Church yacht *Betsey* in 1844 and 1845. In 1844 he found reptile bones in loose blocks opposite the island of Eilean Thuilm at the northern tip of the island; he called this locality Ru-Stoir, a name which does not occur on any map. In 1845 he found the bed *in situ* on the eastern coast of the island about midway between the headland Rudha nan Tri Clach and the settlement of Kildonnan."

Miller (1858) reported crocodilian ribs and plesiosaur bones among those beds of fish teeth and scales. During the 20th century, several workers (G. Barrow, J. D. Hudson, B. Newman, D. S. Brown) collected material from this bed (Benton & Spencer, 1995: 132-133). According to Benton & Spencer (ibid.), "?turtle bones" are present in both the Newman and Brown Collections. However, D. S. Brown (pers. comm., 2006) mentions that there is no material positively identifiable as turtle in these collections, so this record remains unsubstantiated at present.

A RE-EVALUATION OF TURTLE MATERIAL FROM KIRTLINGTON, OXFORDSHIRE, ENGLAND

The following results form part of a collaborative project with Torsten M. Scheyer (Paläontologische Institut und Museum, University of Zurich), which led to a joint publication (Scheyer & Anquetin, 2008). TMS was responsible for the collection and interpretation of shell bone histological data, while I was responsible for the morphological study of the material and the interpretation of our results within the broader context of turtle phylogeny. For the convenience of the reader, a short summary of the results of the histological study is provided. However, it is my duty to stress that the histological study is not the result of my work.

Histological study of the turtle shell remains from Kirtlington

Shell bone histology reveals that two different histomorphs are present within the analysed material. This indicates the presence of two distinct taxa at Kirtlington. The first histomorph possesses the derived histological structure of pleurosternids, which was described for the first time by T. M. Scheyer in Scheyer & Anquetin (2008). This work supports the conclusions of Gillham (1994), who first suggested that the Kirtlington material pertained to pleurosternids. The second histomorph has a more plesiomorphic structure and can only be assigned to Cryptodira *incertae sedis* (see Scheyer & Anquetin, 2008 for further details).

Morphological reassessment of the turtle material from Kirtlington

Kirtlington is a microvertebrate locality that yielded an abundant but very fragmentary turtle material. This material was first studied by Gillham (1994), who provided descriptions of the best-preserved specimens. Gillham (1994) tentatively assigned this material to the Pleurosternidae, based on a combination of characters that did not include any currently accepted pleurosternid synapomorphies (see below). In the light of the histological study of the Kirtlington material (see above), a re-evaluation of both this material and Gillham's arguments is necessary.

Morphological observations on the fragmentary turtle material from Kirtlington do not allow the recognition of more than one taxon in this assemblage. NHM R12404 (fig. 2A, B *in* Gillham, 1994) is a medial fragment of a costal plate that indicates a costal-costal contact along the midline (i.e., it implies the absence of a neural plate). As noted by Gillham (1994), a costal-costal contact is sometimes observed in the pleurosternid *Pleurosternon bullockii* (Owen 1842; e.g., NHM 28618). However, a medial contact between costals in association with the absence of one or more neurals is also observed in numerous pleurodires and trionychoids (Meylan & Gaffney, 1989; Joyce, 2007). Fragments of peripherals are common at Kirtlington. According to Gillham (1994: 585), only around one third of these peripherals bear scale sulci and, when present, those sulci all run perpendicular to the external border of the peripheral (i.e., they are marginal-marginal sulci). This observation suggests that the marginal scales were wide and that they overlapped the costals medially, because pleural-marginal sulci, which would run parallel to the peripheral border, are absent on the peripheral fragments. This morphology is known in three pleurosternid species (Gaffney, 1979a; Milner, 2004): *Pleurosternon bullockii*, *Glyptops plicatulus* (Cope 1877) and *Dinochelys whitei* Gaffney 1979a. However, a similar overlapping of the marginals onto the costals has also been reported for some trionychoids (Meylan & Gaffney, 1989) and xinjiangchelyids (Peng & Brinkman, 1993; Hirayama *et al.*, 2000). Gillham (1994: 586) stated that the mesoplastra of the Kirtlington turtle met in midline (a plesiomorphic feature), but this cannot be verified as the only known specimen is in a private collection and is not figured in the literature. NHM R12407 (fig. 3C *in* Gillham, 1994) is a complete kite-shaped entoplastron that is longer than wide. This morphology differs from that commonly found in known pleurosternids (Gaffney, 1979a; Milner, 2004) where the entoplastron is either wider than long (*Pleurosternon bullockii*) or as wide as it is long (*Glyptops plicatulus*, *Pleurosternon portlandicum* Lydekker 1889). Consequently, none of the shell features mentioned by Gillham (1994) provides unambiguous support for pleurosternid affinities of this material. However, NHM R12407 clearly possesses a surface ornamentation of low vermiculate ridges and tubercles framed by fine linear striations perpendicular to the plate margins. This ornamentation is characteristic for the pleurosternids *Glyptops plicatulus*, *Pleurosternon bullockii* and *Compsemys victa* Leidy 1856, and the baenid *Trinitichelys hiatti* Gaffney 1972 (Gaffney, 1979a; Hutchison & Holroyd, 2003). Overall, the presence of that distinctive ornamentation, not only on NHM R12407 but also on numerous other specimens (unnumbered), is the best morphological argument supporting of the presence of pleurosternids or paracryptodires at Kirtlington.

In contrast to the evidence from gross anatomy, bone histology suggests that at least two species of turtle are present at Kirtlington. Consequently, it is possible that the skull reconstruction

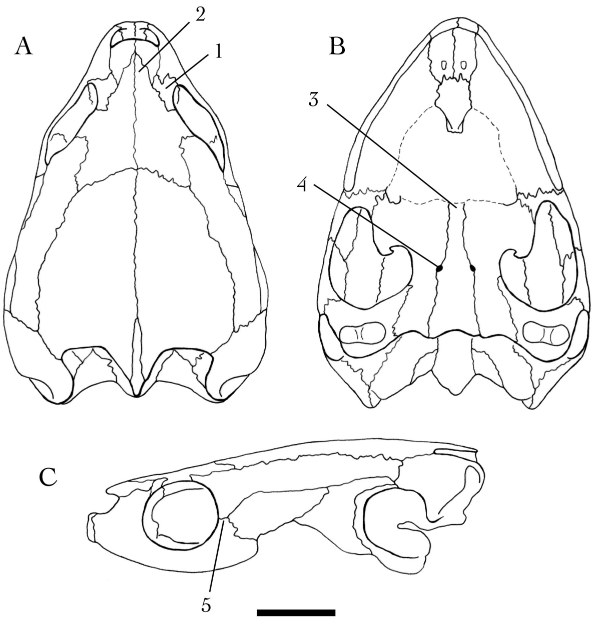


Figure 4.1—Pleurosternid cranial anatomy as exemplified by *Pleurosternon bullockii* (= *Mesochelys durlstonensis* Evans & Kemp 1975). A, dorsal; B, ventral; C, left. 1, small prefrontal lappets; 2, anterior process of frontals that partly separates nasals posteromedially; 3, basisphenoid-vomer contact preventing medial contact of pterygoids; 4, fpcci opening between the basisphenoid and pterygoid; 5, postorbital-maxilla contact preventing jugal from entering the orbital margin. Scale bar: 10 mm. Redrawn from Evans & Kemp (1975) and Gaffney (1979b).

proposed by Gillham (1994: fig. 6) might be composite. Indeed, only isolated skull bones are known at Kirtlington. One of Gillham's strongest arguments in favour of a referral to Pleurosternidae was the presence of reduced prefrontal lappets (Fig. 4.1-1), which is now, however, considered a paracryptodire synapomorphy (Joyce, 2007; see also character 10 in Chapter 5 and Appendix 7). No prefrontal is known from Kirtlington, but Gillham (1994: fig. 7A, B) identified an anterior fragment of frontal (NHM R12414), which could potentially give information on the prefrontal. According to Gillham (1994), NHM R12414 shows that the prefrontal lappets of this species were reduced, as in paracryptodires. However, this specimen is reinterpreted here as a fragment of postorbital: its internal surface shows a strong ridge that delimits the posterior margin of the fossa orbitalis, as occurs in many turtles, whereas no such ridge is present on the frontal. Moreover, this ridge is present on another unmistakable postorbital from Kirtlington (NHM R12419). Hence, the presence of reduced prefrontal lappets cannot be demonstrated on the basis of the available material.

As observed by Gillham (1994), some cranial fragments suggest that the jugal contribution to the orbit was either very small or completely absent. NHM R12419 (fig. 8C, D *in* Gillham, 1994) is a nearly complete left postorbital that possesses a long anteroventral process along the orbital margin, a process that could have prevented the contact of the jugal with the orbital margin. Additionally, NHM R12418, an almost complete jugal (fig. 8A, B *in* Gillham, 1994), lacks a clearly defined orbital border between the postorbital and the maxillary sutural facets. The curved orbital

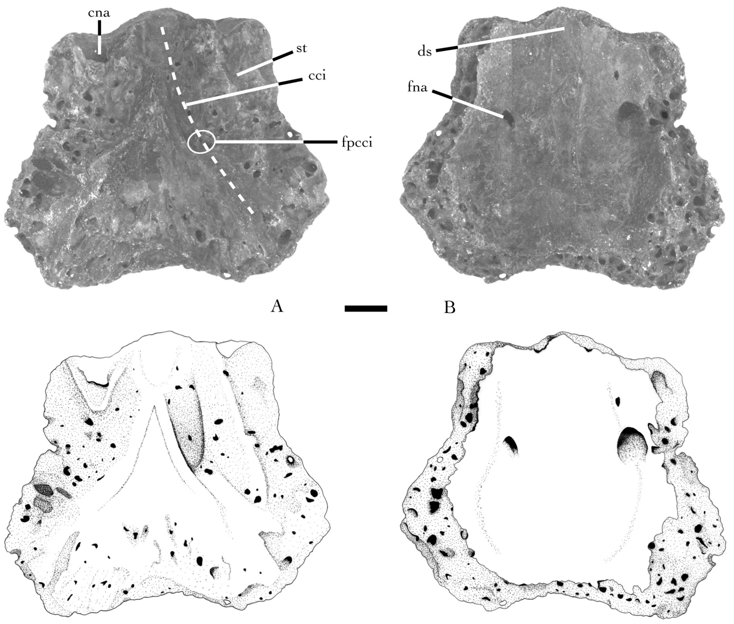


Figure 4.2—NHM R16498, partial basisphenoid, Kirtlington Quarry, Bathonian, Oxfordshire, England. A, ventral view; B, dorsal view. Anterior upward. Scale bar: 1 mm. Abbreviations: cna, canalis nervi abducentis; cci, canalis caroticus internus; ds, dorsum sellae; fna, foramen nervi abducentis; fpcci, foramen posterius canalis carotici interni; st, sutural contact with pterygoid. Dashed line: path of the internal carotid artery.

border described by Gillham (1994: 589) on this specimen is actually limited to the medial (internal) process of the jugal and was probably covered externally by the contact between the maxilla and postorbital. Among pleurosternids, both *Pleurosternon bullockii* (= *Mesochelys durlstonensis* Evans & Kemp 1975; Fig. 4.1-5) and *Glyptops plicatulus* have a jugal that is excluded from the orbit by an anterior contact between the postorbital and maxilla (Gaffney, 1979a). The morphology of *Dinochelys whitei* is unclear (Brinkman *et al.*, 2000). Such a contact between the maxilla and postorbital excluding the jugal from the orbit is uncommon among turtles, but it is also known in the baenid *Eubaena cephalica*, the basal paracryptodire *Arundelemys dardeni* and at least three extant species: *Platysternon megacephalum*, *Emys orbicularis* (see Fig. 2.4) and *Malayemys subtrijuga* (Gaffney, 1979b; Lipka *et al.*, 2006). This feature has not yet been included into a phylogenetic analysis (but see Chapter 5). However, during the Jurassic and Early Cretaceous, such morphology is known only in paracryptodires and could be seen as a possible evidence of their presence at Kirtlington.

In order to find more evidence for the presence of pleurosternids, or at least of paracryptodires, at Kirtlington, I examined part of the unsorted material (currently with S. E. Evans at UCL) from this locality looking especially for cranial material, as synapomorphies of both aforementioned clades concern cranial features (Joyce, 2007; see also Chapter 5). This led to the discovery of NHM R16498, a partial basisphenoid (Fig. 4.2). The posterior part is missing and anteriorly the bone is broken at the level of the dorsum sellae. The ventral surface shows the sutural contact with the two pterygoids and it appears that the latter bones met anteriorly in the midline preventing the basisphenoid from contacting the vomer. In other words, this specimen lacks one of the most important pleurosternid synapomorphies (Joyce, 2007; see Discussion, below). A wide groove extending along the basisphenoid-pterygoid suture on both sides of the element indicates the passage of the internal carotid artery. This groove is divided into two parts. Anteriorly, the groove is deeper and deepens anteromedially. This part corresponds to the canalis caroticus internus where the internal carotid artery penetrates the basisphenoid and ultimately enters the cavum cranii at the posterior end of the sella turcica. Posteriorly, the groove forms only a shallow mark on the ventral surface of the basisphenoid and is positioned more ventrally than the basisphenoid-pterygoid suture, indicating that the internal carotid artery was not floored ventrally in this part but simply extended along the ventral surface of the basicranium. The limit between the anterior and the posterior parts of the groove marks the position of the foramen posterius canalis carotici interni (fpcci). Hence, the fpcci opens along the basisphenoid-pterygoid suture in a configuration known only in paracryptodires (e.g., Brinkman & Nicholls, 1993; Jamniczky *et al.*, 2006).

Discussion

Pleurosternids are well known from the Late Jurassic and Early Cretaceous of western Europe and North America (e.g., Bräm, 1973; Gaffney, 1979a; Brinkman *et al.*, 2000; Milner, 2004), and may be also present in the Late Cretaceous and Early Palaeocene of North America (Hutchison & Holroyd, 2003). Together with the exclusively North American Baenidae they form the monophyletic Paracryptodira, the sister group of the Eucryptodira (the clade containing the crown-group cryptodires). Monophyly of Pleurosternidae is mainly supported by a single synapomorphy, which is the absence of a medial contact between the pterygoids that allows the basisphenoid to contact the vomer (Gaffney, 1979a, 1996; Gaffney & Meylan, 1988; Joyce, 2007; Fig. 4.1-3). In addition, the presence of an anterior projection of the frontals that partly separates the nasals medially is also considered to be a synapomorphy of the clade (Joyce, 2007; Fig. 4.1-2). Paracryptodira (Pleurosternidae + Baenidae) is supported by three synapomorphies: (1) the reduction of the prefrontal exposure on the dorsal surface of the skull (Fig. 4.1-1); (2) a reduced fenestra perilymphatica; and (3) a secondary reduction of the supraoccipital crest (Joyce, 2007). The clade Paracryptodira was originally based on the location of the foramen posterius canalis carotici interni (fpcci) halfway along the suture between the basisphenoid and the pterygoid (Gaffney, 1975; Fig. 4.1-4), whereas the fpcci is formed entirely by the pterygoid and is located near the posterior limit of the basisphenoid in Eucryptodira (Fig. 4.3). Two contradictory scenarios are still currently debated regarding the evolution of this character (Jamniczky *et al.*, 2006): some authors interpret the position of the fpcci in paracryptodires as ancestral in relation to the condition seen in eucryptodires (Evans & Kemp, 1976; Rieppel, 1980; Joyce, 2007), whereas others think that the position of the fpcci evolved independently from the same primitive condition in both paracryptodires and eucryptodires (Gaffney, 1975, 1996; Brinkman & Nicholls, 1993). Current phylogenetic analyses support the hypothesis that a fpcci placed halfway along the basisphenoid-pterygoid suture is a synapomorphy of Paracryptodira + *Dorsetochelys delairi* Evans & Kemp 1976 (Joyce, 2007: 27).

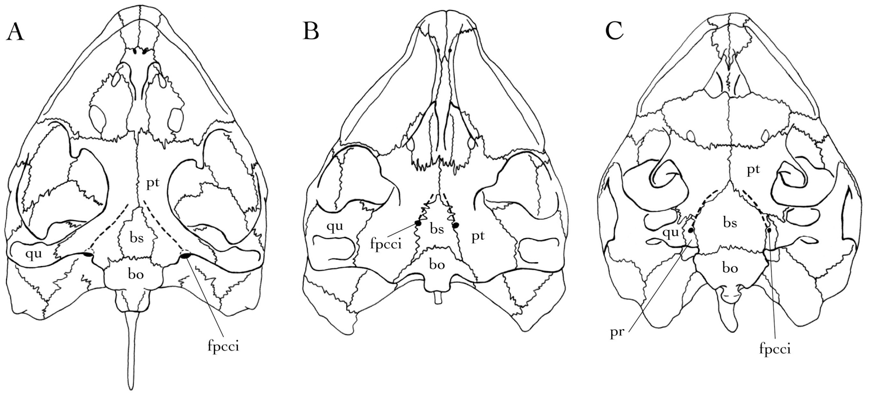


Figure 4.3—Position of the foramen posterius canalis carotici interni (fpcci) in eucryptodires (A), paracryptodires (B) and pleurodires (C). Abbreviations: bo, basioccipital; bs, basisphenoid; fpcci, foramen posterius canalis carotici interni; pr, prootic; pt, pterygoid. Dashed line: canalis caroticus internus.

A review of the available turtle material from Kirtlington shows that there is little anatomical evidence to support the proposed presence of pleurosternids in this locality. Perhaps, the best evidence is the presence of the unique shell ornamentation found in *Glyptops plicatulus*, *Pleurosternon bullockii* and *Compsemys victa* on numerous specimens. Cranial remains suggest the presence of a postorbital-maxilla contact that would have prevented the jugal from entering the orbital border (Fig. 4.1-5). During the Jurassic and Early Cretaceous, this characteristic is mainly, if not exclusively, found in paracryptodires: i.e., *Pleurosternon bullockii* (= *Mesochelys durlstonensis* Evans & Kemp 1975), *Glyptops plicatulus*, *Eubaena cephalica* and *Arundelemys dardeni* (Gaffney, 1979a; Lipka *et al.*, 2006; see also Chapter 5). This would suggest the presence of paracryptodires at Kirtlington, a conclusion supported by a recently discovered isolated basisphenoid (NHM R16498), which possesses a foramen posterius canalis carotici interni that opens along the basisphenoid-pterygoid suture (Fig. 4.2). Although this specimen strongly supports a referral to the paracryptodires, it also tends to prevent a referral to the pleurosternids because of the probable absence of a basisphenoid-vomer contact and the presence of pterygoids meeting along the midline (see above). This specimen can either support the presence of a non-pleurosternid paracryptodire in addition to the pleurosternid identified on the basis of shell bone histology, or, if NHM R16498 pertains to the pleurosternid species, it would suggest that the basisphenoid-vomer contact observed in pleurosternids appeared later in their evolution than their derived shell bone histology. Currently, it is not possible to choose between one of these two hypotheses (but see Chapter 5).

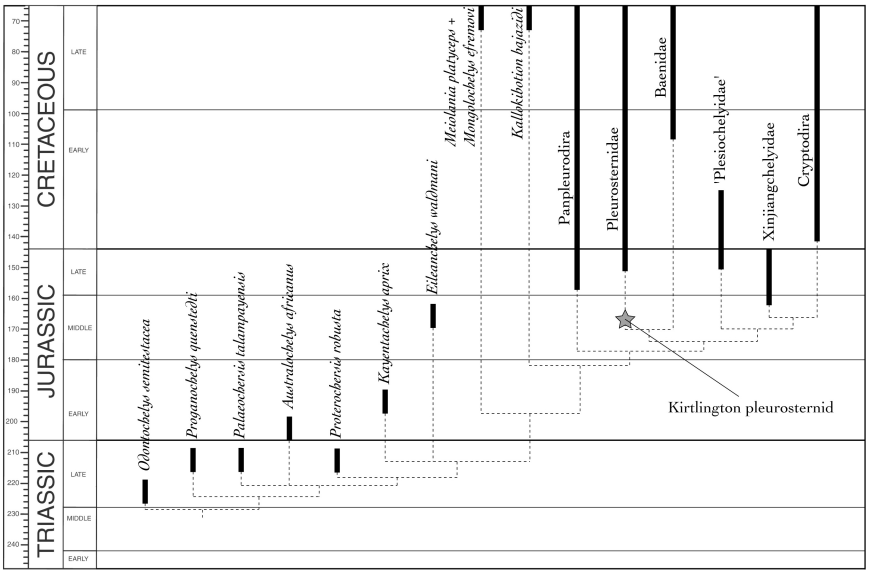


Figure 4.4—Phylogeny and stratigraphic record of basal turtles, including the Kirtlington pleurosternid. Phylogenetic relationships according to Joyce (2007), Li *et al.* (2008) and Anquetin *et al.* (2009).

Phylogenetic interpretation

The presence of pleurosternids at Kirtlington cannot be confirmed unambiguously on the basis of morphological data, but it is strongly supported by histological data. This dual study extends the fossil record of pleurosternids from the Late Jurassic into the Middle Jurassic, as hinted at by Gillham (1994). The presence of paracryptodires had already been suggested by ghost lineages inferred from the phylogenetic relationships of pancryptodires (Fig. 4.4). Indeed, several eucryptodires (Xinjiangchelyidae and Chengyuchelyidae) are known from the Middle Jurassic of Asia (e.g., Nessov, 1995; Tong *et al.*, 2002; Matzke *et al.*, 2005; Danilov & Parham, 2008; see Chapter 1), which indicates that their sister group, the paracryptodires, had already evolved by this time. The Kirtlington material represents the first physical evidence of that presence (Fig. 4.4).

REASSESSMENT OF THE OLDEST BRITISH TURTLE: '*PROTOCHELYS*' FROM THE MIDDLE JURASSIC STONESFIELD SLATE OF STONESFIELD, OXFORDSHIRE, ENGLAND

The Stonesfield Slate is well known as the type locality of the first scientifically described dinosaur, *Megalosaurus* Buckland 1824. This is also one of the richest Middle Jurassic terrestrial reptile localities in Great Britain (Evans & Milner, 1994; Benton & Spencer, 1995). Although most of the taxa from Stonesfield have been well studied, the fact that the Stonesfield Slate also yielded the oldest known British turtle is often overlooked.

Owen (1842: 160) was the first to notice impressions of turtle epidermal scales from the Stonesfield Slate. Blake (1863) confirmed the chelonian nature of these impressions and provided a short general description based on specimens in the British Museum (now housed in the Natural History Museum, London), without indicating which ones he had in hand. In the same issue of *The Geologist*, Mackie (1863) described an isolated coracoid from this locality that he attributed to a new species, *Chelys(?) blakii* Mackie 1863. Later, Phillips (1871: 182) proposed the new species *Testudo stricklandi* Phillips 1871 for epidermal scales from the Stonesfield Slate housed at the Oxford University Museum. In his *Catalogue of Fossil Reptilia and Amphibia*, Lydekker (1889: 220) coined the new genus name *Protochelys* for *T. stricklandi* and provisionally referred the isolated coracoid described by Mackie (1863) to this form (although he did not change *P. stricklandi* to *P. blakii* as he should have according to the Principle of Priority; ICZN, 1999). Since Lydekker (1889), the turtle material from the Stonesfield Slate has been completely overlooked: this material has never been properly described or compared. Only a few authors have mentioned this material during the 20th century: Romer (1956, 1966) and Bergounioux (1955) list *Protochelys*, which they tentatively assign to the Pleurosternidae, but do not discuss it. Benton & Spencer (1995: 144) mention these remains and underline their need for reassessment:

> "The scales are unusual in that they lack bony material, and in that they are supposedly from the crest of the back of a turtle carapace. The coracoid is probably indeed chelonian, but the scales may be remains of invertebrates, though the possibility remains that they might represent shed turtle scutes (certain extant turtles shed their carapace scutes in order to facilitate growth). We have found no recent discussion of the Stonesfield 'chelonians' [...]. Turtles are rare in the Mid Jurassic but, until the exact nature of the Stonesfield specimens is reassessed, nothing can be said of their significance."

Geological setting

The Stonesfield Slate was extracted from a localised series of mines and quarries that lie within a kilometre of the village of Stonesfield, Oxfordshire (Boneham & Wyatt, 1993: fig. 1). The slates were exploited as roofing stones (tiles) between the 17th and the early 20th centuries (Aston, 1974). The Stonesfield Slate consists of fine, calcareous sandstones and siltstones that are locally interbedded with thin and fissile laminae of ooliths (Boneham & Wyatt, 1993). It was previously considered to be a member of either the Taynton Limestone Formation or the underlying Sharp's Hill Formation. More recently, Boneham & Wyatt (1993) demonstrated that the Stonesfield Slate represents a sporadic, recurrent lithofacies of the Taynton Limestone Formation. Based on the ammonite fauna, both the Taynton Limestone Formation and the Stonesfield Slate are referred to the *Procerites progracilis* Biozone, which corresponds to the lower part of the middle Bathonian (Torrens, 1980; Boneham & Wyatt, 1993). The Stonesfield Slate is consequently a little older than Kirtlington and Cladach a'Ghlinne.

The Stonesfield Slate has yielded a mixed assemblage of marine and terrestrial taxa: marine invertebrates (ammonites, belemnites, bivalves, gastropods, crustaceans, etc.), terrestrial plants, insects, fish, marine and terrestrial reptiles, and mammals (Evans & Milner, 1994; Benton & Spencer, 1995). This association suggests a deposit in a shallow inshore marine environment. Stonesfield rapidly became famous following the discovery of fossil mammals and reptiles. Mammals are represented by two small jaws, of two different species, discovered in 1812 which still represent the oldest unquestionable crown-group mammals (Rowe, 1999). Reptiles include marine crocodiles (steneosaurids), plesiosaurs, ichthyosaurs, pterosaurs (rhamphorhynchoids), dinosaurs (including the famous *Megalosaurus*), and turtles (Evans & Milner, 1994; Benton & Spencer, 1995). Fossil vertebrates occur in the three different lithofacies of the Stonesfield Slate (sandstones, siltstones and oolith laminae), without particular differences in faunal composition. The bone preservation is generally good but the material is disarticulated and was probably transported over a short distance (Benton & Spencer, 1995). However, the presence of well-preserved fragile elements like turtle epidermal scales (see below) and terrestrial plants suggests that transport was gentle.

Material and methods

Apart from two isolated bones (a coracoid and a plastron fragment), all of the Stonesfield turtle specimens consist of unassociated, isolated carapacial scales (no plastral scale has been identified). The Stonesfield scales are unique in being the first isolated fossil turtle scales known to date (Anquetin & Claude, 2008; see below). Interestingly, these scales are not imprints, as described by 19th century authors, but thin fossilised layers picked out by iron staining or other mineralisation, in the same way as the majority of terrestrial plant remains from the same locality (Cleal & Rees, 2003). Palaeobotanists use the term 'impression' or 'compression-impression' to designate this type of preservation (Shute & Cleal, 1987; Cleal & Rees, 2003). At Stonesfield, turtle scales are often represented by an association (two slabs) of the fossil scale itself (representing the original morphology of the scale; i.e., growth rings are thin grooves) and an external mould (representing a mould of the external surface of the scale; i.e., growth rings are low ridges).

Turtle shell scales usually possess growth rings (or growth annuli), though these are not always pronounced. Generally, these rings indicate that growth is not equal in all directions, or asymmetrical (Zangerl, 1969: 319). For carapacial scales, mediolateral growth is usually faster laterally (or medially for marginals), whereas anteroposterior growth is faster anteriorly (Fig. 4.5). When scale growth is asymmetrical, this characteristic enables orientation of the scales. This method of orientation has been applied to the Stonesfield scales. In addition to growth rings, vertebral scales from Stonesfield also present an ornamentation of ridges radiating anteriorly from the posteromedial part of the scale.

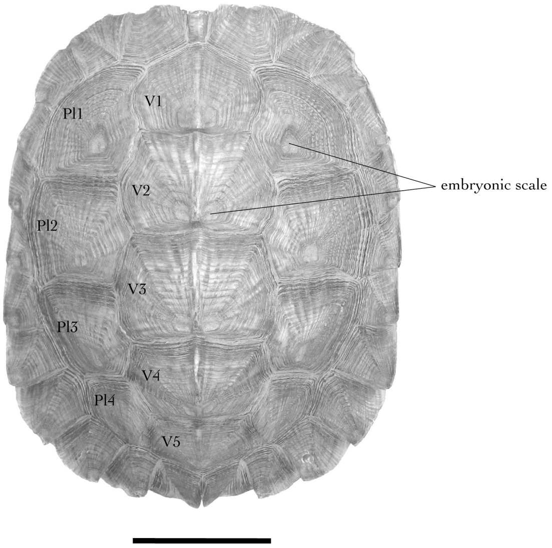


Figure 4.5—Carapace of *Glyptemys insculpta*, the wood turtle (FMNH 83482), illustrating the morphology of carapacial epidermal scales. Scale bar: 50 mm. Abbreviations: Pl, pleural scale; V, vertebral scale.

The major challenge was the identification of the scales. Isolated scales almost never occur in the fossil record (see below) and no studies on modern turtles relating to the identification of isolated scales could be located. Consequently, identification of the Stonesfield scales was based on a comparative study, especially with modern turtles (Fig. 4.5). The first criterion is the symmetry of the scale. On a turtle shell, only the median, unpaired carapacial scales (i.e., the cervical and vertebrals) are symmetrical. Other carapacial scales and all plastral scales are non-symmetrical. The second criterion is the number and morphology of the scale margins. As the turtle shell is a mosaic of geometrical elements (Zangerl, 1969), the margins of a scale indicate its relations to neighbouring scales and consequently give valuable indications on its identification. For example, a third vertebral would generally possess the following features: a more or less arched anterior margin that contacts the second vertebral; a similar posterior margin that contacts the fourth vertebral; and two lateral margins on each side that contact the posteromedial margin of the second pleural anterolaterally and the anteromedial margin of the third pleural posterolaterally. In most turtles, the anterior and posterior margins are of approximately the same length, as are the lateral margins (pers. obs.; Fig. 4.5). This deductive reasoning enabled the identification of most scales found at Stonesfield. The identification of each scale is discussed where appropriate (see below).

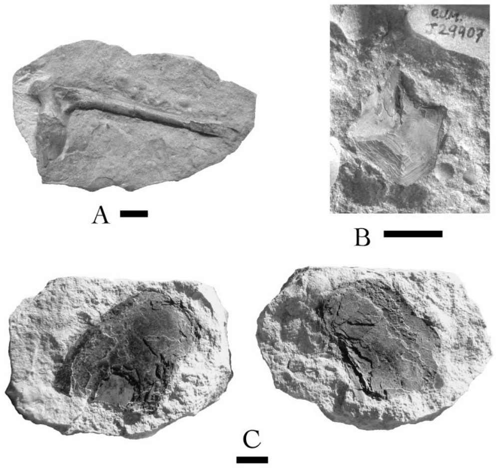


Figure 4.6—Specimens from the Stonesfield Slate misidentified as chelonian. A, NHM R896, specimen identified by Lydekker (1889: 222) as a "scapulo-precoracoid", but more probably an archosaur cervical rib; B, OXFUM J29907, fish scale labelled as a turtle scale; C, OXFUM unnumbered, specimen (two slabs) labelled as a turtle bony plate which consists of a splinter of compact bone maybe from a crocodile osteoderm. Scale bars: 10 mm.

Systematic palaeontology

TESTUDINATA Klein 1760 (*sensu* Joyce *et al.*, 2004)

'*Protochelys blakii*' (Mackie 1863) *nomen dubium*

Chelys (?) blakii Mackie 1863: 41, fig. 1
Testudo stricklandi Phillips 1871: 182, diagram 41
Protochelys stricklandi — Lydekker, 1889: 220

Holotype—NHM 37979, an isolated, slightly crushed right coracoid, figured in Mackie (1863) [holotype by monotypy].

Referred specimens—NHM 37218, complete vertebral (two slabs); NHM 37218a, complete vertebral; NHM R247, half vertebral (two slabs); NHM R247a, half vertebral; NHM 37218b, almost complete vertebral (due to a misreading of the original label, the external mould has been erroneously numbered NHM 39198b after the work of Lydekker (1889); the correct number is used herein); NHM R247b, complete pleural (two slabs); NHM 39198, external mould of a pleural; NHM 39198a, external mould of a small incomplete scale; NHM R5320, isolated fragment of plastron; OXFUM J40407, complete vertebral; OXFUM J37067, complete small vertebral; OXFUM J77375 + J77376, complete vertebral (two slabs, both figured in Phillips, 1871); OXFUM J77377, external mould of a small vertebral; OXFUM J77378, external mould of a half vertebral.

Horizon and age—Stonesfield Slate, Taynton Limestone Formation, Stonesfield, Oxfordshire, England. The Stonesfield Slate is attributed to the lower part of the middle Bathonian (Torrens, 1980; Boneham & Wyatt, 1993).

Remarks—Lydekker (1889: 222) referred to *Protochelys* the specimen NHM R896, which he interpreted as a "chelonian scapulo-precoracoid". In fact, this specimen is not chelonian. It shows pneumatic features and may be interpreted as a possible archosaur cervical rib (Fig. 4.6A). The collections of the OXFUM also hold several other specimens misidentified as chelonian: OXFUM J29907 (a fish scale; Fig. 4.6B) and an unnumbered specimen that consists of a splinter of compact bone (maybe from the base of a crocodilian osteoderm; Fig. 4.6C).

Due to the nature of the specimens, no satisfactory diagnostic characters can be identified. Comparisons with other taxa are also limited (see below). That is why *Protochelys* is considered to be a *nomen dubium* (Anquetin & Claude, 2008). At least as far as the scales are concerned, the consistency of the morphology and preservation suggests that they only represent one taxon. The creation of two separate species for the coracoid and for the scales is arguable. However, this would not improve the current taxonomic situation in any way; it would rather result in another *nomen dubium*. So, it appears sensible to treat all the remains as one taxon, whose affinities are unknown.

Description

Coracoid—NHM 37979, as identified by Carter Blake in Mackie (1863), is a right coracoid presented in dorsal view (Fig. 4.7A). The bone is elongate and slightly crushed dorsoventrally. The proximal head is notably enlarged laterally to form the articular glenoid. Medially, the upper part of the sutural surface with the scapula is clearly visible. Posterior to the proximal head, the main body of the bone is thin and was probably cylindrical before crushing. Distally, the coracoid expands into a dorsoventrally flattened blade that is characteristic of many turtles. Its posterior margin is broken. The bone may have been slightly concave dorsally, but this could be the result of *post-mortem* deformation.

Plastron fragment—NHM R5320 is the only turtle shell bone from the Stonesfield Slate. This is a plastron fragment (hyo- or hypoplastron) probably of the bridge area (Fig. 4.7B). Three spiny projections are present like those that can be found in embryonic or juvenile individuals or in turtles that do not have a fully ossified shell at adult stage. The size of the specimen (40 mm in maximum length) indicates that it does not belong to a hatchling turtle, but it may have belonged to a young individual. The specimen is too fragmentary to reveal much information about its bearer.

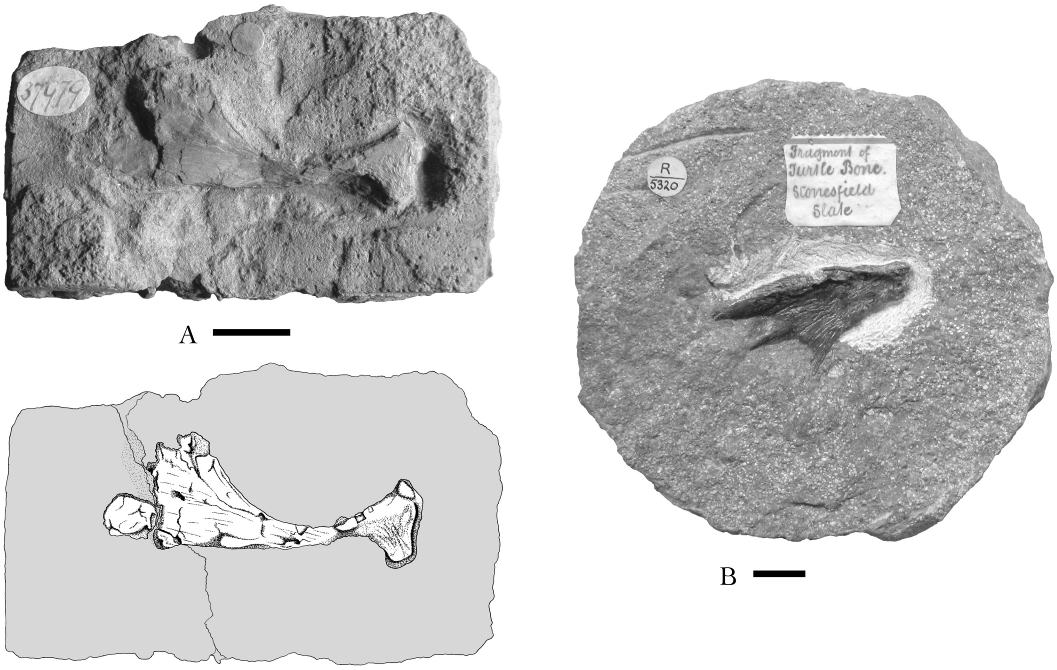


Figure 4.7—Turtle bones from the Stonesfield Slate, middle Bathonian. A, NHM 37979, right coracoid in dorsal view (proximal to the right); B, NHM R5320, plastron fragment (hyo- or hypoplastron) probably from the bridge area. Scale bars: 10 mm.

First vertebral scale**—**NHM 37218b (Fig. 4.8A,B), OXFUM J77375 + J77376 (Phillips, 1871: 182, fig. 41.10, 11; Fig. 4.8C,D) and OXFUM J77377 (Fig. 4.8E) are interpreted as first vertebrals because of their symmetrical, pentagonal shape and their concave posterior margin. The pentagonal shape is characteristic of the first and fifth vertebrals, other vertebrals tend to be hexagonal (pers. obs.). The first vertebral has a posterior contact with the second vertebral, whereas the fifth vertebral has a posterior contact with the left and right last marginals (generally the twelfth). As a consequence, the former usually has a concave posterior margin, whereas the latter generally has a convex posterior margin that is divided into two facets. The bilateral symmetry of the aforementioned specimens is underlined by a pronounced median keel that is stronger anteriorly and ends abruptly just before reaching the posterior margin of the scale. It is likely that the second vertebral overlapped the first, as suggested by the presence of a smooth triangular area on the posterior part of vertebral 1 and by the disappearance of the median keel just anterior to this area. These scales are almost twice as wide as they are long. The anterior margin of vertebral 1 is convex and longer than the posterior margin. The long lateral margin faces posterolaterally and contacts the anteromedial margin of the first pleural. On NHM 37218b (Fig. 4.8A,B), growth rings are poorly preserved on some areas of the scale. A few anteriorly radiating ridges are present on the anteromedial part of the scale. On OXFUM J77375 + J77376 (Fig. 4.8C,D), growth rings and radiating ridges are well preserved. OXFUM J77377 is poorly preserved, but some anteriorly radiating ridges are still visible (Fig. 4.8E).

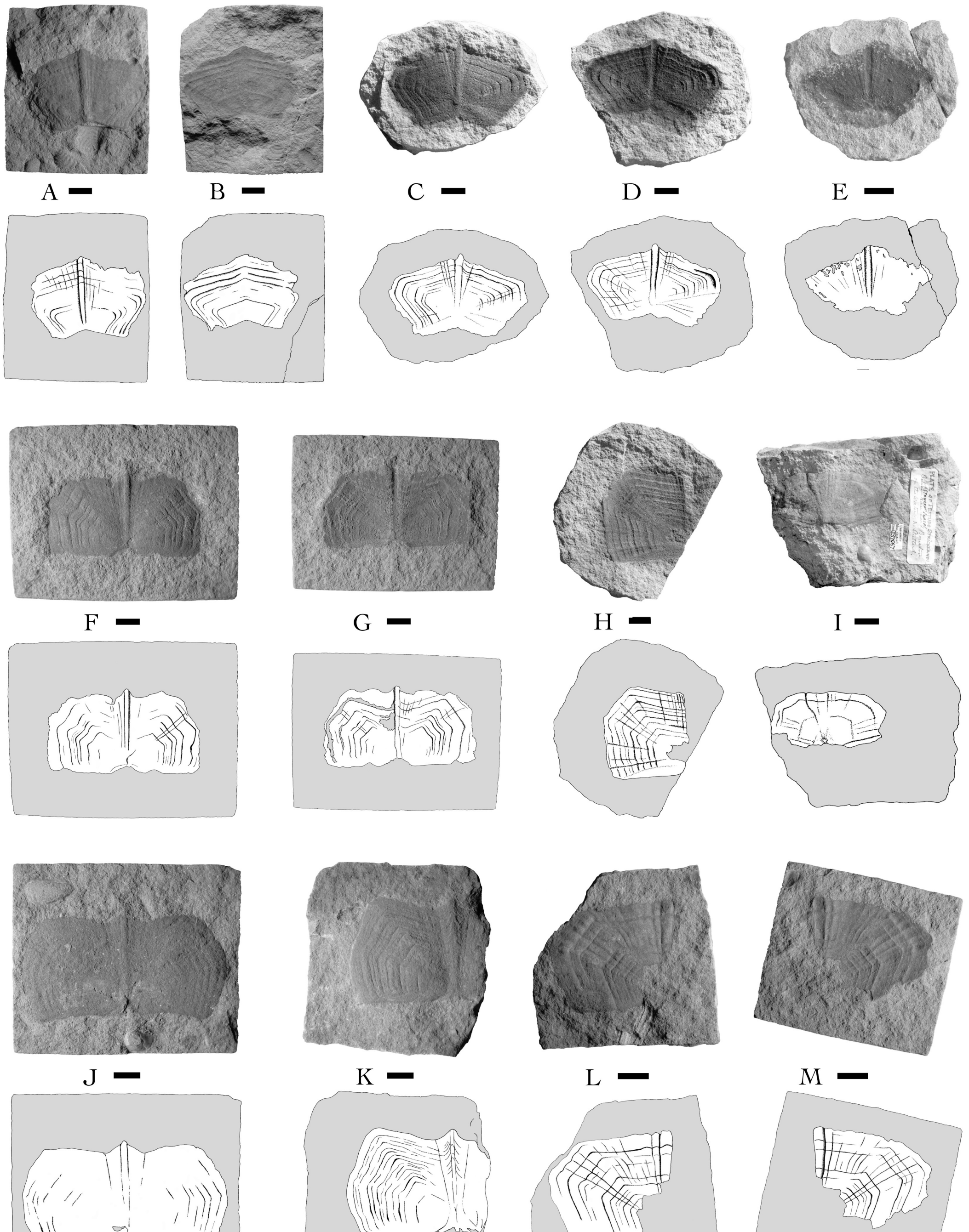


Figure 4.8—Chelonian vertebral scales 1 to 4, Stonesfield Slate, middle Bathonian. A-E, first vertebral; F-I, second vertebral; J, K, third vertebral; L, M, fourth vertebral. A, B, NHM 37218b, almost complete first vertebral (B is the external mould); C, D, OXFUM J77375 + J77376, complete first vertebral (D is the external mould, OXFUM J77376); E, OXFUM J77377, badly preserved external mould of a first vertebral; F, G, NHM 37218, complete second vertebral (G is the external mould); H, OXFUM J77378, external mould of the right half of a second vertebral; I, OXFUM J37067, badly preserved small second vertebral; J, NMH 37218a, complete third vertebral; K, NHM R247a, left half of a third vertebral; L, M, NHM R247, left half of a fourth vertebral (M is the external mould). Scale bars: 10 mm.

Second vertebral scale—NHM 37218 (Fig. 4.8F,G), OXFUM J77378 (Fig. 4.8H) and OXFUM J37067 (Fig. 4.8I) are interpreted as second vertebrals because of their symmetrical, hexagonal shape and their possession of an anterior margin that is shorter than the posterior margin. Usually, vertebrals 2-4 are hexagonal in outline and differ from one another in the relative development of their anterior and posterior margins: vertebral 2 tends to have a shorter anterior margin; vertebral 3 an anterior margin of the same length as the posterior margin; and vertebral 4 a shorter posterior margin. The aforementioned specimens have a straight or slightly concave anterior margin and straight posterior margin. They are twice as wide as long (OXFUM J77378 is incomplete) and have a median keel. The anterolateral margin contacts the posteromedial margin of the first pleural and faces anterolaterally. The posterolateral margin contacts the anteromedial margin of the second pleural and extends parallel to the anteroposterior axis of the scale. The anterolateral margin is slightly shorter than the posterolateral one. The median keel protrudes anteriorly from the anterior margin of the scale. The posterior margin presents a median emargination that probably corresponds to the anterior protrusion of the median keel of the third vertebral (see below). On NHM 37218, growth rings are only slightly apparent medially but are still well defined laterally (Fig. 4.8F,G). Some rings are deeply marked but, between those, thinner rings are often present. The spacing between major growth rings is irregular. A few poorly defined anteriorly radiating ridges are apparent laterally. On OXFUM J77378, growth rings are better preserved, no intercalated thin rings are present, and the spacing between growth rings is relatively regular (Fig. 4.8H). An anteriorly radiating pattern covers the whole surface of the scale. On OXFUM J37067, the presence of the medial ridge is uncertain and the majority of growth rings are badly marked (this specimen is poorly preserved; Fig. 4.8I). A few anteriorly radiating ridges are present on the anteromedial and posterolateral portions of this specimen.

Third vertebral scale—NHM 37218a (Fig. 4.8J) and NHM R247a (Fig. 4.8K) are interpreted as third vertebrals because of their symmetrical, hexagonal shape, and anterior and posterior margins that are equal in length (see discussion in the description of the second vertebral scale above). Both specimens exhibit a median keel that is wider and more pronounced anteriorly. The scale is twice as wide as long with anterior and posterior margins that are almost straight. The median keel protrudes anteriorly from the anterior margins of the scale, whereas a slight median emargination of the posterior margin probably corresponds to the anterior protrusion of the fourth vertebral. Both lateral margins are oblique with respect to the anteroposterior axis of the scale: the anterolateral margin contacts the posteromedial margin of the second pleural, whereas the posterolateral margin contacts the anteromedial margin of the third pleural. The two lateral margins are equal in length. The surface ornamentation of NHM 37218a is poorly preserved, but growth rings are still well preserved on NHM R247a. On the latter, thinner (less marked) rings are intercalated between the rather regularly spaced major growth rings. No radiating pattern is observable, but it should be noted that these specimens are less well preserved than the previously described scales.

Fourth vertebral scale—NHM R247 (Fig. 4.8L,M) is interpreted as a fourth vertebral because of its (original) symmetrical, hexagonal shape, and anterior margin that is wider than the posterior one (see discussion in the description of the second vertebral scale above). The right side of the scale and the emplacement of the embryonic scale are missing. The anterior part of the median keel is visible on the broken side of the scale. The anterior margin is slightly convex, whereas the posterior margin is slightly concave. Both lateral margins are oblique with respect to the anteroposterior axis of the scale: the anterolateral margin contacts the posteromedial margin of the third pleural, whereas the posterolateral margin contacts the anteromedial margin of the fourth pleural. The anterolateral margin is notably shorter than the posterolateral margin. The original scale was approximately twice as wide as long. Due to the preservation, it is unclear whether or not the median keel protrudes anteriorly, but since a slight median emargination is present on the posterior margin of vertebral 3 (see above) it is probable that it did. Growth rings are relatively well defined and thinner rings are often intercalated between major rings. The spacing between major growth rings is irregular. A pattern of anteriorly radiating ridges is present.

Fifth vertebral scale—OXFUM J40407 (Fig. 4.9A) and NHM 39198a (Fig. 4.9B) are interpreted as fifth vertebrals because of their symmetrical, pentagonal shape and their convex posterior margin (see discussion in the description of the first vertebral scale above). OXFUM J40407 has a well-developed median keel that is wider anteriorly than posteriorly. On NHM 39198a (an external mould), an inflexion present on each growth ring near the broken side of the scale indicates the presence of a keel although the latter is not apparent on the specimen (compare with OXFUM J40407). In contrast to the condition in other vertebrals, both the anterior and posterior margins of each aforementioned specimen are convex. The anterior margin contacts the posterior margin of the fourth vertebral. The long and arched posterior part of the scale in fact represents four separate margins that correspond to the contacts with the two last marginals on each side (probably the eleventh and twelfth) at the posterior end of the carapace. The short lateral margin faces anterolaterally and corresponds to the contact with the posteromedial margin of the fourth pleural. The scale is wider than long, but proportionally less wide than vertebrals 2-4. Growth rings are well preserved on OXFUM J40407, although only slightly defined in some areas (Fig. 4.9A). The spacing between major growth rings is irregular and a few anteriorly radiating ridges are present anteromedially. By comparison, only major growth rings are preserved on NHM 39198a and no trace of a radiating pattern is present (Fig. 4.9B).

Pleural scales—NHM R247b (Fig. 4.9C,D) is interpreted as a third right pleural because of its non-symmetrical, squarish shape, its straight anterior and posterior margins, its oblique medial margins, and its short posteromedial margin. The outline of this scale indicates that it contacts two vertebrals medially, one pleural anteriorly, one pleural posteriorly and three marginals laterally. This description corresponds to a second or third pleural (first and fourth pleurals have a very reduced or absent anterior or posterior margin, respectively). The short posteromedial margin of

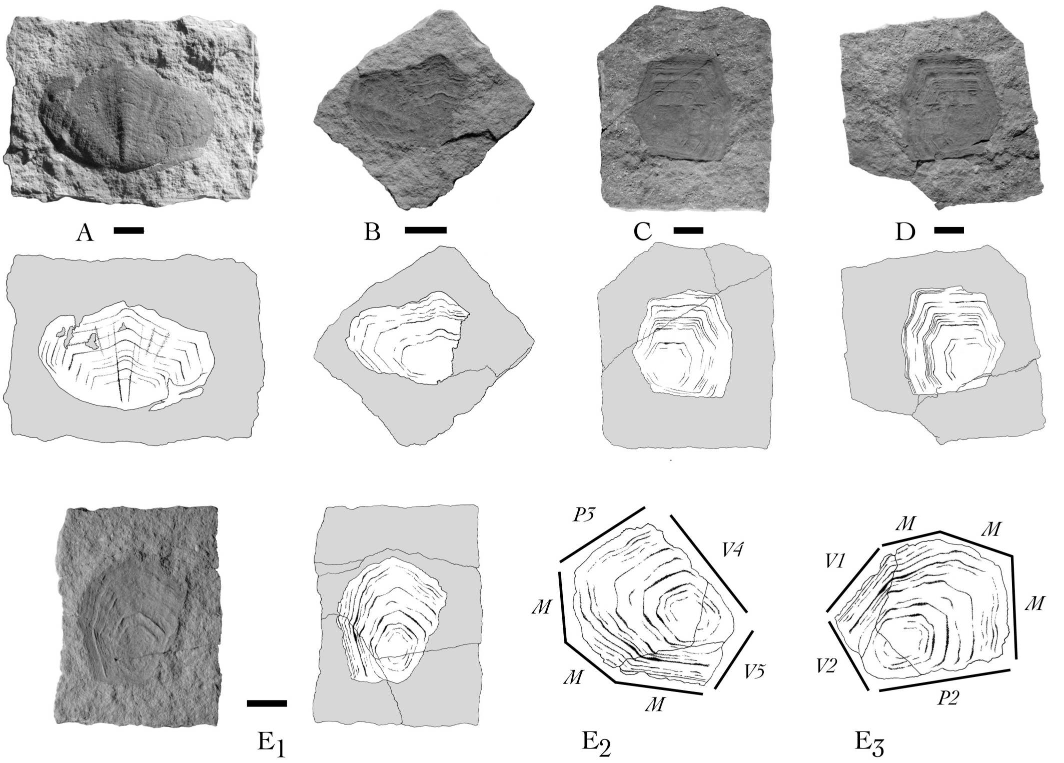


Figure 4.9—Chelonian fifth vertebral and pleural scales, Stonesfield Slate, middle Bathonian. A, B, fifth vertebral; C-E, pleural scales. A, OXFUM J40407, complete fifth vertebral; B, NHM 39198a, external mould of the right half of a fifth vertebral; C, D, NHM R247b, complete right third pleural (D is the external mould); E, NHM 39198, external mould of an almost complete scale (E$_1$, non oriented) which can be interpreted either as a right fourth pleural (E$_2$, preferred hypothesis) or as a left first pleural (E$_3$). Scale bars: 10 mm (E$_2$ and E$_3$ not to scale). Abbreviations: M, marginal scale; P, pleural scale; V, vertebral scale.

NHM R247b indicates that it was in contact with the short lateral margin of vertebral 4, whereas the oblique anteromedial margin could not be in contact with the posterolateral margin of vertebral 2, which is parallel to the anteroposterior axis. This supports the interpretation of NHM R247b as a third pleural scale. This specimen is slightly longer than wide. The anterior margin is as long as the posterior one. The lateral side of the scale is divided into three distinct contacts corresponding to three marginals. Growth rings are well preserved, especially on the external mould. Major rings are irregularly spaced and up to three or four less pronounced rings can be seen between some of them. There is no trace of radiating ridges on the scale.

NHM 39198 (Fig. 4.9E$_1$) is interpreted as a first or fourth pleural because of its non-symmetrical and irregular pentagonal shape. Six margins can be identified: three correspond to contact with marginals, two others to contact with vertebrals, and one to a contact with a pleural scale (anterior or posterior). The original outline of the scale, revealed by growth rings, allows two possible interpretations of this specimen: a right fourth pleural (Fig. 4.9E$_2$) or a left first pleural (Fig. 4.9E$_3$). The following observations weaken the second interpretation: first pleurals are usually more elongate; growth rate should have been more important anteriorly; and the posterior margin that contacts the second pleural should be sub-perpendicular to the anteroposterior axis of

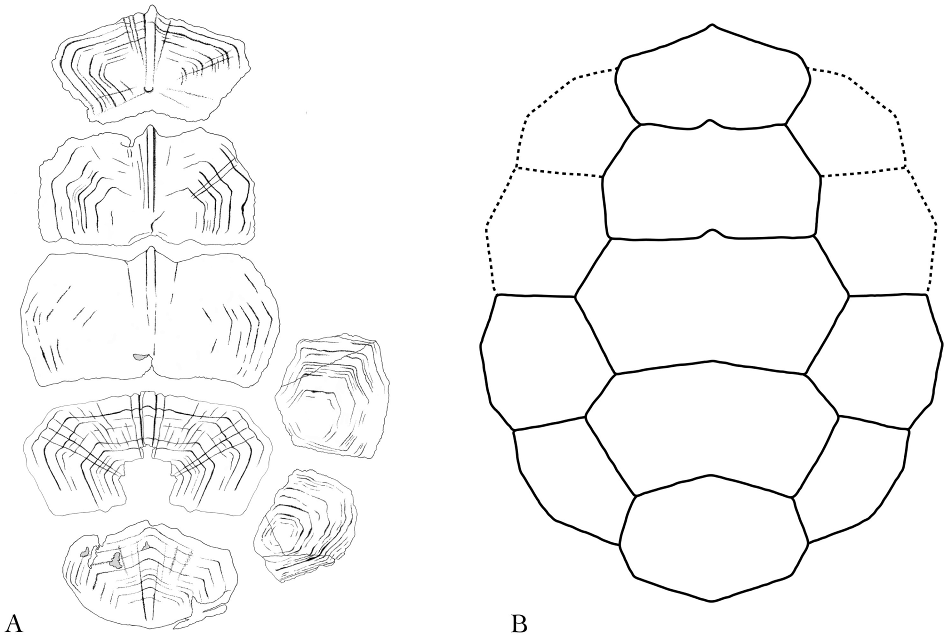


Figure 4.10—Reconstruction of the Stonesfield turtle, middle Bathonian. A, reconstruction based on available specimens (note that these specimens are not from the same individuals nor at the same scale); B, proposed reconstruction of the carapace of the Stonesfield turtle. The morphology of the first and second pleural (dashed lines) can be deduced from that of neighbouring scales. Marginals are unknown at Stonesfield and therefore are not represented on the present reconstruction.

the scale. Consequently, the interpretation of NHM 39198 as a right fourth pleural is favoured. The scale is longer than wide. The anteromedial margin (that contacts the posterolateral margin of the fourth vertebral) is damaged and consequently the anterior margin (that contacts the posterior margin of the third pleural) appears shorter than it was originally. The short posteromedial margin corresponds to the contact with the lateral margin of the fifth vertebral. The lateral margin is divided into three parts corresponding to the contact with three different marginals. Growth rings are relatively well preserved. Major rings are irregularly spaced. A few weaker rings are present but are difficult to distinguish. There is no radiating pattern on the scale.

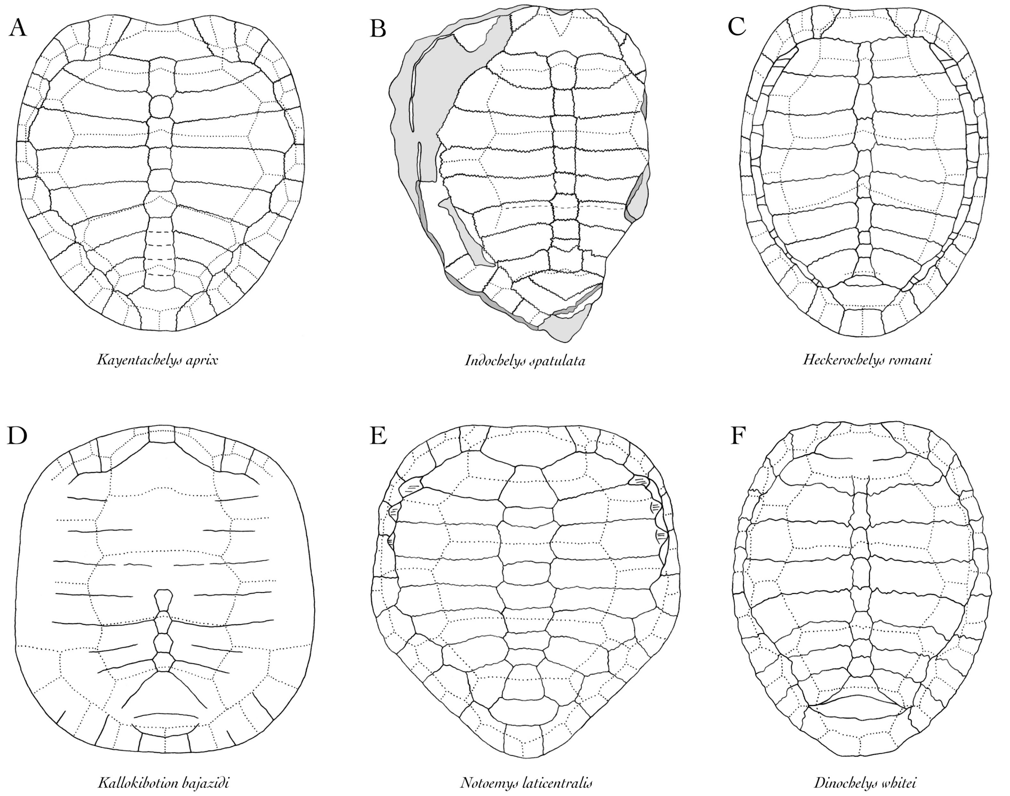
Comparison

It is difficult to compare the turtle scales from the Stonesfield Slate with other taxa because no directly comparable material (i.e., fossil epidermal scales) is known (see below). When describing bony shells, systematists can only access information on the general outline of the scales and mainly use their relative sizes for diagnostic purposes. At Stonesfield, although they match each other fairly well, the scales are isolated and obviously pertain to different individuals: they show different growth rates, different sizes and there is no indication that all of the scales come from the same stratigraphical horizon. Consequently, the relative sizes of the Stonesfield scales cannot be assessed. However, the detailed description provided above enables some comparisons.

A tentative reconstruction of the carapace of the Stonesfield turtle is provided in figure 4.10. The most important characteristic of this turtle is that vertebrals are wider than long, whereas pleurals are slightly longer than wide. This is a rather primitive scheme commonly found in stem turtles and basal crown-group turtles. More derived turtles tend to have vertebrals that are longer than wide and pleurals that are wider than long.

Among turtles with wide vertebrals and narrow pleurals, the Stonesfield turtle most closely resembles the stem turtles *Kayentachelys aprix* Gaffney *et al.* 1987, *Indochelys spatulata* Datta *et al.* 2000, *Heckerochelys romani* Sukhanov 2006, and *Kallokibotion bajazidi* Nopcsa 1923, the panpleurodire *Notoemys laticentralis* Cattoi & Freiberg 1961, and the pleurosternid *Dinochelys whitei* (Fig. 4.11). The aforementioned species share the following features with the Stonesfield turtle: large vertebral 1 with a convex anterior margin that is at least as long as the posterior margin; vertebral 2 with a posterolateral margin more or less parallel to the anteroposterior axis of the shell; vertebral 4 with a significantly short anterolateral margin; vertebral 5 wider than long with an anterior margin as long as the posterior margin. The Stonesfield turtle differs from each of these species in several respects. Vertebrals 2-4 of *Kayentachelys aprix* and *Indochelys spatulata* are wider than those of the Stonesfield turtle, whereas they are narrower in *Kallokibotion bajazidi* (Gaffney *et al.*, 1987; Gaffney & Meylan, 1992; Datta *et al.*, 2000). In *Kayentachelys aprix*, vertebral 1 is at least three times wider than long and has three distinct margins anteriorly (one for each marginal 1 and one for the cervical scale). Vertebral 1 of *Dinochelys whitei* and *Notoemys laticentralis* is also wider than that of the Stonesfield turtle (Gaffney, 1979a; Fernandez & de la Fuente, 1994; Brinkman *et al.*, 2000; Lapparent de Broin *et al.*, 2007). In *Kallokibotion bajazidi*, vertebral 1 is narrower and more elongated than that of the Stonesfield turtle and its lateral margin is parallel to the anteroposterior axis of the shell. In *Notoemys laticentralis*, the lateral margin of vertebral 1 is also parallel to the anteroposterior axis of the shell and all intervertebral sulci are straight. *Dinochelys whitei* also has straight intervertebral sulci. *Heckerochelys romani* differs from the Stonesfield turtle in having a longer vertebral 2, a vertebral 3 with a strongly concave posterior margin and a vertebral 4 with only one lateral margin (Sukhanov, 2006).

None of the aforementioned species is known to have scale ornamentation, although it is possible that such ornamentation does not always leave a trace on the bony plates of the shell. The anterior margin of vertebrals 2-5 of *Kayentachelys aprix* presents a well-defined, short median protrusion similar to that of the Stonesfield turtle and that could indicate the presence of a median keel on those scales. Other turtles known to have scale ornamentation consisting of anteriorly radiating ridges on the vertebrals do not match the morphology of the Stonesfield turtle: e.g., *Proganochelys quenstedti* (Gaffney, 1990), *Platychelys oberndorferi* (BSPG AS I 1438), *Desmemys bertelsmanni* (Wegner, 1911), some plesiochelyids (e.g., Bräm, 1965) and chengyuchelyids (e.g., IVPP V6507).



Kayentachelys aprix
Indochelys spatulata
Heckerochelys romani
Kallokibotion bajazidi
Notoemys laticentralis
Dinochelys whitei

Figure 4.11—Carapace morphology of select basal turtles. A, *Kayentachelys aprix*, redrawn from Joyce (2007); B, *Indochelys spatulata*, redrawn from Datta *et al.* (2000); C, *Heckerochelys romani*, redrawn from Sukhanov (2006); D, *Kallokibotion bajazidi*, redrawn from Gaffney & Meylan (1992); E, *Notoemys laticentralis*, redrawn from Lapparent de Broin *et al.* (2007); F, *Dinochelys whitei*, redrawn from Gaffney (1979a).

Romer (1956, 1966) and Bergounioux (1955) referred the turtle from Stonesfield to the Pleurosternidae. *Pleurosternon bullockii, Glyptops plicatulus* and "*Glyptops*" *typocardium* (Seeley 1869) (Gaffney, 1979a; Milner, 2004) all have vertebrals that are reduced in width and pleurals that are wider than long, which differs significantly from the Stonesfield turtle. Among pleurosternids, only the Late Jurassic *Dinochelys whitei* has a scale pattern that is somewhat similar to that of the Stonesfield turtle (see above). However, as demonstrated above, it is also the case for several other species ranging from Early Jurassic stem turtles to basal panpleurodires. This suggests that this scale pattern is rather plesiomorphic and that a referral of the Stonesfield turtle to the pleurosternids is not better supported than a referral to the stem Testudines or the Panpleurodira.

Taphonomy

The preservation of turtle epidermal scales in the fossil record is exceptionally rare. I am aware of only two other cases: a shell fragment from the Pleistocene of northeastern Thailand (J. Claude, pers. comm., 2007) and a shell of *Neurankylus* from the early Paleocene of New Mexico (Sullivan *et al.*, 1988). In the latter case, the scales are preserved on approximately 85% of the carapace, are rich in iron and manganese, and are apparently preserved with the original colour pattern (Sullivan *et al.*, 1988: fig. 3). In both of the aforementioned cases, the scales are preserved as a thin layer on the surface of the bony shell, but the Stonesfield specimens are isolated scales (i.e., separated from the neighbouring scales and from the underlying bony plates). This is the only known example of such preservation in the fossil record. *A priori*, isolated epidermal scales can result from two processes: shedding during growth or *post-mortem* disarticulation.

To my knowledge, no detailed studies of the post-hatching development of shell scales have been published. In a recent review on the use of growth rings to estimate turtle age, Wilson *et al.* (2003) discuss the lack of literature on epidermal scale growth. Two patterns of development are seen in extant turtles (Wilson *et al.*, 2003: fig. 1). In some turtles (e.g., *Terrapene carolina*), scales do not shed and old scale layers are retained on the external surface of new ones. In such cases, growth rings correspond to the superposition of successively larger and younger scales. Consequently, such scales become thicker with age, although old scale layers are often worn progressively by abrasion. In other turtles (e.g., *Trachemys*, *Orlitia*, *Chrysemys*), the old scale layer is shed while the new one grows beneath it. Although the mechanism is not yet understood, the old layers leave an impression, corresponding to the growth ring, on the new scale.

It is more likely that the Stonesfield scales result from disarticulation rather than shedding. Shed scales consist of thin, translucent and flexible keratinous layers that are therefore less likely to become fossilised than complete scales. Moreover, I was unable to find any reference mentioning the persistence of shed scale layers in the environment, which might suggest that they are quickly destroyed after shedding. Additionally, extant shedding turtles tend to have smooth epidermal scales (i.e., without ornamentation) with poorly developed growth rings. If this can be transposed to Mesozoic forms, the important ornamentation and well-defined growth rings of the Stonesfield scales would indicate that they probably do not belong to a shedding form.

Turtle taphonomy is poorly studied and the few available studies deal primarily with bones, which is of little help in the case of the Stonesfield material. Frustratingly, most taphonomical studies on extant species often fail to mention epidermal scales at all (see Brand *et al.*, 2003 for a more detailed review). Bourn & Coe (1979) reported the disarticulation sequence of *Geochelone gigantea* (the Aldabra tortoise) and stated that, at some point in the sequence, scales detach themselves from each other and from the bony plates before falling. Dodd (1995) documented the disarticulation patterns of 80 turtle carcasses, representing three families (emydids, testudinids and trionychids), in a terrestrial sandhill habitat in North Florida. As noted by Bourn & Coe (1979), Dodd (1995) observed that the keratinous scales of emydids and testudinids eventually detach themselves individually from the shell (trionychids have no scales but a leathery skin covering the shell). He noted that the vertebrals and pleurals generally detach simultaneously, or the former closely followed by the latter. Marginals are often the first group to detach, although they persist longer than the vertebrals and pleurals in the testudinid *Gopherus polyphemus*. Dodd (1995: 383) observed that disarticulated scales may remain close to the carcass for an extended period of time. Brand *et al.* (2003) carried out an experimental study to compare the disarticulation processes of *Trachemys scripta* (the common slider turtle) in different environments. They observed that separation between scales and shell bones occurred at the same time as shell disarticulation. Unfortunately, the detached elements were removed immediately from the experimental area so that there was no estimation of the time that disarticulated scales could remain in the environment.

Hence, taphonomic studies on turtles have not so far explained the fate of scales once detached, or even shed. For example, it is unknown how long keratinous scales can remain in the environment, how they are affected by transport or what conditions may be conducive to their preservation. The preservation of isolated keratinous elements is unusual in the fossil record and probably requires particular burial environments and transport conditions. In addition, there are currently no detailed taphonomic analyses of the Stonesfield biota in general that could explain the preservation of these scales, although the similar preservation seen in plant remains from the same locality is striking (Cleal & Rees, 2003).

CONCLUSIONS

The Middle Jurassic turtle fossil record is relatively sparse, except perhaps in China (Danilov & Parham, 2008; see Chapter 1), but the British Isles are remarkable in having several Middle Jurassic localities that yielded turtle remains. Although these remains are often too fragmentary to be exploited, at least three localities have produced exploitable material: Cladach a'Ghlinne (see Chapter 3) in Scotland, and Kirtlington and Stonesfield in England (Oxfordshire). A morphological revision of the material from the Mammal Bed at Kirtlington indicates the presence of paracryptodires and maybe of pleurosternids. The presence of pleurosternids is further supported by shell bone histology (Scheyer & Anquetin, 2008). By adjusting the stratigraphical appearance of pleurosternids from the Late Jurassic (Kimmeridgian) to the Middle Jurassic (Bathonian), this dual study erases the previous ghost lineage of the Paracryptodira - the earliest eucryptodires are from the Middle Jurassic of China (see Danilov & Parham, 2008 for a review).

A reassessment of the available material from the Middle Jurassic Stonesfield Slate shows that *Protochelys blakii* (Mackie 1863) cannot be distinguished from other taxa and is consequently considered as a *nomen dubium*. The Stonesfield turtle possesses a plesiomorphic carapacial scale pattern with vertebrals that are twice as wide as long, pleurals that are reduced in width and a fifth vertebral with an anterior margin as long as the posterior margin. These features are commonly found in stem turtles and some basal crown-group turtles. A phylogenetic assignment of the Stonesfield turtle is therefore difficult to achieve, but the combination of these primitive features suggests a basal phylogenetic position. Although the Stonesfield scales have limited systematic value, they are important in terms of taphonomy. These remains are the only known examples of isolated fossil turtle scales. They probably result from disarticulation processes as such scales are thicker, more resistant and more likely to become fossilised. These results also highlight the fact that the taphonomic literature generally overlooks the fate of shed scale layers and disarticulated scales. This should be taken into consideration by future taphonomic studies on extant turtles.

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CHAPTER 5: PHYLOGENETIC RELATIONSHIPS OF BASAL TURTLES

INTRODUCTION

The phylogenetic relationships of *Eileanchelys waldmani* were investigated by Anquetin *et al.* (2009), who incorporated this new turtle into the analysis presented by Joyce (2007). The latter represents the most complete analysis of turtle relationships so far, in terms of both the number of included taxa and characters (see Chapter 1). Anquetin *et al.* (2009) found *Eileanchelys waldmani* to be nested within the stem of Testudines (crown-group turtles). More precisely, *E. waldmani* was recovered as more derived than *Palaeochersis talampayensis*, *Australochelys africanus* and *Proterochersis robusta*, and formed a polytomy with *Kayentachelys aprix* and a clade containing all remaining turtles (Fig. 5.1A). The inclusion of *Heckerochelys romani* and *Condorchelys antiqua*, two recently described Middle Jurassic turtles (see Chapter 1), in the analysis resulted in a similar topology (Anquetin *et al.*, 2009): in the strict consensus tree, *Kayentachelys aprix*, *Eileanchelys waldmani*, *Heckerochelys romani*, *Condorchelys antiqua* and a clade consisting of all more derived turtles formed an unresolved polytomy (Fig. 5.1B). However, the Adams consensus tree supported the existence of a clade formed by *Eileanchelys waldmani* and *Heckerochelys romani* (Fig. 5.1C), which indicated that this relationship was strictly supported by the data matrix. The strict reduced consensus method revealed that the relationships of *Condorchelys antiqua* were unstable with respect to this clade and resulted in its collapse in the strict consensus tree (Anquetin *et al.*, 2009).

Joyce (2007) constructed his phylogenetic analysis to provide a comprehensive data set that summarised previous attempts to resolve turtle relationships. Most available phylogenetic analyses were scanned for characters and additional characters were derived from original descriptions of several species. Additionally, as the computational limitations that had restricted previous analyses were no longer an issue, Joyce (2007) was able to include species as terminals, rather than higher taxa, such as genera or families, and was therefore able to test the monophyly of numerous turtle clades. Previous studies had assumed the monophyly of these clades prior to analysis. The sampling of fossil species was also significantly improved in comparison with previous studies and reached a total of 45, together with 22 extant species. For all these reasons, the analysis of Joyce (2007) represented a major advance in our understanding of turtle relationships.

Since Joyce (2007) was published, several new stem turtles have been described: *Heckerochelys romani* (Sukhanov, 2006), *Condorchelys antiqua* (Sterli, 2008), *Odontochelys semitestacea* (Li *et al.*, 2008) and *Eileanchelys waldmani* (Anquetin *et al.*, 2009). Joyce (2007) excluded several early turtles whose relationships were uncertain: e.g., *Indochelys spatulata* (Datta *et al.*, 2000), chengyuchelyids (e.g., Ye, 1994; Danilov & Parham, 2008), *Siamochelys peninsularis* (Tong *et al.*, 2002), and *Otwayemys cunicularius* (Gaffney *et al.*, 1998). Here, a new cladistic analysis is presented

Figure 5.1—Phylogenetic relationships of *Eileanchelys waldmani* according to Anquetin *et al.* (2009). A, strict consensus tree (data matrix of Joyce, 2007 plus *E. waldmani*); B, strict consensus tree after the inclusion of *Heckerochelys romani* and *Condorchelys antiqua*; C, Adams consensus tree after the inclusion of *Heckerochelys romani* and *Condorchelys antiqua*.

in order to test the relationships of these recently described and previously omitted species (for more details see Taxon sampling, below). The main objective of this analysis is to provide a more thorough exploration of basal turtle relationships. It is based largely on a revised version of Joyce (2007) data matrix. The taxon sample has been increased to include all sufficiently well-known pre-Late Jurassic species as well as some more recent species that might conceivably represent relatively basal taxa (see below). Seven non-chelonian taxa are included as outgroups in lieu of *Proganochelys quenstedti* and the hypothetical ancestor used by Joyce (2007; see 'Choice of the outgroups', below). In order to encompass the newly added taxa, characters from previous analyses, as well as seven new characters, are included in the data matrix. Finally, the coding of some characters used in Joyce (2007) is revised in an attempt to reduce the effects of *a priori* assumptions on the analysis (see Coding strategy and Characters, below).

TAXA, CHARACTERS, AND CODING STRATEGY

Taxon sampling

The phylogenetic analysis of Joyce (2007) was the first attempt to produce a broad-scale analysis of the relationships between some of the best-known Mesozoic turtles and representatives of extant turtle clades. Although Gaffney & Meylan (1988) and especially Gaffney *et al.* (1991) attempted to reach a similar goal, Joyce's (2007) analysis was more comprehensive and less constrained by assumptions regarding the monophyly of numerous turtle clades because it included only species as terminal taxa. However, partly because it coincided with new discoveries (see Chapters 1 and 3) and partly because of the aim of the study itself (i.e., producing a reasonably resolved, broad-scale phylogeny), the taxon sampling of Joyce (2007) was incomplete, especially with respect to the most basal species whose potential relationships are poorly known.

The present analysis is intended to complement the analysis of Joyce (2007) by focusing on early turtles from the Triassic and Jurassic. In addition to the 45 fossil and 22 extant species scored by Joyce (2007), 19 other fossil species have been added to the present study (for a list of specimens and references used for scoring, see Appendix 3). Four of these newly added species are stem turtles that have been discovered subsequent to the publication of Joyce (2007) and were therefore not included in that analysis: *Odontochelys semitestacea* (Li *et al.*, 2008), *Eileanchelys waldmani* (Anquetin *et al.*, 2009), *Heckerochelys romani* (Sukhanov, 2006), and *Condorchelys antiqua* (Sterli, 2008). The present analysis also scores *Indochelys spatulata*, a shell-based species from the Early Jurassic of India that is reputed to be close to *Kayentachelys aprix* (Datta *et al.*, 2000). Asia (mostly China) has proven to be a prolific place for Middle Jurassic turtle discoveries (see Chapter 1). However, most of these species have been overlooked by phylogeneticists because they are often only briefly described, consist mostly of shells lacking associated crania, and are often difficult to access for direct observation. However, I was lucky enough to be granted access to some specimens of several Chinese species (see Appendix 3). The following species from Asia are included in the present phylogenetic analysis: *Sichuanchelys chowi* (Ye & Pi, 1997), *Chengyuchelys baenoides* (Young & Chow, 1953; Ye, 1994), *Chengyuchelys zigongensis* (Ye, 1982, 1994), *'Chengyuchelys' dashanpuensis* (Fang, 1987), *Siamochelys peninsularis* (Tong *et al.*, 2002), *Annemys levensis* (Sukhanov, 2000; Sukhanov & Narmandakh, 2006), *Xinjiangchelys tianshanensis* (Nessov, 1995), and *Xinjiangchelys qiguensis* (Matzke *et al.*, 2004). All but two of these species are from the Middle Jurassic, whereas *A. levensis* and *X. qiguensis* are from the Late Jurassic. In contrast to Matzke *et al.* (2004), *Annemys levensis* is included in the analysis rather than *Annemys latiens* (the type species of the genus) because cranial material of this species is known. *Sichuanchelys chowi*, *Chengyuchelys zigongensis*, *'Chengyuchelys' dashanpuensis* and *Siamochelys peninsularis* are included into a phylogenetic analysis for the first time. The remaining six newly added species are younger than the Jurassic. *Arundelemys dardeni*, from the Early Cretaceous of Maryland, USA, was described by Lipka *et al.* (2006) as a basal paracryptodire. The meiolaniids *Ninjemys oweni* from the Pleistocene of Australia and *Niolamia* *argentina* from the Eocene of Argentina (Gaffney, 1996) are included in order to partly bridge the temporal and morphological gap between *Meiolania platyceps* and other turtles. *Otwayemys cunicularius* from the Early Cretaceous of Australia and *Chubutemys copelloi* from the Early Cretaceous of Argentina are included in order to test their supposed relationships with meiolaniids (Gaffney *et al.*, 2007). Finally, *Naomichelys speciosa*, a large turtle from the Early Cretaceous of North America, is tentatively included in a phylogenetic analysis for the first time based on the observation of an undescribed, complete individual (FMNH PR273). This specimen is currently under formal description by S. D. Chapman (pers. comm., 2009), so I will not provide further details on the anatomy of this specimen here. *Naomichelys speciosa* is believed to be close to *Helochelydra*, a probable pancryptodire genus from the Early Cretaceous of western Europe (e.g., Hirayama *et al.*, 2000; Milner, 2004).

Some of the newly added taxa are relatively poorly known and are represented only by shell material (e.g., *Indochelys spatulata*, *Sichuanchelys chowi*, *Chengyuchelys baenoides*, *C. zigongensis*, *'C.' dashanpuensis*, *Otwayemys cunicularius*). This explains why they have been generally ignored in previous phylogenetic analyses, which have tended to concentrate on taxa with cranial remains. Their inclusion in the matrix results in an increased proportion of missing data (e.g., *Otwayemys cunicularius* and *Sichuanchelys chowi* can only be scored for 26% and 20% of characters, respectively), which can ultimately lead to an increased number of equally parsimonious trees and a decrease of resolution (e.g., Kitching *et al.*, 1998). However, the aim of this analysis is not to produce a better-resolved phylogeny than previous studies, but to obtain a more comprehensive view of the relationships among the most basal members of the turtle clade.

Choice of the outgroups

Most phylogenetic analyses that considered the whole turtle clade have used *Proganochelys quenstedti* and/or a chimaeric hypothetical ancestor consisting of a mixture of *P. quenstedti* and other amniotes as the outgroup (e.g., Dryden, 1988; Gaffney *et al.*, 1991; Rougier *et al.*, 1995; Gaffney, 1996; Shaffer *et al.*, 1997; Brinkman & Wu, 1999; Hirayama *et al.*, 2000; Gaffney *et al.*, 2007; Joyce, 2007; Sterli *et al.*, 2007). Character polarisation aside, the general premise for outgroup comparison rests on the testing of ingroup monophyly, as long as more than one outgroup is used. However, this is not as relevant for turtles as it can be for other clades as turtle monophyly has not been seriously questioned (e.g., Gaffney & Meylan, 1988; Joyce, 2007). Consequently, previous authors justified their choice of *Proganochelys quenstedti* as the outgroup because it was indisputably the most primitive turtle known to date, which in phylogenetic terms can be translated as '*P. quenstedti* is the sister group to all other turtles' (e.g., Gaffney, 1990; Joyce, 2007). However, choosing *Proganochelys quenstedti* as the outgroup precludes any possibility that at least part of its morphology may be derived. In other words, choosing *P. quenstedti* as the outgroup is equivalent to accepting that this species represents the ancestral morphotype of turtles because characters would be polarised based on the assumed plesiomorphic morphology of this species.

With the recent discovery of *Odontochelys semitestacea* (Li *et al.*, 2008), *Proganochelys quenstedti* can no longer be used as an outgroup for the rest of the turtle clade. The presence of teeth on the premaxilla, maxilla and dentary of this species is strong evidence that it is more basal than *Proganochelys quenstedti*. Moreover, the postcranial morphology of *Odontochelys semitestacea* suggests that *Proganochelys quenstedti* may not represent the ancestral morphotype of turtles (Li *et al.*, 2008; but see also Reisz & Head, 2008), which contradicts some previous assumptions regarding the ancestral state of certain characters. For example, Joyce (2007: 50) proposed that a phalangeal formula with most digits reduced to two phalanges (a probable terrestrial adaptation) was plesiomorphic for turtles because it is the morphology found in *Proganochelys quenstedti* and *Palaeochersis talampayensis*. However, the manual phalangeal formula of *Odontochelys semitestacea* is 2-3-4-4-3, a condition found in no other turtle and one that is intermediate between the phalangeal formula found in most turtles (2-3-3-3-3) and the common reptilian formula of 2-3-4-5-3 (Li *et al.*, 2008; see also character 175, below).

In order to avoid the *a priori* assumptions on character polarisation that would result from the choice of a basal turtle as the outgroup to all other species, outgroups must be taken from other amniote clades that are closely related to turtles. However, the highly derived body plan of turtles renders the analysis of their relationships with other amniotes difficult (for a review, see Rieppel, 2008). Over the past thirty years, based on morphological arguments only, turtles have been proposed as close relatives of captorhinids (Gaffney & McKenna, 1979; Gaffney & Meylan, 1988; Gauthier *et al.*, 1988), procolophonids (Reisz & Laurin, 1991; Laurin & Reisz, 1995), pareiasaurs (Lee, 1993, 1995, 1996, 1997), sauropterygians (Rieppel & deBraga, 1996; deBraga & Rieppel, 1997, Rieppel & Reisz, 1999) and lepidosaurs (Müller, 2004; Hill, 2005). In addition, numerous molecular studies have supported archosaurian affinities for turtles (for a complete list, see Rieppel, 2008: 348). Sterli (2008) recently proposed a partial revision of the phylogenetic analysis of Joyce (2007) in which she used four non-chelonian outgroups (*Sphenodon punctatus*, *Simosaurus gaillardoti*, *Anthodon serrarius* and *Owenetta kitchingorum*). The present analysis follows this proposal and extends it to include representatives of all clades that have been proposed as the closest relatives of turtles. *Anthodon serrarius* (Lee, 1997), *Owenetta kitchingorum* (Reisz & Scott, 2002) and *Simosaurus gaillardoti* (Rieppel, 1994) represent pareiasaurs, procolophonids and sauropterygians, respectively. The extant *Sphenodon punctatus* is replaced by the Early Jurassic *Gephyrosaurus bridensis* (Evans, 1980, 1981), a basal rhynchocephalian, as representative of lepidosaurs. A combined Captorhinidae is scored based on *Captorhinus aguti* (Fox & Bowman, 1966), *Captorhinus laticeps* (Heaton, 1979) and *Concordia cunninghami* (Müller & Reisz, 2005). Araeoscelidia, representing basal 'diapsids', is scored based on the description of *Araeoscelis* by Reisz *et al.* (1984). Finally, early archosauromorphs are represented by *Protorosaurus speneri* (Gottmann-Quesada & Sander, 2009).

Coding strategy

Coding strategies have been intensively debated in the literature (e.g., Pimentel & Riggins, 1987; Meier, 1994; Pleijel, 1995; Wilkinson, 1995d; Hawkins *et al.*, 1997). Two main schools of thought on character construction can be identified (Wilkinson, 1995d; Kitching *et al.*, 1998): the first considers that characters should be coded as multistate, additive variables, whereas the second sees the characters only as binary variables. Those that defend the multistate coding consider the characters as transformation series where each stage of the transformation is coded as a separate character state. Consequently, multistate characters are often ordered to respect this logical series. The coding of multistate character requires the acceptance prior to the analysis that this transformation series is a true reflection of what happened during evolutionary history. This also implies that the homology between character states is accepted *a priori*, without possibility of being tested by the analysis (Pleijel, 1995). Apart from imposing the aforementioned constraints on the analysis, the multistate coding also carries the risk of underweighting characters if two or more independent features are falsely united as a single multistate character (Wilkinson, 1995d). Additionally, the question of the ordering of these multistate characters needs to be considered. Those that defend the binary coding suggest that each variable should be coded as a separate character and tested for congruence against other variables (Pleijel, 1995). The advantages of this methodology are that it minimises *a priori* assumptions about homology and that the character hierarchy emerges from the result rather than it being part of the original input (Kitching *et al.*, 1998). However, this coding could potentially overweight some features if characters are not independent from one another (Pleijel, 1995; Wilkinson, 1995d). Using one character construction or the other depends mostly on a philosophical choice and "neither approach has a monopoly of advantages or dangers" (Wilkinson, 1995d: 307). Regardless of the preferred coding strategy, characters must be constructed with great care in order to minimise the effects of the identified pitfalls associated with each method (see above). Ideally, any character (binary or multistate) should code for a single feature in order to avoid supporting clades with assemblage of potentially unrelated variables and character states should be mutually exclusive, so that neither can co-occur in the same taxon (Freudenstein, 2005).

Although multistate coding imposes constraints on the resulting topologies, these constraints can be tolerated if they are sufficiently supported by the available data. However, the constraints imposed on the analysis by multistate characters (especially if they are ordered) could have a great influence on the result by restricting the possible topologies (usually toward a pattern that is congruent with our ideas about the interrelationships of the group under study). A review of multistate characters coded by Joyce (2007; see Table 5.1) shows that many of them could be recoded so as to avoid imposing unnecessary *a priori* assumptions on the analysis, while some others have problematic definitions (e.g., unwarranted homology between character states, non-homologous derived states producing similar morphologies, and uninformative character states). These characters are recoded herein as binary variables following the coding 'C' of Pleijel (1995), or 'conventional' coding of Hawkins *et al.* (1997), for which the presence/absence of a feature is coded separately from its various attributes (e.g., colour, shape). According to Hawkins *et al.* (1997), this coding represents the most appropriate method to translate morphological observations into cladistic characters.

Rationale for recoding	**Characters**
Presence/absence considered as a separate variable from other attributes	7*(9-10)*; 27*(41-42)*; 36*(52-53-54)*; 43*(63-64)*; 54 *(76-77)*; 65*(96-97-98)*; 68*(93-94)*; 70*(102-103)*; 85 *(120-121-122)*; 98*(136-137)*; 120*(162-163)*
Unwarranted homology between character states	24*(34-35)*; 35*(51)*; 36*(52-53-54)*; 68*(93-94)*; 113 *(155)*; 119*(160)* [18*(rejected)*]
Non-homologous morphologies united in single multistate character	31*(47-60)*; 56*(79-80-81)*; 62*(89-90)*; 100*(139-140)*
Quantitative character, scoring difficult to reproduce	33*(49)*; 61*(88)*; 133*(177)* [134*(rejected)*]
Disagreement over scoring, character partly uninformative	60*(87)*; 71*(105)*; 86*(123)*; 93*(131)*; 112*(152)*

Table 5.1—Summary of characters from Joyce (2007) that are recoded in the present analysis and rationale for recoding. Numbers correspond to character numbers used by Joyce (2007), corresponding characters in the present analysis are italicised. For rejected characters, see Appendix 6.

Characters

Although most of the characters used in the present analysis are taken from Joyce (2007), substantial changes to the original data set have been made. All characters used in the present study are listed below and modifications are discussed where necessary. In order to encompass newly added taxa and outgroups, several characters have been taken from other studies and details are also provided where appropriate. Additionally, seven new characters are proposed. A shortened, more practical, list of characters can be found in Appendix 4.

CRANIUM

NASAL

Character 1

Nasals: 0 = present; 1 = absent (Joyce, 2007, ch. 1; and references therein).

Character 2

Medial contact of nasals: 0 = nasals contact one another medially along their entire length; 1 = medial contact of nasals partly or fully prevented by an anterior process of the frontal (Joyce, 2007, ch. 2; and references therein).

Comments: *Dorsetochelys delairi* is scored state 1, in contrast to Joyce (2007, state 0). The anterior process of the frontal in that species is similar in development to that of *Arundelemys dardeni* (Evans & Kemp, 1976: fig. 1A; Lipka *et al.*, 2006: fig. 2A, F).

Character 3

Size of nasals: 0 = dorsal exposure of nasals large, about the same size or larger than that of frontal; 1 = dorsal exposure of nasals greatly reduced relative to that of frontals (Joyce, 2007, ch. 3; and references therein).

Comments: According to personal observations (MNA V1558, MNA V2664 and TMM 43670-2) and recently published studies (Sterli & Joyce, 2007; Sterli, 2008), *Kayentachelys aprix* has been scored state 1 in the present analysis, in contrast to Joyce (2007; state 0).

Character 4

Nasomaxillary sinus: 0 = absent; 1 = present (Gaffney, 1996, ch. M12; Gaffney *et al.*, 2007, ch. 4).

Comments: Nasomaxillary sinuses are paired lateral pockets of the fossa nasalis extending posterolaterally into the bone and opening anteriorly just behind the apertura narium interna (Gaffney, 1983: 403). They are formed by the nasal dorsally and maxilla ventrally. These structures are found only in meiolaniids: they are present in *Meiolania platyceps* and *Ninjemys oweni*, but it is not known whether or not they were present in *Niolamia argentina* (Gaffney, 1996).

PREFRONTAL

Character 5

Medial contact of prefrontals on the dorsal skull surface: 0 = absent; 1 = present, absence of contact between the nasal or apertura narium externa and the frontal (Joyce, 2007, ch. 4; and references therein).

Character 6

Prefrontal-vomer contact: 0 = absent; 1 = present (Joyce, 2007, ch. 5; and references therein).

Comments: Sterli & Joyce (2007: 680) tentatively proposed that a prefrontal-vomer contact was present in *Kayentachelys aprix*. However, the actual contact is not preserved in any specimens (Sterli & Joyce, 2007; and personal observation) and the state of preservation of the material prevents any definitive conclusion on this matter (see description of the vomer of *Eileanchelys waldmani* in Chapter 3). Consequently, *Kayentachelys aprix* is scored unknown in the present analysis.

Character 7

Prefrontal-palatine contact: 0 = present; 1 = absent (Laurin & Reisz, 1995, ch. 6; deBraga & Rieppel, 1997, ch. 20; Müller, 2004, ch. 130; Hill, 2005, ch. 70; Joyce, 2007, ch. 6; and references therein).

Character 8

Foramen orbito-nasale: 0 = absent; 1 = present (Laurin & Reisz, 1995, ch. 10; Hill, 2005, ch. 79).

Comments: This character is included for outgroup comparison. The foramen orbito-nasale is an opening between the fossa nasalis and the fossa orbitalis that is usually formed by the prefrontal, palatine and maxilla in turtles. It may be entirely surrounded by bone, as it is usual in turtles (Gaffney, 1979), or only developed as a notch, as in captorhinids (Laurin & Reisz, 1995). Most parareptiles have a foramen orbito-nasale that is developed between the prefrontal, lacrimal and palatine, whereas diapsids lack this foramen (Laurin & Reisz, 1995). The lacrimal also enters the margin of the foramen in *Proganochelys quenstedti* (Gaffney, 1990).

Character 9

Dorsal prefrontal exposure: 0 = present; 1 = absent or near absent (modified from Joyce, 2007, ch. 7; and references therein).

Comments: Joyce (2007) coded the dorsal prefrontal exposure as an ordered multistate character (dorsal prefrontal exposure large / reduced to small lappets / absent or near absent). Although it may seem logical at first glance to follow this coding (especially when considering the reduced prefrontal lappets of pleurosternids and *Neurankylus eximius* and the absence of dorsal exposure of the prefrontal in baenids), it almost automatically implies that the condition in baenids is derived from some group with state 1, because deriving the baenids from a group with state 0 would cost one more step (0 -> 1 -> 2). In order to avoid such an unnecessary *a priori* assumption (see Coding strategy, above), the development of the dorsal exposure of the prefrontal is coded with two binary characters (characters 9 and 10). The present character codes for the presence or absence of dorsal exposure of the prefrontal. Only some baenids are known lack a dorsal exposure of the prefrontal.

Character 10

Dorsal prefrontal exposure: 0 = large; 1 = reduced to small lappets (modified from Joyce, 2007, ch. 7; and references therein).

Comments: See character 9 for a discussion. Most turtles have an exposure of the prefrontal on the dorsal skull roof and this exposure is usually large. However, the reduction of the dorsal prefrontal exposure to small lappets occurred several times within turtles. It is present in *Kayentachelys aprix*, *Eileanchelys waldmani*, *Arundelemys dardeni*, *Dorsetochelys delairi*, pleurosternids, *Neurankylus eximius*, *Sinemys lens*, *Ordosemys leios*, and at least some chelids. In contrast to Joyce (2007; state 0), *Dorsetochelys delairi* is scored state 1 in the present analysis. Taxa that lack a dorsal exposure of the prefrontal are scored inapplicable for this character.

LACRIMAL

Character 11

Lacrimal: 0 = present; 1 = absent (Joyce, 2007, ch. 9; and references therein).

Character 12

Lacrimal: 0 = elongate, enters the border of the external nares (apertura narium externa of turtles) and prevents the contact between maxilla and nasal and/or prefrontal; 1 = short, does not enter the border of the external nares and allows extensive contact between maxilla and nasal and/or prefrontal (Gauthier *et al.*, 1988, ch. 33; Laurin & Reisz, 1995, ch. 9; deBraga & Rieppel, 1997, ch. 17; Lee, 1997, ch. 26; Müller, 2004, ch. 6; Hill, 2005, ch. 98, 107).

Comments: This character is included for outgroup comparison. With the exception of *Proganochelys quenstedti*, *Palaeochersis talampayensis* and *Australochelys africanus*, turtles lack a lacrimal bone and are consequently scored inapplicable for this character.

FRONTAL

Character 13

Frontal contribution to orbit: 0 = absent, contact between prefrontal and postorbital; 1 = present (Joyce, 2007, ch. 10; and references therein).

POSTFRONTAL

Character 14

Postfrontal: 0 = present; 1 = absent (Dryden, 1988, ch. 26; Gaffney & Meylan, 1988, ch. A4-8; Gauthier *et al.*, 1988, ch. 9; Hill, 2005, ch. 77).

Comments: This character is included for outgroup comparison. The postfrontal is present in all outgroups, but absent in all turtles.

TEMPORAL FENESTRATION

Character 15

Temporal fenestration: 0 = absent; 1 = present (Gauthier *et al.*, 1988, ch. 35, 37; Laurin & Reisz, 1995, ch. 29, 30; deBraga & Rieppel, 1997, ch. 50, 51; Lee, 2001, ch. 50, 51; Müller, 2004, ch. 9, 17; Hill, 2005, ch. 109, 110; Sterli, 2008, ch. 69).

Comments: This character is included for outgroup comparison. Within the context of the present analysis, there is no reason to code two different characters (one for the upper, one for the lower fenestra) as is usual because both characters would have exactly the same repartition. This situation may change with a different choice of outgroup and in that case two characters should be coded. Temporal fenestration is present in Araeoscelidia (this analysis follows the scoring of Gauthier *et al.*, 1988, Laurin & Reisz, 1995, deBraga & Rieppel, 1997, and Lee, 2001, for the presence of temporal fenestrae in this group), *Protorosaurus speneri*, *Simosaurus gaillardoti* and *Gephyrosaurus bridensis*, and absent in *Anthodon serrarius*, *Owenetta kitchingorum*, Captorhinidae and all turtles.

PARIETAL

Character 16

Parietal-squamosal contact: 0 = present, upper temporal emargination absent or poorly developed; 1 = absent, upper temporal emargination well developed (Joyce, 2007, ch. 11; and references therein).

Character 17

Parietal contact with the pterygoid, epipterygoid, or palatine: 0 = absent, foramen nervi trigemini usually developed as a notch; 1 = present, foramen nervi trigemini clearly formed by the processus inferior parietalis (Joyce, 2007, ch. 12; and references therein).

Comments: This character codes for the development of the processus inferior parietalis, which is typical of turtles (e.g., Gaffney, 1979). Whereas in basalmost taxa (e.g., *Proganochelys quenstedti*, *Palaeochersis talampayensis*) it is only an incipient structure, in more derived forms the processus inferior parietalis extends ventrally to meet the epipterygoid and/or pterygoid, enclosing the foramen nervi trigemini with bone. In *Meiolania platyceps*, the morphology of this region is different: the processus inferior parietalis is poorly developed, but the foramen nervi trigemini is defined anteriorly by the large epipterygoid that extends upward to meet the parietal (Gaffney, 1983: 419 and fig. 47). As discussed by Sterli & Joyce (2007), this may represent an intermediate state between the rod-like, free-ending epipterygoid found in most amniotes and the morphology found in most turtles where the parietal sends a long ventral process to meet the pterygoid and the laminar epipterygoid (when present). Consequently, and in contrast to Joyce (2007; state 1), *Meiolania platyceps* is scored state 0 in relation to the incipient development of the processus inferior parietalis. According to Woodward's (1901: 172) description this morphology might also be found in *Niolamia argentina*, but this species is scored unknown here. Based on published descriptions (Khosatzky, 1997; Sukhanov, 2000) and photographs of the PIN material kindly provided by W. G. Joyce, the morphology of *Mongolochelys efremovi* is unclear, so it is scored unknown for this character. Joyce (2007) scored *Mongolochelys efremovi* with state 1.

Character 18

Length of anterior extension of the lateral braincase wall: 0 = short, processus inferior parietalis only produces a narrow strut anterior to the foramen nervi trigemini, usually absence of contact with palatine; 1 = elongate, processus inferior parietalis produces an extended process anterior to the foramen nervi trigemini, contact with palatine commonly present (Joyce, 2007, ch. 13; and references therein).

POSTPARIETAL

Character 19

Postparietal: 0 = present; 1 = absent (Dryden, 1988, ch. 27; Gaffney & Meylan, 1988, ch. A4-3; Gauthier *et al.*, 1988, ch. A36; Laurin & Reisz, 1995, ch. 4; deBraga & Rieppel, 1997, ch. 52; Müller, 2004, ch. 14; Hill, 2005, ch. 93).

Comments: This character is included for outgroup comparison. Postparietals are absent in all turtles, as well as in *Protorosaurus speneri*, *Gephyrosaurus bridensis* and *Simosaurus gaillardoti*.

JUGAL

Character 20

Jugal-squamosal contact: 0 = present; 1 = absent, contact between postorbital and quadratojugal commonly present (Joyce, 2007, ch. 14; and references therein).

Character 21

Jugal participation in the rim of the upper temporal emargination: 0 = absent; 1 = present, upper temporal emargination extensive (Joyce, 2007, ch. 15).

QUADRATOJUGAL

Character 22

Deep lower temporal emargination extending above the upper limit of the cavum tympani: 0 = absent; 1 = present, generally associated with a loss of the quadratojugal (modified from Joyce, 2007, ch. 16; and references therein).

Comments: Character 16 of Joyce (2007) codes for the presence/absence of a quadratojugal in relation to the development of a deep lower temporal emargination. According to his scoring, the quadratojugal is lost only in chelids and state 1 is a synapomorphy of this clade. However, as described by Joyce (2007: 14), the quadratojugal is also lost in some testudinoids as well as in

Sinemys lens and *S. gamera*. This appears to be related to the lack of ossification of the temporal bar in these taxa (Joyce, 2007). In order to avoid confusion, the character has been reworded here.

Character 23

Quadratojugal-maxilla contact: 0 = absent; 1 = present (Joyce, 2007, ch. 17; and references therein).

Character 24

Quadratojugal-squamosal contact below the cavum tympani: 0 = absent; 1 = present (Gaffney & Meylan, 1988, ch. C11-3; Gaffney, 1996, ch. M17; Joyce, 2004, ch. Quadratojugal B; Sterli, 2008, ch. 18).

Comments: *Meiolania platyceps* and *Ninjemys oweni* are unique among turtles in having a posteroventral process of the quadratojugal that extends below the cavum tympani and contacts the squamosal. The condition in *Niolamia argentina* is unknown, although it is probable that this contact was present.

SQUAMOSAL

Character 25

Squamosal-supraoccipital contact: 0 = absent; 1 = present (Joyce, 2007, ch. 19; and references therein).

Character 26

Meiolaniid 'horns': 0 = absent; 1 = present (Gaffney & Meylan, 1988, ch. C11-1; Gaffney, 1996, ch. M5; Joyce, 2004, ch. Squamosal B; Gaffney *et al.*, 2007, ch. 16).

Comments: The most striking feature of the meiolaniid skull is the development of horn-like projections of the squamosal (e.g., Gaffney, 1983, 1996). In the present taxon sample, these structures are only found in *Meiolania platyceps*, *Ninjemys oweni* and *Niolamia argentina*.

POSTORBITAL

Character 27

Postorbital-palatine contact: 0 = absent; 1 = present, foramen palatinum posterius situated posterior to the orbital wall (Joyce, 2007, ch. 20; and references therein).

Character 28

Postorbital-maxilla contact preventing the jugal from entering the orbital margin: 0 = absent; 1= present (NEW - derived from Scheyer & Anquetin, 2008).

Comments: A contact between the maxilla and postorbital that excludes the jugal from the orbital margin is relatively uncommon among turtles. It is known in at least three extant species: *Platysternon megacephalum*, *Emys orbicularis* and *Malayemys subtrijuga* (Gaffney, 1979). Among fossil taxa scrutinised for this analysis, the occurrence of this contact is limited to some paracryptodires. A maxilla-postorbital contact is present in *Arundelemys dardeni*, *Pleurosternon bullockii* (= *Mesochelys durlstonensis* Evans & Kemp, 1975), *Glyptops plicatulus* and the baenid *Plesiobaena antiqua*. This condition is also known in *Eubaena cephalica* (e.g., Gaffney, 1972; Lyson & Joyce, 2009). The morphology of *Dinochelys whitei* regarding this character is unclear (Brinkman *et al.*, 2000: 272), whereas in *Dorsetochelys delairi* the jugal enters the orbital margin according to the reconstruction provided by Evans & Kemp (1976).

Character 29

Postorbital-supratemporal contact: 0 = present; 1 = absent (Gauthier *et al.*, 1988, ch. 24; Laurin & Reisz, 1995, ch. 12; deBraga & Rieppel, 1997, ch. 30; Müller, 2004, ch. 184; Hill, 2005, ch. 95).

Comments: This character is included for outgroup comparison. Among the outgroups that have a supratemporal (see also character 30), this contact is present in *Anthodon serrarius* and *Owenetta kitchingorum*, whereas it is absent in Captorhinidae and Araeoscelidia. *Odontochelys semitestacea*, *Proganochelys quenstedti* and *Palaeochersis talampayensis* are the only turtles where a supratemporal is known and this bone does not contact the postorbital in these species. Taxa that have lost the supratemporal (see character 30, below) are scored inapplicable for this character.

SUPRATEMPORAL

Character 30

Supratemporal: 0 = present; 1 = absent (Gaffney & Meylan, 1988, ch. A2-2; Gauthier *et al.*, 1988, ch. 23; Laurin & Reisz, 1995, ch. 18; deBraga & Rieppel, 1997, ch. 30, 53; Müller, 2004, ch. 21; Hill, 2005, ch. 95; Joyce, 2007, ch. 21; and references therein).

PREMAXILLA

Character 31

Subdivision of the apertura narium externa by an internarial process of the premaxilla: 0 = present; 1 = absent (Joyce, 2007, ch. 22; and references therein).

Comments: The present analysis differs from that of Joyce (2007; state 0) in scoring *Meiolania platyceps* and *Kallokibotion bajazidi* as lacking an internarial process formed by the premaxilla (state 1). Although the apertura narium externa is indeed divided in these two species, the separation appears to be formed by the nasal and premaxilla in *M. platyceps* (Gaffney, 1983, 1996) and apparently by the nasal in *K. bajazidi* (Gaffney & Meylan, 1992). The condition in these two taxa is hypothesised as non-homologous to the plesiomorphic amniote condition (state 0) where the premaxillae send a dorsal internarial process that partly separates the nasals anteromedially (Gaffney, 1996: 120). In the present analysis, the condition seen in meiolaniids is coded as a separate character (see character 32, below). In contrast to Joyce (2007; state 0), Sterli *et al.* (2007; state 0) and Sterli (2008; state 0), *Australochelys africanus* is scored unknown for this character. Personal observation of the holotype and only known specimen (BP/1/4933) reveals that it is not possible to determine which bones participate in the formation of the internarial septum in this species.

Character 32

Apertura narium externa subdivided by an internarial process formed by the nasal and premaxilla and somewhat recessed within the apertura: 0 = absent; 1 = present (Gaffney, 1996, ch. M15; Sterli *et al.*, 2007, ch. 1; Sterli, 2008, ch. 23).

Comments: An internarial process formed by the nasal and premaxilla is found only in *Meiolania platyceps* and *Ninjemys oweni*. The apertura narium externa is single in *Niolamia argentina*. The condition in *Kallokibotion bajazidi* appears non-homologous to that of *Meiolania platyceps*: the internarial septem seems to be formed by the nasal only and it is not recessed within the apertura (Gaffney & Meylan, 1992; Gaffney, 1996). In order to avoid favouring any scenario, *K. bajazidi* is scored unknown for this character. *Naomichelys speciosa* is also scored unknown for this character because, although as preserved the apertura is not subdivided in FMNH PR273, a small anteroventral process of the nasal is present and might represent the remnant of a medial septum dividing the apertura narium externa.

Character 33

Fusion of the premaxillae: 0 = absent; 1 = present (Joyce, 2007, ch. 23; and references therein).

Character 34

Foramen praepalatinum: 0 = present; 1 = absent (modified from Joyce, 2007, ch. 24; and references therein).

Comments: Joyce (2007) coded an unordered multistate character for the presence/absence of the foramen praepalatinum (present/absent, premaxillary well ossified/absent, foramen intermaxillaris present). The foramen praepalatinum is present in the majority of turtles. In most cheloniids (here only in *Chelonia mydas* and *Caretta caretta*), the premaxillae are well ossified but the foramina praepalatinum are absent. A different morphology is found in Trionychia (*sensu* Joyce *et al.*, 2004) in which the foramina praepalatinum appear to be absent because of the poorly ossified anterior palate forming a gaping single medial opening called the foramen intermaxillaris (e.g., Gaffney, 1979; Joyce, 2007; see also Appendix 1). Coding these three morphologies into a single multistate character assumes the homology between the three states (e.g., Pleijel, 1995), so that somehow the foramen intermaxillaris corresponds to modified foramina praepalatinum. This homology statement is neither supported nor contradicted by available data. According to the coding strategy adopted here (see above), this multistate character is recoded as two binary characters (characters 34 and 35). The present character codes for the presence/absence of the foramen praepalatinum and representatives of Trionychia are scored inapplicable for it. Although Heaton (1979: fig. 7) identified a "prepalatal foramen" within the premaxilla of *Captorhinus laticeps*, the homology of the chelonian foramen praepalatinum in other reptiles has yet to be assessed and none of the recent phylogenetic analyses of amniote relationships consider this problem. Consequently, each outgroup is scored unknown for this character.

Character 35

Foramen intermaxillaris: 0 = absent; 1 = present (Meylan & Gaffney, 1989, ch. 8; modified from Joyce, 2007, ch. 24).

Comments: See character 35 for a discussion. The foramen intermaxillaris is an unpaired medial opening in the anterior part of the palate found in *Carettochelys insculpta* and most trionychids.

Character 36

Exclusion of the premaxillae from the apertura narium externa: 0 = absent; 1 = present (Joyce, 2007, ch. 25; and references therein).

Comments: In contrast to Joyce (2007; state 0), *Australochelys africanus* is scored unknown for this character because this area of the skull is not preserved in the only known specimen (BP/1/4933).

Character 37

Distinct medial premaxillary hook along the labial margin of the premaxillae: 0 = absent; 1 = present (Joyce, 2007, ch. 26; and references therein).

Comments: Although a premaxillary hook was most probably absent, this region is not sufficiently preserved in any specimen of *Palaeochersis talampayensis* (Sterli *et al.*, 2007) or *Australochelys africanus* (BP/1/4933), so these two taxa are scored as unknown in the present analysis. This contrasts with Joyce (2007) who scored these species with state 0.

MAXILLA

Character 38

Accessory ridge on triturating surface: 0 = absent; 1 = present (Gaffney, 1996, ch. M16; Hirayama *et al.*, 2000, ch. 13; Gaffney *et al.*, 2007, ch. 22).

Comments: In turtles, the maxilla can be described as a triradiate element. It consists of an anterodorsal prefrontal process forming the anteroventral part of the fossa orbitalis, a ventral alveolar process consisting of a thin, sharp blade (the labial ridge) that is enclosed by the rhamphotheca (i.e., the horny beak), and a medial, horizontal palatine process forming the floor of the fossa orbitalis (Gaffney, 1979). The ventral surface of the palatine process of the maxilla is often referred to as the triturating surface because it is covered ventrally by the rhamphotheca and serves as a crushing surface for the mandible. The triturating surface usually bears a lingual ridge that is variably developed among turtles (Gaffney, 1979). Some meiolaniids have at least one additional ridge on the triturating surface (the accessory ridge of Gaffney, 1983). Remarkably, *Niolamia argentina* lacks an accessory ridge (Woodward, 1901; Gaffney, 1996). Khosatzky (1997) proposed that *Mongolochelys efremovi* had an accessory ridge similar to that of meiolaniids. This proposition has been followed by subsequent workers (Hirayama *et al.*, 2000; Gaffney *et al.*, 2007; this work). Accessory ridges are also present sporadically within crown-group turtles in some pleurodires, testudinids, batagurids and emydids (Gaffney, 1979, 1996), but none of the relevant taxa are included in the present analysis.

Character 39

Teeth on the upper and lower jaws (maxilla, premaxilla and dentary): 0 = present; 1 = absent (Dryden, 1988, ch. 3; Gaffney & Meylan, 1988, ch. A4-5; Gauthier *et al.*, 1988, ch. A41; deBraga & Rieppel, 1997, ch. 3; Hill, 2005, ch. 193; Sterli, 2008, ch. 68).

Comments: This character is included for outgroup comparison. All turtles but *Odontochelys semitestacea* lack marginal teeth.

Character 40

Maxillary contribution to orbital margin: 0 = maxilla entirely or largely excluded from the orbital margin by a lacrimal-jugal contact; 1 = maxilla forms most of the anteroventral edge of the orbit (Lee, 1995, ch. 21; deBraga & Rieppel, 1997, ch. 15; Lee, 1997, ch. 28; Müller, 2004, ch. 128; Hill, 2005, ch. 103; Sterli *et al.*, 2007, ch. 15).

VOMER

Character 41

Vomer: 0 = present; 1 = absent or vestigial (modified from Joyce, 2007, ch. 27; and references therein).

Comments: Joyce (2007) scored a single ordered multistate character for the morphology of the vomer (paired/single/single, greatly reduced or absent). This coding may appear logical in view of what is known of turtle phylogeny: a paired vomer is only found in most basal turtles, then all turtles have a single vomer and finally some groups lost the vomer. However, it implies *a priori* statements (i.e., that the loss of the vomer was derived from a condition where a single vomer was present) that are unnecessary and weight against any other possibility. According to the methodology followed here (see Coding strategy, above), the presence/absence of the vomer (character 41) and the fact that this bone may be paired or single (character 42) are kept as separate characters. Within the analysed taxon sample, the vomer is missing or vestigial only in Pelomedusoides (i.e., *Podocnemis expansa*, *Erymnochelys madagascariensis* and *Pelomedusa subrufa*).

Character 42

Vomer: 0 = paired; 1 = single (modified from Joyce, 2007, ch. 27; and references therein).

Comments: See character 41 for a discussion. Taxa that have lost the vomer are scored inapplicable for this character. According to Gaffney & Kitching (1995) and personal observation (BP/1/4933), the vomer appears to have been paired in *Australochelys africanus*. However, this species is cautiously scored as unknown for this character until further evidence is available.

Character 43

Vomer shape: 0 = flat blade, either convex dorsally or horizontal; 1 = develops a ventral median septum and often a ventral horizontal plate contributing to an incipient secondary palate (NEW).

Comments: This character results directly from observation of the morphology in *Eileanchelys waldmani* (see Discussion in Chapter 3). State 0 corresponds to the plesiomorphic amniote morphology and is found in basalmost turtles like *Proganochelys quenstedti*, *Kayentachelys aprix* and *Eileanchelys waldmani*. All more derived turtles, starting with *Meiolania platyceps* and *Mongolochelys efremovi*, have a vomer that acquires a three-dimensional shape by developing at least a ventral median septum dividing the meatus choanae and sometimes a ventral horizontal plate (the dumbbell-shape of Gaffney, 1979). Taxa that have lost the vomer are scored inapplicable for this character.

Character 44

Vomer-pterygoid contact in palatal view: 0 = present; 1 = absent, medial contact of palatines present (Joyce, 2007, ch. 28; and references therein).

Comments: In contrast to Joyce (2007; states 0, 0, and 1, respectively), *Australochelys africanus*, *Palaeochersis talampayensis* and *Sandownia harrisi* are scored as unknown for this character. In *Australochelys africanus*, it is unclear whether the bone anterior to the interpterygoid vacuity is the pterygoid or the palatine (BP/1/4933). In *Palaeochersis talampayensis*, the vomer-pterygoid contact is probably present, but it is not actually observable in the material (Sterli *et al.*, 2007). In *Sandownia harrisi*, the development of an extensive secondary palate obscures the palate roof and prevents the proper scoring of this character (Meylan *et al.*, 2000: figs. 2 and 3). According to Gaffney & Meylan (1992: 13), the vomer does not separate the palatines to meet the pterygoids in *Kallokibotion bajazidi*. This species is consequently scored state 1 in the present analysis, whereas it was scored state 0 in Joyce (2007). State 1 is also found in *Chubutemys copelloi*, *Solnhofia parsonsi*, '*Thalassemys*' *moseri*, *Santanachelys gaffneyi* and Trionychia (*sensu* Joyce *et al.*, 2004). Taxa that have lost the vomer are scored inapplicable for this character.

Character 45

Vomerine and palatine teeth: 0 = present; 1 = absent (Joyce, 2007, ch. 29; and references therein).

Comments: Following Li *et al.* (2008), *Odontochelys semitestacea* is scored unknown for this character. According to the original description (ibid.), some teeth are preserved on the vomer, but the condition for the palatine is unknown. *Proganochelys quenstedti* is unique among turtles in having teeth on the vomer and palatines, a plesiomorphic condition in reptiles (Romer, 1956). Consequently, in the context of this analysis, splitting this character in two (one for vomerine and one for palatine teeth) would unnecessarily overweight this feature.

PALATINE

Character 46

Palatine contribution to the anterior extension of the lateral braincase wall: 0 = absent; 1 = present, well-developed (Joyce, 2007, ch. 30; and references therein).

QUADRATE

Character 47

Ventromedial process of the quadrate and/or ventral expansion of the prootic that partly floors the cavum acustico-jugulare: 0 = absent; 1 = present (modified from Joyce, 2007, ch. 31; and references therein).

Comments: The cavum acustico-jugulare corresponds to the medial part of the middle ear cavity in turtles (see Appendix 1). In basal forms, the cavum is not floored so that it is apparent in ventral view (e.g., *Proganochelys quenstedti*, *Kayentachelys aprix*, *Eileanchelys waldmani*). In more derived turtles, a flooring of the cavum acustico-jugulare often develops and results in a bracing of the braincase. However, two different morphologies exist within turtles (Gaffney, 1979: 210). The flooring of the cavum acustico-jugulare can be produced by a more or less extensive posterior process of the pterygoid, the latter often contacting the basioccipital posteriorly. This morphology can be found in all pancryptodires as well as some basal turtles (e.g., *Meiolania platyceps*, *Mongolochelys efremovi* and *Kallokibotion bajazidi*). The second morphology consists of a generally less extensive flooring of the cavum acustico-jugulare formed by a ventromedial process of the quadrate and/or a ventral expansion of the prootic. This morphology is found in most pleurodires. Gaffney (1975a) conceived this character complex in order to support the dichotomy between cryptodires and pleurodires, but subsequent workers recognised the absence of homology between these two morphologies and consequently refrained from coding them into a single multistate character (see Joyce, 2007: 19). In contrast, Joyce (2007) coded a multistate character for the flooring of the cavum acustico-jugulare (absent/produced by pterygoid/produced by quadrate and prootic). His rationale is based on the fact that if the two derived morphologies are coded separately then the plesiomorphic state of each character is composite: for example in the case of the pleurodire-type flooring, the plesiomorphic state encompasses both the absence of flooring found in basal turtles and the presence of a floor formed by the posterior process of the pterygoid (Joyce, 2007: 19). Although the remark is accurate, this is actually not a problem. Because these two types of flooring are, according to available evidence, not homologous, the absent/present coding used here does not imply any assumption on the morphology of taxa scored absent, it simply asks whether or not a particular derived morphology is present in the considered taxa. In other words, the perspective of the present work is reversed relative to that of Joyce (2007): the coded feature is not whether the cavum is floored (i.e., the *a posteriori* interpreted character complex) but whether or not the quadrate produces a ventromedial process that braces the braincase (character 47), or whether or not the pterygoid has a well-developed posterior process that often contacts the basioccipital (character 60). The result of both derived states produces a similar morphology: the flooring of the cavum acustico-jugulare. In the present analysis, *Notoemys laticentralis* is scored state 0 because its basicranial morphology is very similar to that of *Eileanchelys waldmani* or *Kayentachelys aprix*, for example (Lapparent de Broin *et al.*, 2007: fig. 2). This differs from Joyce (2007) who scored *N. laticentralis* as having the pleurodire-type flooring, which would correspond to state 1 in the present analysis.

Character 48

Central constriction of the middle ear by the quadrate: 0 = absent; 1 = present (Joyce, 2007, ch. 32; and references therein).

Comments: Sterli (2008) proposed that characters 32 and 33 of Joyce (2007; characters 48 and 49 herein) were not independent and united them as her character 34. This may be true, but some morphological observations tend to indicate that it is possible to code two characters: in *Australochelys africanus* and *Palaeochersis talampayensis*, the cavum tympani is incipient but the central constriction of the quadrate around the columella auris has not begun (Gaffney & Kitching, 1995; Joyce, 2007; Sterli *et al.*, 2007). Until this matter is further investigated, the present analysis follows that of Joyce (2007) in coding two separate characters. In contrast to Joyce (2007), characters 48, 49, 50, 52, 53 and 54 (see below) are scored unknown for *Dinochelys whitei* because the relevant morphological areas are not preserved on the only known skull of this species (Brinkman *et al.*, 2000).

Character 49

Cavum tympani: 0 = absent; 1 = present (modified from Joyce, 2007, ch. 33; and references therein).

Comments: The development of the cavum tympani is very difficult to code because it appears to represent a truly continuous character. *Proganochelys quenstedti* is interpreted as lacking a cavum tympani (e.g., Gaffney, 1990; Joyce, 2007), although a shallow recessed area is present along the posterior edge of the quadrate (SMNS 16980). In *Autralochelys africanus*, an incipient cavum tympani is present as a well-defined recessed area along the posterior part of the quadrate (BP/1/4933). In *Palaeochersis talampayensis*, the cavum tympani is even more marked, although it does not reach the development seen in all other turtles (Sterli *et al.*, 2007). Coding quantitative characters can be difficult when no real separation can be drawn between potential states, as it is the case for the development of the cavum tympani. Joyce (2007), following Rougier *et al.* (1995), coded an ordered multistate character with an intermediate state 'cavum tympani partly developed'. Joyce (2007) scored *Australochelys africanus* and *Palaeochersis talampayensis* as having the intermediate state, although the development of the cavum tympani is clearly not equivalent in both taxa (see above). In contrast, Rougier *et al.* (1995) assigned the intermediate state only to *P. talampayensis*, *A. africanus* being scored as lacking a cavum tympani. Given the fact that there is no consensus, only the absence/presence of the cavum tympani is scored here and both *A. africanus* and *P. talampayensis* are scored state 1.

Character 50

Precolumellar fossa: 0 = absent; 1 = present (Joyce, 2007, ch. 34; and references therein).

Character 51

Antrum postoticum: 0 = absent; 1 = present (modified from Joyce, 2007, ch. 35; and references therein).

Comments: Joyce (2007) coded an ordered multistate character for the development of the antrum postoticum and its constitution (absent/present, quadrate does not fully enclose the anterior perimeter of the antrum/present, quadrate fully encloses the anterior perimeter). According to Joyce (2007: 21), the intermediate state is present in stem turtles and an eclectic mix of pancryptodires, whereas the state in which the quadrate forms the anterior perimeter of the antrum is found in pleurodires and numerous cryptodires. However, the reality is not so simple and this feature appears to be highly variable among turtles, especially among pancryptodires. According to Joyce's (2007) scoring, many pancryptodires are polymorphic (presenting states 1 and 2) and the repartition of the character states is very homoplastic (consistency index of 0.16; ibid.). For these reasons, the present analysis follows the simple absent/present coding of previous authors (Dryden, 1988, ch. 29; Rougier *et al.*, 1995, ch. 29). Sterli (2008, ch. 36) attempted to code the development of the antrum postoticum in a multistate character and scored it as incipient (her intermediate state) only in *Kayentachelys aprix*. No rationale was proposed for this coding.

Character 52

Incisura columellae auris: 0 = absent; 1 = present (modified from Joyce, 2007, ch. 36; and references therein).

Comments: Joyce (2007) proposed an unordered multistate character for the absence/presence of the incisura columellae auris and its morphology (absent/present, open posteroventrally/present and closed, only enclosing the stapes/present and closed, enclosing both the stapes and the Eustachian tube). This is a systematic character: it regroups all observed morphologies into one character complex, which can be used to recognise or emphasise differences between different groups. According to the coding strategy followed herein, such characters must be translated so as to minimise *a priori* assumptions on character evolution and possible linkage between characters that could constrain the resulting topology (see Coding strategy, above). The original multistate character of Joyce (2007) can be divided into three binary characters: the absence/presence of the incisura (character 52); whether the incisura is open posteroventrally or closed (character 53); and, where the incisura is closed, whether the quadrate also encloses the Eustachian tube or not (character 54). This coding offers a better representation of the morphological observations and allows the different hypotheses of homology to be tested by congruence independently.

Character 53

Incisura columellae auris: 0 = open posteroventrally; 1 = closed by the quadrate (modified from Joyce, 2007, ch. 36; and references therein).

Comments: See character 52 for a discussion. Joyce (2007), Sterli (2008) and all previous authors who coded the morphology of the incisura columellae auris (see references in Joyce, 2007) followed Gaffney's (1983) description and scored *Meiolania platyceps* as having a closed incisura columellae auris enclosing both the stapes and Eustachian tube (see also character 54). However, in this species the closing of the incisura columellae auris is, according to all evidence, not homologous to that seen in other turtles. In *Meiolania platyceps*, the incisura is closed laterally by the extension of the quadratojugal and squamosal below the cavum tympani (Gaffney, 1983: 415), not by the posteroventral surrounding of the columella auris by the quadrate as in other turtles. Hence, the extension of the quadratojugal and squamosal below the cavum tympani gives the impression that the incisura is closed in lateral view, but figures 38, 42 and 45 in Gaffney (1983) rather show an open incisura. According to these observations, *Meiolania platyceps* is tentatively scored state 0 in the present analysis. Taxa without incisura columellae auris are scored inapplicable for this character.

Character 54

Eustachian tube contained within the incisura columellae auris alongside the stapes: 0 = absent; 1 = present (modified from Joyce, 2007, ch. 36; and references therein).

Comments: See character 52 and 53 for a discussion. Taxa that have an open incisura columellae auris are scored unknown for this character.

EPIPTERYGOID

Character 55

Epipterygoid: 0 = present; 1 = absent (Joyce, 2007, ch. 37; and references therein).

Character 56

Shape of the epipterygoid: 0 = stout and pillar-shaped; 1 = laminar (modified from Sterli, 2008, ch. 39).

Comments: This character was proposed by Sterli (2008) following observations on *Kayentachelys aprix* by Sterli & Joyce (2007). A stout, pillar-shaped epipterygoid (plesiomorphic amniote condition) is known in *K. aprix* and *Meiolania platyceps* (Gaffney, 1983; Sterli & Joyce, 2007). This morphology was probably also present in *Proganochelys quenstedti* (Gaffney, 1990). The condition in *Mongolochelys efremovi* is scored as unknown, but photographs of the PIN material provided by W. G. Joyce suggest that a similar morphology to that of *Meiolania platyceps* may have been present.

PTERYGOID

Character 57

Pterygoid teeth: 0 = present: 1 = absent (Joyce, 2007, ch. 38; and references therein).

Comments: Based on Rougier *et al.* (1995), Joyce (2007) scored *Palaeochersis talampayensis* as possessing pterygoid teeth. However, according to a recent redescription of the material by Sterli *et al.* (2007), the structures described as denticles by Rougier *et al.* (1995) are artefacts. Consequently, and considering the relatively poor preservation of this area in available specimens (Sterli *et al.*, 2007), *Palaeochersis talampayensis* is scored as unknown regarding this character.

Character 58

Basipterygoid articulation: 0 = open; 1 = fused (Joyce, 2007, ch. 39; and references therein).

Character 59

Interpterygoid vacuity: 0 = present; 1 = absent (Joyce, 2007, ch. 40; and references therein).

Character 60

Posterior process of the pterygoid that floors the cavum acustico-jugulare: 0 = absent; 1 = present (modified from Joyce, 2007, ch. 31; and references therein).

Comments: See character 47 for a discussion. As preserved, the posterior process of the pterygoid in *Chubutemys copelloi* has a limited extent and does not contact the basioccipital posteriorly. However, according to Gaffney *et al.* (2007), the posterior margin of this process is broken so that it may have floored the cavum acustico-jugulare entirely and contacted the basioccipital. Consequently, *Chubutemys copelloi* is cautiously scored unknown for characters 60 and 61 (see below).

Character 61

Pterygoid-basioccipital contact: 0 = absent; 1 = present (Joyce, 2007, ch. 41; and references therein).

Comments: See character 60.

Character 62

Processus trochlearis pterygoideus: 0 = absent; 1 = present (Joyce, 2007, ch. 42; and references therein).

Character 63

Foramen palatinum posterius: 0 = present; 1 = absent (modified from Joyce, 2007, ch. 43; and references therein).

Comments: In order to minimise *a priori* assumptions (see Coding strategy, above), the original unordered multistate character of Joyce (2007; foramen palatinum posterius present/open laterally/absent) is recoded as two binary characters (characters 63 and 64). A foramen palatinum posterius that is open laterally (character 64) is found only in *Plesiochelys solodurensis*, *'Thalassemys' moseri* and *Santanachelys gaffneyi*, whereas the absence of the foramen palatinum posterius characterises extant chelonioids. This repartition suggests two derived morphologies that evolved separately and hence justifies the coding of two separate characters (see Joyce, 2007). Joyce (2007) scored *Sandownia harrisi* as having a foramen palatinum posterius that is open laterally. In contrast, Meylan *et al.* (2000) described the foramen palatinum posterius as being a narrow opening situated just lateral to the apertura narium interna, in which case the foramen would be entirely surrounded by bone in this species. The palatal region of *Sandownia harrisi* is highly modified because of the presence of a very extensive secondary palate, so that only a direct examination of the only known specimen could clarify this situation. In the meantime, *Sandownia harrisi* is scored unknown for characters 63, 64 and 66 of the present analysis. According to Rieppel (1993), during early stages of ossification of the palate, the foramen palatinum posterius of turtles appears in the same topological position as the suborbital fenestra of other reptiles. Following Laurin & Reisz (1995) and Rieppel (1993, 1994: 44), the foramen palatinum posterius and suborbital fenestra are considered homologous herein. This allows the scoring of the outgroups for this character.

Character 64

Foramen palatinum posterius open laterally: 0 = absent; 1 = present (modified from Joyce, 2007, ch. 43; and references therein).

Comments: See character 63 for a discussion. Taxa that have lost the foramen palatinum posterius are scored inapplicable for this character.

Character 65

Medial contact of pterygoid: 0 = present, pterygoids in medial contact with one another for at least part of their length; 1 = absent, contact of the basisphenoid with the vomer and/or palatines present (Joyce, 2007, ch. 44; and references therein).

Comments: *Australochelys africanus* is scored unknown for this character (see discussion for character 44, above). In contrast to Joyce (2007; state 1), but following Sukhanov & Narmandakh (1974) and Sukhanov (2000), *Hangaiemys hoburensis* is scored as having a medial contact between the pterygoids (state 0).

Character 66

Pterygoid contribution to foramen palatinum posterius: 0 = present; 1 = absent (Joyce, 2007, ch. 45; and references therein).

Comments: Joyce (2007) scored *Meiolania platyceps* as polymorphic for this character. This is probably the result of the lack of precision of the illustrations published by Gaffney (1983) that sometimes represent the pterygoid forming part of the foramen palatinum posterius and sometimes not. However, Gaffney's (1983) description is less ambiguous and states that the pterygoid forms part of the foramen palatinum posterius in this species. Consequently, *Meiolania platyceps* is scored state 0 in the present analysis.

Character 67

Intrapterygoid slit: 0 = absent; 1 = present (Gaffney & Meylan, 1988, ch. C11-2; Gaffney, 1996, ch. M13; Gaffney *et al.*, 2007, ch. 38).

Comments: The intrapterygoid slit is a feature unique to meiolaniids. It consists of a "thin sheet of bone formed by the pterygoids that encloses a space ventral to the basisphenoid" (Gaffney, 1983: 429). It is found in *Meiolania platyceps*, *Ninjemys oweni* and *Niolamia argentina*.

SUPRAOCCIPITAL

Character 68

Crista supraoccipitalis: 0 = poorly developed; 1 = protruding significantly posterior to the foramen magnum (Joyce, 2007, ch. 46; and references therein).

Character 69

Large supraoccipital exposure on dorsal skull roof: 0 = absent; 1 = present (Joyce, 2007, ch. 47; and references therein).

Comments: According to Joyce (2007), a large supraoccipital exposure on the skull roof is present in *Meiolania platyceps* and *Mongolochelys efremovi*. However, as pointed out by Gaffney *et al.* (2007), the dorsal exposure of the supraoccipital is not as well developed in *Mongolochelys efremovi* as it is in *Meiolania platyceps*. In the present analysis, only *Meiolania platyceps* and *Ninjemys oweni* are scored state 1, whereas *Niolamia argentina* is scored unknown.

EXOCCIPITAL

Character 70

Medial contact of exoccipitals dorsal to foramen magnum: 0 = absent; 1 = present (Joyce, 2007, ch. 48; and references therein).

OPISTHOTIC

Character 71

Processus paroccipitalis: 0 = loosely articulated to squamosal and quadrate; 1 = tightly sutured to squamosal and quadrate (Joyce, 2007, ch. 49; and references therein).

BASISPHENOID

Character 72

Rostrum basisphenoidale: 0 = flat; 1 = rod-like, thick and rounded (Joyce, 2007, ch. 50; and references therein).

Character 73

Paired pits on ventral surface of basisphenoid: 0 = absent; 1 = present (Joyce, 2007, ch. 51; and references therein).

Character 74

Basispterygoid process: 0 = present; 1 = absent (modified from Sterli, 2008, ch. 41).

Comments: Sterli (2008) proposed a modification of character 39 of Joyce (2007) in coding the absence/presence of a basipterygoid process along with the fusion of the basipterygoid articulation into a single multistate character. However, the absence/presence of a basipterygoid process is probably an independent character, as suggested by the persistence of this process in some taxa with a fused basipterygoid articulation (e.g., *Kayentachelys aprix*, *Condorchelys antiqua*, *Pleurosternon bullockii* and *Glyptops plicatulus*). Consequently, the absence/presence of basipterygoid process is coded here as a separate character from the fusion of the basipterygoid articulation (see character 58, above).

STAPEDIAL ARTERY

Character 75

Position of the canalis stapedio-temporalis: 0 = posterior to fenestra ovalis between the paroccipital process of the opisthotic and the quadrate; 1 = anterior to fenestra ovalis between the quadrate and the prootic (Joyce, 2007, ch. 53; and references therein).

Character 76

Foramen stapedio-temporale: 0 = present; 1 = absent (modified from Joyce, 2007, ch. 54; and references therein).

Comments: Joyce (2007) coded the morphology of the foramen stapedio-temporale as an ordered multistate character (foramen relatively large/foramen significantly reduced/foramen absent). This coding entails that the loss of the foramen stapedio-temporale evolved through the reduction of the size of the foramen and weights against any other possible scenario. This *a priori* assumption can be easily avoided by coding two separate binary characters (character 76 and 77). These characters would then be tested for congruence along with other hypotheses of homology and the resulting topology would (ideally) indicate whether or not the loss of foramen stapedio-temporale in some taxa derives from a reduction of the size of this foramen in less inclusive clades (e.g., Kitching *et al.*, 1998: 37).

Character 77

Size of the foramen stapedio-temporale: 0 = relatively large (the size of a blood foramen); 1 = significantly reduced in size (modified from Joyce, 2007, ch. 54; and references therein).

Comments: See character 76 for a discussion. Taxa that have lost the foramen stapedio-temporale are scored inapplicable for this character.

JUGULAR FORAMINA

Character 78

Foramen jugulare posterius formed by bone: 0 = absent; 1 = present, formed mostly by the exoccipital (modified from Joyce, 2007, ch. 55; and references therein; Sterli, 2008, ch. 62).

CANALIS CAROTICUS

Character 79

Foramen posterius canalis carotici interni formed by the prootic only: 0 = absent; 1 = present (modified from Joyce, 2007, ch. 56; and references therein).

Comments: Characters related to the carotid arterial system have consistently been used by systematists in order to resolve relationships within turtles (e.g., Gaffney, 1979). This is especially true with respect to the position of the foramen posterius canalis carotici interni (fpcci), the foramen through which the internal carotid artery enters the cranium (see Appendix 1). Four morphologies can be recognised among turtles (Gaffney, 1979). The plesiomorphic amniote condition (i.e., fpcci formed entirely within the basisphenoid) is found in most stem turtles, some panpleurodires and maybe also some pancryptodires (if these species are correctly interpreted as belonging to this clade). Most pleurodires show a condition where the fpcci is formed by the prootic only. Paracryptodires (i.e., baenids, pleurosternids and closely related species) have a fpcci that opens between the basisphenoid and pterygoid, halfway along the suture between these two bones (see Chapter 4). Finally, the fpcci of eucryptodires and *Meiolania platyceps* is formed mostly or fully by the pterygoid and is located near the posterior edge of this bone. The interpretation of potential homologies between these different morphologies have varied and the debate is not yet closed (see Jamniczky *et al.*, 2006). As *Notoemys laticentralis*, the only stem pleurodire in which the skull is known, and some extant pleurodires (e.g., *Erymnochelys madagascariensis*, *Podocnemis expansa*) retain the plesiomorphic amniote condition, it is reasonable to conclude that the condition where the fpcci opens within the prootic evolved independently within crown-group pleurodires. Concerning the two morphologies found within pancryptodires, it has been proposed that the paracryptodire condition was an intermediate state toward eucryptodire morphology (e.g., Evans & Kemp, 1976; Rieppel, 1980; Gaffney & Meylan, 1988; Gaffney *et al.*, 1991). However, available evidence suggests that the two conditions evolved separately from the plesiomorphic amniote condition (Brinkman & Nicholls, 1993; Jamniczky *et al.*, 2006). Consequently, the more sensible solution is to code this character complex into three binary characters, one representing each derived morphology (characters 79, 80 and 81 herein). This coding broadly corresponds to that used by Gaffney *et al.* (1991), Gaffney (1996) and Brinkman & Wu (1999). In contrast, Dryden (1988), Hirayama *et al.* (2000), Joyce (2007) and Sterli *et al.* (2007) coded a single, unordered multistate character regrouping all of the four aforementioned morphologies. This coding is not appropriate because it assumes *a priori* that all morphologies are homologous to one another (while evidence suggests this is probably not the case, see above) and that the transition from any derived state to the other is possible in theory and as likely to happen as the transformation from the plesiomorphic condition into one of the derived morphology (i.e., 1 step). *Chubutemys copelloi* is scored unknown for characters 79, 80 and 81 because the exact position of the fpcci is not known in this species (Gaffney *et al.*, 2007: 19). In *Annemys levensis*, the only xinjiangchelyid for which a skull has been described, the fpcci opens within the basisphenoid and posteriorly "the internal carotid arteries are situated in an open ventral groove formed by the basisphenoid" (Sukhanov, 2000: 314 and fig. 17.2). *Annemys levensis* is consequently scored state 0 for characters 79, 80 and 81.

Character 80

Foramen posterius canalis carotici interni positioned halfway along the suture between the basisphenoid and the pterygoid: 0 = absent; 1 = present (modified from Joyce, 2007, ch. 56; and references therein).

Comments: See character 79 for a discussion.

Character 81

Foramen posterius canalis carotici interni formed by the pterygoid and positioned near the posterior edge of this bone: 0 = absent; 1 = present (modified from Joyce, 2007, ch. 56; and references therein).

Comments: See character 79 for a discussion. Joyce (2007) scored *Santanachelys gaffneyi* as having a fpcci formed by the pterygoid (i.e., state 1), but the original description and illustrations of the only known specimen of this species (Hirayama, 1998) indicate that the fpcci opens between the basisphenoid and pterygoid (i.e., the paracryptodire morphology; see character 80, above). Furthermore, Hirayama (1998: 707) stated that all protostegids are characterised by a fpcci opening between the basisphenoid and pterygoid. Known protostegid skulls are not currently well described in the literature, which prevents the resolution of this disagreement between Hirayama (1998) and Joyce (2007). In order to avoid favouring one interpretation or the other, *Santanachelys gaffneyi* is scored unknown for the present character as well as for characters 79 and 80 (see above).

FENESTRA PERILYMPHATICA

Character 82

Fenestra perilymphatica: 0 = large; 1 = reduced in size to that of a small foramen (Joyce, 2007, ch. 57; and references therein).

Comments: The fenestra perilymphatica is not defined by bone either in *Proganochelys quenstedti* or in *Australochelys africanus* (Gaffney, 1990; Gaffney & Kitching, 1995), so that these taxa are scored inapplicable for this character. Similarly, all of the outgroups are scored inapplicable for this character.

DENTARY

Character 83

Medial contact of dentaries: 0 = fused; 1 = open suture (Joyce, 2007, ch. 58; and references therein).

Comments: All turtles, with the exception of chelids (here *Chelodina oblonga*, *Phrynops geoffroanus* and *Elseya dentata*), have dentaries that are strongly fused together medially. In chelids, an open suture is present between the two dentaries (Romer, 1956; Gaffney, 1979). Li *et al.* (2008) are followed here in scoring *Odontochelys semitestacea* as unknown for this character. The distinction between a sutural or symphyseal medial contact of the dentaries is not informative for turtle interrelationships, consequently all outgroups are scored with state 1.

SPLENIAL

Character 84

Splenial: 0 = present; 1 = absent (Joyce, 2007, ch. 59; and references therein).

ANGULAR

Character 85

Lateral exposure of angular: 0 = exposed along one-third of the lateral surface of the posterior part of the mandible; 1 = exposed only as a small sliver (dorsoventrally short) or absent along the lateral surface of the mandible (Gauthier *et al.*, 1988, ch. 99; deBraga & Rieppel, 1997, ch. 89; Müller, 2004, ch. 167; Hill, 2005, ch. 180).

Comments: This character is included for outgroup comparison. It is invariant among turtles, which all possess state 1. Among other amniotes, only the lepidosauromorphs (here *Simosaurus gaillardoti* and *Gephyrosaurus bridensis*) are known to have this derived condition (e.g., deBraga & Rieppel, 1997: 316). However, stem lepidosaurs appear to lack this feature, so the conditions in lepidosaurs and sauropterygians are probably independently acquired (S. E. Evans, pers. comm., 2009).

SHELL

Character 86

Bony turtle shell (i.e., a dorsal carapace, formed by neural bones fused to the neural arches of the underlying vertebra, costal bones fused to the underlying ribs, and generally peripheral elements connected laterally by a bridge to a ventral plastron formed by the clavicles, interclavicles and a series of three to five paired plates; see Zangerl, 1939, 1969; Gaffney & Meylan, 1988: 161): 0 = absent; 1 = present (Dryden, 1988, ch. 35; Gaffney & Meylan, 1988, ch. A4-1; Hill, 2005, ch. 344; Sterli, 2008, ch. 72).

Comments: This character is included for outgroup comparison. *Odontochelys semitestacea* is problematic: according to Li *et al.* (2008), its shell morphology is somehow intermediate between a hypothetical shell-less ancestor and more derived turtles with a complete shell (e.g., *Proganochelys quenstedti*). However, as proposed by Reisz & Head (2008), *Odontochelys semitestacea* could as well be interpreted as a primitive stem-turtle with a highly derived shell morphology. Given the fact that *O. semitestacea* has ossified neural plates and a complete plastron, this species is considered here to have a bony turtle shell (state 1). Similarly, although the shell of *Dermochelys coriacea* is highly derived (Zangerl, 1939), this species is scored state 1 for this character. Because they do not have a turtle shell, all of the outgroups are scored inapplicable for the following characters related to this structure (i.e., characters 87 to 140, 153 to 155, 163, 168, 170 and 172).

CARAPACE

Character 87

Carapacial scale sulci: 0 = present; 1 = absent or poorly developed (modified from Joyce, 2007, ch. 60; and references therein).

Comments: Joyce (2007) originally coded the absence/presence of carapacial scales in fossil taxa by scoring the absence/presence of scale sulci, so the definition of the character has been reworded in order to be more in phase with the available information in fossil taxa. Joyce (2007) coded an ordered multistate character (carapacial scales present/partly present/absent), the intermediate state being attributed to *Mesodermochelys undulatus*, *Pseudasnosteira pulchra* and *Carettochelys insculpta*. I disagree with these conclusions in some respects as the carapacial scale sulci are present in *Pseudanosteira pulchra* (e.g., Hay, 1908; Clark, 1932) and absent in *Carettochelys insculpta* (e.g., Bonin *et al.*, 2006). With regard to these considerations, the present study follows Shaffer *et al.* (1997, ch. 78) and Kear & Lee (2006, ch. 80) in coding only the absence/presence of scale sulci on the carapace. The condition in *Odontochelys semitestacea* is unknown (Li *et al.*, 2008). Very few carapacial scale sulci are present in *Mesodermochelys undulatus* (Hirayama & Chitoku, 1996) and this species is consequently scored state 1. This follows the scoring of Kear & Lee (2006).

Character 88

Tricarinate carapace: 0 = absent; 1 = present (modified from Joyce, 2007, ch. 61; and references therein).

Comments: Joyce (2007: 28) coded an ordered multistate character for this feature (absent/present, but only poorly developed/present and pronounced). Joyce's (2007) scoring is not reproducible because he did not provide any quantification of the relative development of the tricarination of the carapace. For the moment, the absent/present coding of Meylan & Gaffney (1989, ch. 19) and Shaffer *et al.* (1997, ch. 93) appears to be more appropriate and is followed here.

NUCHAL

Character 89

Articulation of nuchal with neural spine of eighth cervical vertebra along a blunt facet: 0 = present; 1 = absent (modified from Joyce, 2007, ch. 62; and references therein).

Comments: All turtles, with the exception of stem turtles and panchelonioids, lack an articulation between the eighth cervical vertebra and the nuchal plate. In stem turtles (e.g., *Proganochelys quenstedti*, *Kayentachelys aprix* and *Mongolochelys efremovi*), the articulation is formed along a blunt facet on the visceral surface of the nuchal. In contrast, the eighth cervical vertebra of panchelonioids articulates with a raised pedestal formed on the ventral surface of the nuchal. According to the available evidence, these two morphologies are not homologous (Joyce, 2007: 29) and should consequently be coded as two separate characters (characters 89 and 90).

Character 90

Raised pedestal on the visceral surface of the nuchal for the articulation with the neural spine of the eighth cervical vertebra: 0 = absent; 1 = present (modified from Joyce, 2007, ch. 62; and references therein).

Comments: See character 89 for a discussion.

Character 91

Elongate costiform processes of the nuchal: 0 = absent; 1 = present, process crosses peripheral 1 to contact peripheral 2 and sometimes peripheral 3 (Joyce, 2007, ch. 63; and references therein).

NEURAL

Character 92

Neural formula 6>4<6<6<6<6: 0 = absent; 1 = present (Joyce, 2007, ch. 64; and references therein).

Character 93

Neurals: 0 = present; 1 = absent, allowing medial contact of all costals (modified from Joyce, 2007, ch. 68; and references therein).

Comments: Joyce (2007) coded the absence/presence of medial contact between costal bones as an ordered multistate character (absence of medial contact/medial contact of up to three posterior costals/medial contact of all costals, neurals absent). This coding assumes that the condition where all neurals are missing, which is found only in some chelids (only in *Chelodina oblonga* and *Elseya dentata* herein), evolved from a condition where only some posterior neurals were absent, allowing a partial contact between posterior costals. The latter condition is found in all other extant pleurodires included in the present analysis, but also in numerous pancryptodires (see character 94, below). Although the aforementioned hypothesis regarding the origin of the condition in some chelids might be correct, it is nevertheless an unnecessary *a priori* assumption that constrains the resulting topologies. In the present analysis, the complete absence of neurals (character 93) is coded separately from the partial reduction of posterior neurals (character 94).

Character 94

Partial reduction of the posterior neurals allowing medial contact of up to three posterior costals: 0 = absent; 1 = present (modified from Joyce, 2007, ch. 68; and references therein).

Comments: See character 93 for a discussion. Available evidence suggests that the partial reduction of posterior neurals allowing medial contact of posterior costals appeared several times within turtles. It is found in numerous extant pleurodires as well as in eleven of the pancryptodiran taxa included in the present analysis (see Appendix 5). The present study differs from that of Joyce (2007; states 0 and 1, respectively) in the scoring of *Mesodermochelys undulatus* and *Peltochelys duchastelli*. In *M. undulatus* the posterior neurals are reduced and allow a medial contact of some posterior costals (Hirayama & Chitoku, 1996), whereas *P. duchastelli* has a complete row of neural that prevents any medial contact of costals (Meylan, 1988).

SUPRAPYGAL

Character 95

Lateral contact of suprapygal 1 with peripherals: 0 = absent; 1 = present (NEW).

Comments: In most turtles, the first suprapygal does not contact the peripherals laterally. A contact between the first suprapygal and the peripherals is present in *Eileanchelys waldmani* (see Chapter 3), *Kallokibotion bajazidi*, *Naomichelys speciosa*, *Plesiochelys solodurensis* and *Xinjiangchelys latimarginalis*.

PERIPHERAL

Character 96

Peripherals: 0 = present; 1 = absent (modified from Joyce, 2007, ch. 65; and references therein).

Comments: Joyce (2007) coded the number of peripherals into a four-state ordered character (more than 11 pairs/11 pairs/10 pairs/less than 10 pairs). Taxa scored as having less than 10 pairs of peripherals are actually those in which ossified peripherals are absent (i.e., trionychids and *Dermochelys coriacea*). The ordered multistate character of Joyce (2007) implies that this condition derived from a state where only 10 pairs of peripherals were present, as appears to be the case for trionychids. This is an unnecessary *a priori* assumption that is partly contradicted by the fact that, according to all evidence (Hirayama & Chitoku, 1996; Joyce, 2007: 31), *Dermochelys coriacea* derives from taxa with 11 pairs of peripherals. Moreover, for the complete absence of peripherals to be considered homologous to the reduction from 11 to 10 pairs of peripherals without any other evidence, a more or less continuous series of intermediates should be known. Consequently, the absence of peripherals is coded here as a separate character from the number of peripherals. Additionally, the hypothetical progressive reduction from more than 11 pairs to 11 pairs then to 10 pairs of peripherals, the first three ordered states of Joyce (2007), is also considered here to be an unnecessary assumption. This pattern should emerge *a posteriori* from the results of the cladistic analysis after being tested for congruence against other characters rather than being an assumption that is accepted *a priori* (e.g., Kitching *et al.*, 1998). For this reason, the number of peripherals is coded as two separate binary characters in the present analysis (see characters 97 and 98, below). Hence, the present study partly follows the coding of Shaffer *et al.* (1997, 83, 95). *Odontochelys semitestacea* is scored unknown until further investigation reveals whether its shell morphology is primitive (peripheral bones not yet developed - i.e., scoring inapplicable) or derived (peripheral bones lost - i.e., state 1).

Character 97

Number of peripherals: 0 = more than 11 pairs; 1 = 11 pairs or less (modified from Joyce, 2007, ch. 65; and references therein).

Comments: See character 96 for a discussion. Taxa that lack peripherals are scored inapplicable for this character.

Character 98

Number of peripherals: 0 = 11 pairs or more; 1 = reduced to 10 pairs (modified from Joyce, 2007, ch. 65; and references therein).

Comments: See characters 96 and 97 for a discussion. Taxa that lack peripherals are scored inapplicable for this character.

Character 99

Anterior peripherals incised by musk ducts: 0 = absent; 1 = present (Joyce, 2007, ch. 66; and references therein).

COSTAL

Character 100

Medial contact of the first pair of costals: 0 = absent; 1 = present, but complete set of neurals present (Joyce, 2007, ch. 67).

Character 101

Reduction of costal ossification: 0 = absent, costals fully or almost fully ossified, costal fontanelles small or absent; 1 = present, costals ossified only two thirds the length of the costal ribs, costal fontanelles well developed (Joyce, 2007, ch. 69; and references therein).

Comments: *Odontochelys semitestacea* is scored unknown until further investigation reveals whether its shell morphology is primitive (costal bones not yet developed - i.e., scoring inapplicable) or derived (ossification of costal bones reduced - i.e., state 1).

CERVICAL

Character 102

Cervical: 0 = present; 1 = absent, carapacial scales otherwise present (modified from Joyce, 2007, ch. 70; and references therein).

Comments: Joyce (2007) coded an unordered multistate character for the absence/presence and number of cervical scales (one cervical scale/cervical scale absent/more than one cervical scale). According to the methodology of character construction followed herein (see Coding strategy, above), the absence/presence of cervical scales and the number of these scales are considered as two separate binary characters (characters 102 and 103). According to Milner (2004) and personal observations (e.g., NHM 28618, 38733, 43621, R3413, R3727 and R 6895), *Pleurosternon bullockii* is scored as lacking a cervical scale. This contrasts with Joyce (2007).

Character 103

Number of cervical scales: 0 = one cervical scale; 1 = more than one cervical scale present (modified from Joyce, 2007, ch. 70; and references therein).

Comments: *Chengyuchelys baenoides* is scored as having only one cervical scale (based on personal observation of IVPP V6507). This is in contradiction to Danilov & Parham (2008) who describe three cervical scales in this specimen. Taxa that lack a cervical scale are scored inapplicable for this character.

MARGINAL

Character 104

Marginal scales overlap onto costal plates: 0 = absent, marginals restricted to peripheral plates; 1 = present (Matzke *et al.*, 2004, ch. 7; Danilov & Parham, 2008, ch. Marginal B; see also Meylan & Gaffney, 1989, ch. 47, and Peng & Brinkman, 1993).

Comments: In the context of the present analysis, marginal scales overlapping onto costal bones are known in pleurosternids, *Xinjiangchelys latimarginalis*, *X. qiguensis* and *Adocus beatus*.

SUPRAMARGINAL

Character 105

Supramarginals: 0 = present; 1 = absent (modified from Joyce, 2007, ch. 71; and references therein).

Comments: Joyce (2007) coded the absence/presence of supramarginal scales as an ordered multistate character (complete row present/partial row/supramarginals absent). According to Joyce (2007), *Proterochersis robusta*, *Platychelys oberndorferi* and *Macrochelys temminckii* have a partial row of supramarginals, whereas *Proganochelys quenstedti* and *Palaeochersis talampayensis* have a complete row of supramarginals. In their recent redescription of *Palaeochersis talampayensis*, Sterli *et al.* (2007) showed that it is unknown whether a complete or partial row of supramarginals was present: only three supramarginals are visible on each sides of the only available shell of this species. This contrasts with the coding of Joyce (2007). *Proganochelys quenstedti* is consequently the only species with a complete row of supramarginals and it is impossible to know whether this is a plesiomorphic or autapomorphic condition (uninformative). Following these observations, the coding of a simple absent/present character for the supramarginals appears to be more appropriate for the moment. The number of supramarginals in *Macrochelys temminckii* appears to be highly variable (e.g., Bonin *et al.*, 2006) and these additional scales may actually be absent in some specimens, according to personal observation (FMNH dried skeleton collection). Nevertheless, *M. temminckii* is conservatively scored state 0 in the present analysis. According to personal observation of BSPG AS I 1438, the presence of a partial row of supramarginals in *Platychelys oberndorferi* is dubious. This specimen appears to have only one supernumerary scale that is located anterior to the first pleural. This observation is confirmed by illustrations of the lost holotype of this species published in Meyer (1860: pl. XVIII.4) and Wagner (1861: taf. IV). Whether this additional scale corresponds to a true suprapygal or to the supernumerary pleural scale found anterior to the first pleural in *Palaeomedusa testa*, *Thalassemys marina* and *Caretta caretta* (see Joyce, 2003, 2007) remains unknown. Joyce (2003: 6) considered this additional scale in *Platychelys oberndorferi* to be a supernumerary pleural, whereas Joyce (2007: 33) interpreted it as a supramarginal. Consequently, *Platychelys oberndorferi* is scored unknown for this character. Finally, *Boremys pulchra* is scored as having supramarginals (Gaffney, 1972; Lyson & Joyce, 2009).

VERTEBRAL

Character 106

Shape of vertebrals: 0 = vertebrals 2 to 4 significantly broader than pleurals; 1 = vertebrals 2 to 4 as narrow as, or narrower than, pleurals (Joyce, 2007, ch. 73; and references therein).

Comments: *Palaeochersis talampayensis* is scored unknown for this character because the vertebrals are not apparent in available specimens (Rougier *et al.*, 1995; Sterli *et al.*, 2007). This scoring differs from that of Joyce (2007; state 0).

Character 107

Position of vertebral 3-4 sulcus in taxa with five vertebrals: 0 = sulcus positioned on neural 6; 1 = sulcus positioned on neural 5 (Joyce, 2007, ch. 74).

Comments: Although the vertebral 3-4 sulcus crosses neural 5 in the published reconstruction of *Heckerochelys romani*, the original description and photographs fail to confirm this characteristic (Sukhanov, 2006). Considering the fact that most basal taxa have a vertebral 3-4 sulcus on neural 6 (see Appendix 5), *Heckerochelys romani* is cautiously scored unknown for this character.

Character 108

Vertebral 3-4 sulcus with a distinct medial embayment: 0 = absent; 1 = present (NEW).

Comments: A distinct, U-shaped medial embayment of the vertebral 3-4 sulcus is known in *Chengyuchelys baenoides*, *C. zigongensis* and *Annemys levensis* (Young & Chow, 1953; Ye, 1982, 1994; Sukhanov, 2000; Sukhanov & Narmandakh, 2006). It is also present in *Annemys latiens*, which is not included in the present analysis (see Sukhanov, 2000).

Character 109

Vertebral 5: 0 = overlaps onto peripherals and often pygal posteriorly; 1 = does not overlap onto peripherals and pygal (modified from Matzke *et al.*, 2004, ch. 6).

Comments: Matzke *et al.* (2004) used this character in their analysis of xinjiangchelyid relationships. According to them, most xinjiangchelyids can be distinguished from other turtles by a fifth vertebral that does not overlap, or only slightly overlaps, the peripherals. However, the broader taxon sample considered in the present analysis shows that vertebral 5 usually overlaps the peripherals to a limited extent in most turtles. With regards to these observations, the character has been redefined herein so that the supposed derived state is restricted to those taxa in which the fifth vertebral does not overlap either the peripherals or the pygal. Following this new definition, state 1 is present only in *Xinjiangchelys latimarginalis* and *X. tianshanensis* among xinjiangchelyids. However, this state is also found in *Mongolochelys efremovi*, *Pleurosternon bullockii*, *Glyptops plicatulus*, *Naomichelys speciosa*, *Siamochelys peninsularis*, *Zangerlia neimongolensis* and *Adocus beatus* (see Appendix 5).

PLASTRON

Character 110

Connection between carapace and plastron: 0 = osseous; 1 = ligamentous (Joyce, 2007, ch. 75; and references therein).

Comments: *Odontochelys semitestacea* is scored unknown because there is no evidence as to whether or not a connexion between the plastron and the almost non-existent carapace of this species was present (Li *et al.*, 2008). *Xinjiangchelys qiguensis* is also scored unknown for this character because the original description of Matzke *et al.* (2004) is unclear on that particular matter.

Character 111

Central plastral fontanelle: 0 = absent in adult individuals; 1 = present, even in adult individuals (Joyce, 2007, ch. 76; and references therein).

Comments: In their reconstruction of *Indochelys spatulata*, Datta *et al.* (2000: fig. 5) depicted a plastron without a fontanelle. However, the central plastral area of the only known specimen of this species is preserved as a gaping hole, which prevents any conclusion on the absence or presence of a central plastral fontanelle (Datta *et al.*, 2000: fig. 3). Consequently, *Indochelys spatulata* is scored unknown for this character. In her reassessed version of Joyce's (2007) matrix, Sterli (2008) scored *Condorchelys antiqua* as having a central plastral fontanelle. Although no mention of this feature is present in the published description (Sterli, 2008), I follow this scoring in the present analysis. Although the presence of a fontanelle may be a true synapomorphy for some clades (e.g. panchelonioids), the fact that fontanelles are very commonly present in young individuals and that it is apparently easy for aquatic species to retain this feature in adult individuals suggest that this character should be used carefully or even excluded from future phylogenetic analyses. Many fossil species are known by a limited number of individuals so that the conclusion that a fontanelle is present in adult individuals is often questionable. *Eileanchelys waldmani* is a perfect example of this phenomenon: a central plastral fontanelle may have been present in one individual but it is entirely absent in other specimens (see Chapter 3). Not only that this can lead to inaccurate scoring of some species, but it can result in unwarranted grouping of some species as it may be the case for *Heckerochelys romani* and *Condorchelys antiqua* in the present study (see Discussion, below).

Character 112

Plastral kinesis: 0 = absent, scale sulci and bony sutures do not overlap; 1 = present, scale sulci coincide with epiplastral-hyoplastral contact (Joyce, 2007, ch. 77; and references therein).

Comments: See restrictions for the scoring of this character in Joyce (2007: 35).

ENTOPLASTRON

Character 113

Anterior entoplastral process: 0 = present, medial contact of epiplastra absent; 1 = absent, medial contact of epiplastra present (Joyce, 2007, ch. 78; and references therein).

Comments: Sterli (2008) scored *Condorchelys antiqua* as having an anterior process of the entoplastron, however in the description of this species she states that the epiplastra actually meet medially (ibid.: 288). Consequently, *Condorchelys antiqua* is scored state 1 in the present analysis.

Character 114

Size of the posterior entoplastral process: 0 = posterior process long, reaching as far posteriorly as the mesoplastra; 1 = posterior process reduced in length (Joyce, 2007, ch. 79; and references therein).

Character 115

Entoplastron: 0 = massive and cross- to diamond-shaped; 1 = strap like and V-shaped (Joyce, 2007, ch. 81; and references therein).

Character 116

Dagger-shaped entoplastron: 0 = absent; 1 = present (NEW).

Comments: *Chengyuchelys baenoides* and *C. zigongensis* are unique among turtles in having an entoplastron shaped like a short dagger (e.g., Danilov & Parham, 2008: fig. 2B; these authors described the entoplastron as being leaf-shaped). Anteriorly, the entoplastron has an anterior process, that is probably not homologous to the anterior entoplastral process of more basal turtles (see character 113), which corresponds to the ‘handle’ of the dagger. At the level of the medialmost point of the epiplastron-hyoplastron suture, the entoplastron has a short lateral projection on each side that recalls the 'guard' of the dagger. Finally, the posterior part of the entoplastron tapers progressively posteriorly, corresponding to the shortened blade of the imaginary dagger. The posterolateral margins of the entoplastron are not straight but rather slightly sinuous.

Character 117

Entoplastron: 0 = present; 1 = absent (Joyce, 2007, ch. 82).

EPIPLASTRON

Character 118

Shape and contact of epiplastra: 0 = epiplastra sub-square in outline, minor posterior contact with hyoplastra; 1 = epiplastra elongate in shape, long posteromedial contact with hyoplastra (Joyce, 2007, ch. 83; and references therein).

Comments: Based on personal observation of dried skeletons at the Field Museum in Chicago (e.g., FMNH 51627), *Platysternon megacephalum* is scored state 1 in the present analysis, in contrast to Joyce (2007; state 0). Although the elongate shape of the epiplastra in *P. megacephalum* is less pronounced than that of *Protochelydra zangerli* or *Chelydra serpentina*, it is similar to the condition in *Meiolania platyceps*, *Mongolochelys efremovi* and *Hangaiemys hoburensis*, which are all scored state 1 in both Joyce (2007) and the present study.

HYOPLASTRON

Character 119

Contacts of axillary buttresses: 0 = peripherals only; 1 = peripherals and first costal (Joyce, 2007, ch. 84; and references therein).

Comments: *Siamochelys peninsularis* is scored as unknown because Tong *et al.* (2002: 691) expressed doubts on whether or not the axillary buttress contacts the first costal in this species.

MESOPLASTRON

Character 120

Mesoplastron: 0 = present; 1 = absent (modified from Joyce, 2007, ch. 85; and references therein; Sterli *et al.*, 2007, ch. 70).

Comments: Joyce (2007: 38) coded the number, development and presence of mesoplastra as an ordered multistate character (one or two pairs present/one pair of mesoplastra not meeting in midline/mesoplastra absent). Sterli *et al.* (2007: 59) followed a similar approach, although they scored the presence of two pairs of mesoplastra as a separate state (which was uninformative) and ran the character unordered. Following the character construction methodology followed here (see Coding strategy, above), the absence/presence, the number, and the development of mesoplastra are kept as separate characters so that each of them constitutes a potential synapomorphy to be tested for congruence against other characters included in the analysis (Kitching *et al.*, 1998: 37). By coding the absence/presence of mesoplastra as a simple binary character, the present analysis follows the majority of previous cladistic analyses of turtle relationships (Dryden, 1988, 44; Gaffney *et al.*, 1991, 31; Gaffney, 1996, 34; Brinkman & Wu, 1999, 34; Hirayama *et al.*, 2000, 74; Gaffney *et al.*, 2007, 103). *Siamochelys peninsularis* was reported to have one pair of mesoplastra meeting medially (Tong *et al.*, 2002), but I. G. Danilov (in Danilov & Parham, 2008) seriously questioned the presence of mesoplastra after seeing the few known specimens of this species. In order to avoid favouring one hypothesis or the other, *Siamochelys peninsularis* is scored unknown for characters 120 to 122.

Character 121

Mesoplastron: 0 = one pair present; 1 = two pairs present (NEW).

Comments: Until the discovery of *Odontochelys semitestacea* (Li *et al.*, 2008), *Proterochersis robusta* was the only turtle known to have two pairs of mesoplastra. Before this discovery, coding the number of mesoplastra as a separate character would have been uninformative and the presence of two pairs of mesoplastra would have been an autapomorphy of *Proterochersis robusta*. Following the discovery of *Odontochelys semitestacea* (Li *et al.*, 2008), the present analysis is the first to consider the number of mesoplastra as a separate character. The presence of two pairs of mesoplastra in *Odontochelys semitestacea*, arguably the most basal turtle known to date (Li *et al.*, 2008; Reisz & Head, 2008), could have dramatic implications for the relationships of basalmost turtles: it suggests that the presence of two pairs of mesoplastra may be the plesiomorphic condition for turtles. Taxa in which the mesoplastra are lost are scored inapplicable for this character.

Character 122

Medial contact of mesoplastra: 0 = present, or virtually present when a central plastral fontanelle is present, absence of contact between hyoplastron and hypoplastron; 1 = absent, partial contact between hyoplastron and hypoplastron present (modified from Gaffney *et al.*, 1991, ch. 30; Joyce, 2007, ch. 85; Sterli *et al.*, 2007, ch. 70).

Comments: Previous analyses that considered the absence/presence of a medial contact between the mesoplastra made no distinction between the condition in which mesoplastra are reduced and restricted to the lateral part of the plastron, hence allowing a broad medial contact between hyoplastra and hypoplastra, and the condition in which the mesoplastra do not meet at the midline because of the presence of a central plastral fontanelle, in which case there is no contact between hyoplastra and hypoplastra (Gaffney *et al.*, 1991, 30; Joyce, 2007, 85; Sterli *et al.*, 2007, 70). The definition of the present character is intended so that only taxa with reduced mesoplastra that actually do not contact each other medially and allow a contact between hyoplastra and hypoplastra are scored state 1. It is assumed that species in which the mesoplastra reach the central plastral fontanelle without any indication of medial tapering would have presented a median contact of these plates if the fontanelle was closed (e.g., *Heckerochelys romani* and *Mongolochelys efremovi*). These species are consequently scored state 0 in the present analysis. According to this new definition, the absence of medial contact of the mesoplastra is exclusively found in *Kallokibotion bajazidi* and Panpleurodires, with the exception of chelids that have lost the mesoplastra. Joyce (2007) scored *Baena arenosa* as lacking a medial contact of the mesoplastra. Indeed, Gaffney (1972: fig. 31) depicted a shell of a juvenile specimen of *Baena arenosa* in which the mesoplastra are reduced and do not contact one another medially. However, he clearly stated in the caption of this figure that "mesoplastra meet in midline in all other known *B. arenosa* shells" (Gaffney, 1972: 282). *Baena arenosa* is consequently scored state 0 in the present analysis. Taxa in which the mesoplastra are lost are scored inapplicable for this character.

HYPOPLASTRON

Character 123

Contacts of inguinal buttresses: 0 = peripherals only; 1 = peripherals and costals (modified from Joyce, 2007, ch. 86; and references therein).

Comments: Joyce (2007) followed Shaffer *et al.* (1997, ch. 55) in coding an unordered multistate character for the contacts of the inguinal buttress (contact with peripherals only/peripherals and costal 5/peripherals, costal 5 and costal 6). However, no taxon appears to possess the third state either in the description of the character, or in the matrix (Joyce, 2007: 39 and 90-91). Consequently, the binary coding used by Dryden (1988, ch. 47), Hirayama *et al.* (2000, ch. 66) and Sterli *et al.* (2007, ch. 66) appears to be more appropriate.

XIPHIPLASTRON

Character 124

Distinct anal notch: 0 = absent; 1 = present (Joyce, 2007, ch. 87; and references therein).

Comments: In contrast to Joyce (2007), *Pleurosternon bullockii* is scored state 1 because all specimens at the NHM (including the holotype NHM R911) in which this area of the plastron is preserved have distinct processes of the xiphiplastra that frame an anal notch. The present study also differs from that of Joyce (2007; state 1) in scoring *Mongolemys elegans* and *Chrysemys picta* as lacking an anal notch (state 0).

Character 125

Shape of xiphiplastra: 0 = elongate rectangles; 1 = narrow struts that frame a xiphiplastral fontanelle (Joyce, 2007, ch. 88; and references therein).

PLASTRAL SCALES

Character 126

Plastral scales: 0 = present; 1 = absent (Joyce, 2007, ch. 89; and references therein).

Character 127

Midline sulcus of plastral scales: 0 = straight; 1 = distinctly sinuous, at least for part of its length (Matzke *et al.*, 2004, ch. 14; Joyce, 2007, ch. 90; and references therein; see also Peng & Brinkman, 1993).

Comments: A sinuous midline sulcus of the plastral scales is known in *Xinjiangchelys latimarginalis*, *X. tianshanensis*, *X. qiguensis*, *Siamochelys peninsularis*, *Annemys levensis*, *Zangerlia neimongolensis*, *Basilemys variolosa*, *Adocus beatus* and *Peltochelys duchastelli* (see Appendix 5).

GULAR

Character 128

Plastral scale set 1, gulars: 0 = one medially situated pair of scales present; 1 = one medially situated single scale present (Joyce, 2007, ch. 91; and references therein).

Character 129

Plastral scale set 1, gulars: 0 = extending posteriorly onto entoplastron; 1 = limited to epiplastra only (modified from Matzke *et al.*, 2004, ch. 15).

Comments: In most turtles, the gulars extend posteriorly onto the entoplastron. In contrast, the gulars are limited to the epiplastra and do not extend posteriorly onto the entoplastron in *Mongolochelys efremovi*, *'Chengyuchelys' dashanpuensis*, *Siamochelys peninsularis*, *Xinjiangchelys latimarginalis*, *X. tianshanensis*, *X. qiguensis* and *Annemys levensis* (see Appendix 5).

EXTRAGULAR

Character 130

Plastral scale set 2, extragulars: 0 = present; 1 = absent (Joyce, 2007, ch. 92; and references therein).

Character 131

Medial contact of plastral scale set 2, extragulars: 0 = absent; 1 = present, extragulars contacting one another posterior to gulars (modified from Joyce, 2007, ch. 93).

Comments: Joyce (2007) coded an unordered multistate character for the absence/presence of a medial contact of the extragulars (medial contact absent/present, anterior to gulars/present, posterior to gulars). Within the context of the present analysis, as well as in that of Joyce (2007), a medial contact of the extragulars anterior to the gulars is only known in *Chelodina oblonga* and is consequently uninformative. Moreover, a medial contact of the extragulars anterior to the gulars should probably not be considered homologous to a medial contact posterior to gulars. Future studies should consider the medial contact of extragulars anterior to the gulars as a separate character. In the present analysis, *Chelodina oblonga* is scored as missing a medial contact of extragulars posterior to gulars (state 0).

Character 132

Anterior plastral tuberosities: 0 = present; 1 = absent (Joyce, 2007, ch. 94; and references therein).

Comments: The short epiplastral projections seen in *Chengyuchelys baenoides* (Danilov & Parham, 2008: fig. 2) are not considered homologous to the plastral tuberosities seen in *Odontochelys semitestacea*, *Proganochelys quenstedti*, *Palaeochersis talampayensis* and *Proterochersis robusta*.

INTERGULAR

Character 133

Plastral scale set 8, intergulars: 0 = absent; 1 = present (Joyce, 2007, ch. 95).

HUMERAL

Character 134

Plastral scale set 3, humerals: 0 = one pair present; 1 = two pairs present, subdivided by a plastral hinge (Joyce, 2007, ch. 96).

PECTORAL

Character 135

Plastral scale set 4, pectorals: 0 = present; 1 = absent (Joyce, 2007, ch. 97; and references therein).

ABDOMINAL

Character 136

Plastral scale set 5, abdominals: 0 = present; 1 = absent (modified from Joyce, 2007, ch. 98; and references therein).

Comments: Joyce (2007, ch. 98), following Meylan & Gaffney (1989, ch. 34), coded both the absence/presence of abdominals and their medial contact with one another as an ordered multistate character (present, in medial contact/present, medial contact absent/abdominals absent). This coding introduces unnecessary *a priori* assumptions: for example, the loss of the abdominals is assumed to have evolved through the reduction of these scales so that they do not meet one another medially. Such assumptions can be avoided by keeping the absence/presence of abdominals and the absence/presence of medial contact between these scales as two separate potential synapomorphies to be tested for congruence against other observations. The present coding corresponds to that of character 94 of Shaffer *et al.* (1997).

Character 137

Plastral scale set 5, abdominals: 0 = contact one another medially; 1 = absence of medial contact between abdominals (modified from Joyce, 2007, ch. 98; and references therein).

Comments: See character 136 for a discussion. The present coding corresponds to that of character 41 of Brinkman & Wu (1999). Taxa that have lost abdominals are scored inapplicable for this character.

ANAL

Character 138

Plastral scale set 7, anals: 0 = only cover parts of the xiphiplastra; 1 = overlap anteromedially onto the hypoplastra (Joyce, 2007, ch. 99; and references therein).

INFRAMARGINAL

Character 139

Inframarginal scales: 0 = present; 1 = absent (modified from Joyce, 2007, ch. 100; and references therein).

Comments: The presence and number of inframarginals has been variously discretized as a character by successive authors. Dryden (1988, ch. 46) simply coded the inframarginals as absent/present. Meylan & Gaffney (1989, ch. 35) considered the number of inframarginals (five to four/four to three/three to two), with obvious problems regarding the necessary mutual exclusivity between character states (see Freudenstein, 2005). Shaffer *et al.* (1997, ch. 101) coded only the absence/presence of a complete row of inframarginals, without differentiating the condition in panpleurodires where the inframarginals are lost and the condition in testudinoids where two pairs of inframarginals (axillaries and inguinals) are present. Hirayama *et al.* (2000, ch. 65) attempted to unify previously proposed codings into a multistate character (4 to 3 pairs/2 pairs, axillaries and inguinals/inframarginals absent). Joyce (2007, ch. 100) broadly followed this latter proposition in coding an unordered multistate character (more than two pairs, complete row of inframarginals/ two pairs present, limited contact between plastral scales and marginals/inframarginals absent, unlimited contact between plastral scales and marginals). However, all evidence suggests that the loss of inframarginals in panpleurodires is not homologous to the reduction to two pairs of inframarginals in testudinoids. In other words, these conditions probably result from two independent evolutionary processes and should not be coded as two states of the same character (e.g., Pleijel, 1995). Consequently, the present analysis codes two separate binary characters for the inframarginals (character 139 and 140).

Character 140
Inframarginals scales: 0 = complete row present; 1 = only two pairs present (axillary and inguinal), limited contact between plastral scales and marginals present (modified from Joyce, 2007, ch. 100; and references therein).
Comments: See character 139 for a discussion. Taxa that have lost the inframarginals are scored inapplicable for this character.

AXIAL SKELETON

CERVICAL RIBS

Character 141
Cervical ribs: 0 = large cervical ribs present; 1 = cervical ribs reduced or absent (Joyce, 2007, ch. 101; and references therein).
Comments: Joyce (2007) scored *Palaeochersis talampayensis* as having large cervical ribs, yet the recent redescription of the material by Sterli *et al.* (2007) states that no specimen has cervical ribs preserved. Consequently, *P. talampayensis* is scored unknown in the present analysis.

CERVICAL VERTEBRAE

Character 142
Position of the transverse processes: 0 = middle of the centrum; 1 = anterior end of the centrum (Joyce, 2007, ch. 102; and references therein).

Character 143

Posterior cervicals with strongly developed ventral keels: 0 = absent; 1 = present (Joyce, 2007, ch. 103; and references therein).

Character 144

Eighth cervical centrum significantly shorter than seventh: 0 = absent; 1 = present (Joyce, 2007, ch. 104; and references therein).

CERVICAL ARTICULATION

Character 145

Central articulations of cervical vertebrae: 0 = articulations not formed, cervical vertebrae amphicoelous or platycoelous; 1 = articulations formed, cervical vertebrae procoelous or opisthocoelous (Joyce, 2007, ch. 105; and references therein).

Characters 146 to 151 code for the shape of the articulation between successive centra of cervical vertebrae. Articular arrangements are given following the notation of Walther (1922) as implemented by Joyce (2007). This notation imitates the shape of the articular surfaces: the articulation between the centrum of the second cervical vertebra and that of the third is either convex anteriorly [i.e., 2(3] or concave anteriorly [i.e., 2)3]. Taxa that have amphicoelous or platycoelous cervical vertebrae are scored as inapplicable for these characters.

Character 146

Articulation between the centra of the second and third cervicals: 0 = 2(3; 1 = 2)3 (Joyce, 2007, ch. 106).

Character 147

Articulation between the centra of the third and fourth cervicals: 0 = 3(4; 1 = 3)4 (Joyce, 2007, ch. 107).

Character 148

Articulation between the centra of the fourth and fifth cervicals: 0 = 4(5; 1 = 4)5 (Joyce, 2007, ch. 108).

Character 149

Articulation between the centra of the fifth and sixth cervicals: 0 = 5(6; 1 = 5)6 (Joyce, 2007, ch. 109).

Character 150

Articulation between the centra of the sixth and seventh cervicals: 0 = 6(7; 1 = 6)7 (Joyce, 2007, ch. 110).

Character 151

Articulation between the centra of the seventh and eighth cervicals: 0 = 7(8; 1 = 7)8 (Joyce, 2007, ch. 111).

Character 152

Articulation between the eighth cervical and the first dorsal vertebrae: 0 = along the vertebral centra and zygapophyses; 1 = along zygapophyses only (modified from Joyce, 2007, ch. 112).

Comments: Joyce (2007) coded an unordered multistate character for the articulation between the eighth cervical and first dorsal vertebrae (8(dorsal/8)dorsal/contact only at zygapophyses). The majority of turtles have an 8)dorsal articulation, whereas in tryonichids the vertebrae only meet along the zygapophyses (ibid.: 45). *Adocus beatus* is unique among turtles in having an 8(dorsal articulation and this state is uninformative in the context of the present analysis. Consequently, the character has been redefined to focus only on the loss of central vertebral articulation in trionychids.

DORSAL RIBS

Character 153

Length of the first dorsal rib: 0 = long, extends full length of the first costal and may even contact the peripherals distally; 1 = short, extends less than halfway across the first costal (modified from Dryden, 1988, ch. 37; Gaffney *et al.*, 1991, ch. 35; Rougier *et al.*, 1995, ch. 49; Gaffney, 1996, ch. 32; Brinkman & Wu, 1999, ch. 32; Hirayama *et al.*, 2000, ch. 45; Gaffney *et al.*, 2007, ch. 87; Joyce, 2007, ch. 113; Sterli *et al.*, 2007, ch. 72).

Comments: The first dorsal rib of turtles does not fuse to the costal bones in contrast to the other dorsal ribs, but simply extends over the visceral surface of the first costal. In stem turtles, as well as numerous basal crown-group species, the first dorsal rib is of similar length to the remaining dorsal ribs, extending the full length of the first costal and often contacting the peripherals laterally. In more derived turtles, including all extant forms, the first dorsal rib is considerably reduced in length and extends less than halfway across the first costal. However, in some taxa (e.g., *Platychelys oberndorferi* and some baenids), the morphology is somewhat complicated by the development of a large axillary buttress that prevents the first dorsal rib from extending the full length of the first costal bone, despite the fact that the rib is well developed (Joyce, 2007: 45). Joyce (2007, ch. 113) tried to encompass the latter condition in coding an unordered multistate character (first dorsal rib long, extends full length of first costal/intermediate, in contact with axillary buttress/intermediate to short, extends less than halfway across the first costal). Coded that way, this character becomes partly dependent on character 119 of the present analysis (character 84 of Joyce, 2007), which codes for the contacts of the axillary buttress (see above). Moreover, a survey of the taxa included in the analysis shows that the development of the axillary buttress is highly variable among turtles and that it cannot be used as a stable landmark to score the length of the first dorsal rib. Sterli *et al.* (2007, ch. 72) also coded the length of the first dorsal rib as a multistate character (extends to peripherals or nearly so and lies close to the tip of the axillary buttress/extends more than halfway across the first costal, but is far from the axillary buttress/extends less than halfway across the first costal). The intermediate state of Sterli *et al.* (2007) is only present in *Notoemys laticentralis* and is consequently uninformative in both their analysis and the present study. Neither the coding of Joyce (2007) nor that of Sterli *et al.* (2007) appears to be appropriate. The present character is derived from Dryden (1988, ch. 37), Gaffney *et al.* (1991, ch. 35), Gaffney (1996, ch. 32), Brinkman & Wu (1999, ch. 32) and Gaffney *et al.* (2007, ch. 87), and distinguishes taxa with a long first dorsal rib from taxa in which the rib is significantly reduced. Taxa with a well developed axillary buttress, which prevents the rib from extending the full length of the first costal, are scored state 0 because the first dorsal rib is always well developed in length in those taxa and it would certainly run the full length of the first costal if it was not for the buttress.

Character 154

Contact of dorsal ribs 9 and 10 with costals: 0 = present; 1 = absent (Joyce, 2007, ch. 114; and references therein).

Character 155

Dorsal rib 10: 0 = long, spanning full length of costals and contacting peripherals distally; 1 = short, not spanning farther distally than pelvis (Joyce, 2007, ch. 115; and references therein).

Comments: In contrast to Joyce (2007; state 1), *Santanachelys gaffneyi* is scored unknown because published description does not allow indisputable scoring of this character (Hirayama, 1998).

Character 156

Contact between dorsal vertebrae and dorsal ribs: 0 = transverse processes of all dorsal vertebrae in the middle or anterior part of the vertebral centra; 1 = dorsal ribs in contact with two successive vertebral centra (NEW - derived from Rieppel & Reisz, 1999; Li *et al.*, 2008; Joyce *et al.*, 2009).

Comments: All turtles, with the notable exception of *Odontochelys semitestacea*, are characterised by a peculiar relationship between the dorsal vertebral centra and ribs: each dorsal rib contacts the vertebrae on the boundary between two successive centra (Hoffstetter & Gasc, 1969; Rieppel & Reisz, 1999: 15; Joyce *et al.*, 2009: 509; see also Chapter 2). This apparently results from the forward migration by half a segment of neural arches in the dorsal region of the vertebral column (Rieppel & Reisz, 1999: 14; and references therein). In *Odontochelys semitestacea* (Li *et al.*, 2008: 497-498) and the majority of other reptiles (e.g., Romer, 1956), the transverse process of each dorsal vertebra is located around the middle of the centrum. According to Joyce *et al.* (2009), the contact of dorsal ribs with two successive centra is only incipient in the Norian turtle *Chinlechelys tenertesta* (not included in the present analysis given the fragmentary nature of the material). According to Gaffney (1990: 119) this articulation between dorsal ribs and two successive centra "occurs in all turtles *[known at that time]* to some extent but usually the posterior thoracics tend to lose the articulation with the posterior ribs and maintain a complete articulation with their own rib anteriorly" (see also Hoffstetter & Gasc, 1969). This is confirmed by *Palaeochersis talampayensis* in which dorsal ribs 6 through 9 articulate with their own centrum, whereas at least dorsal ribs 2 and 10, the others being lost, articulate with two successive centra (Sterli *et al.*, 2007: 32 and fig. 8).

DORSAL VERTEBRAE

Character 157

Anterior articulation of the first dorsal centrum: 0 = faces at most slightly anteroventrally; 1 = faces strongly anteroventrally (Joyce, 2007, ch. 116; and references therein).

CHEVRONS

Character 158

Chevrons: 0 = present on nearly all caudal vertebrae; 1 = absent, or only poorly developed, along the posterior caudal vertebrae (Joyce, 2007, ch. 117; and references therein).

CAUDAL VERTEBRAE

Character 159

Tail club: 0 = present; 1 = absent (Joyce, 2007, ch. 118; and references therein).

Character 160

Caudal centra: 0 = amphicoelous; 1 = procoelous or opisthocoelous (Sterli, 2008, ch. 130; and references therein).

Comments: The evolution of the caudal vertebral articulations of turtles is very complex and successive authors have tried to anatomise it in many ways (see Joyce, 2007: 47; and references therein). For example, Joyce (2007, ch. 119) coded an unordered multistate character regrouping, according to him, the four basic patterns of caudal vertebral articulations found in turtles (all centra amphicoelous/all centra procoelous/all centra opisthocoelous/anterior centra procoelous, posterior centra opisthocoelous). He also suggested (ibid.: 47) that a condition with opisthocoelous anterior centra and procoelous posterior centra might be present in *Meiolania platyceps*. Beyond the problems of unwarranted character state homology, the mere repartition of the different states suggests a high level of homoplasy resulting in a very complex evolutionary history (see Joyce, 2007: 47). Moreover, characters related to caudal vertebral articulation are often difficult to score for fossil taxa, because caudal vertebrae are sparsely preserved and complete caudal column very rare. In this context, the simple coding proposed by Sterli (2008, ch. 130), although not entirely satisfactory, is preferred here. This coding distinguishes taxa with amphicoelous caudal vertebrae from those with formed caudal articulations (i.e., procoelous and/or opisthocoelous).

GIRDLES

PECTORAL GIRDLE

Character 161

Morphology of the scapulocoracoid: 0 = horizontal blade with a dorsal process, not triradiate; 1 = triradiate in shape, with the development of an acromial process (Sterli *et al.*, 2007, ch. 76; Sterli, 2008, ch. 131; and references therein).

Comments: The present study disagrees with Sterli *et al.* (2007) and Sterli (2008) in the scoring of *Proganochelys quenstedti* and *Palaeochersis talampayensis*. In both species the morphology of the scapulocoracoid is similar (see Sterli *et al.*, 2007: 36) and there is an incipient acromial process, so that the pectoral girdle of these species is indeed triradiate in shape (state 1). Li *et al.* (2008) described the acromial process as missing in *Odontochelys semitestacea*, but the pectoral girdle of this species does not appear to be fundamentally different from that of *Proganochelys quenstedti* and a similarly developed acromial process appears to be present (Li *et al.*, 2008: fig. 3c). The acromial process of turtles is believed not to be homologous with the acromial process found in pareiasaurs (deBraga & Rieppel, 1997: 302).

CLEITHRUM

Character 162

Cleithrum: 0 = present; 1 = absent (modified from Joyce, 2007, ch. 120; and references therein).

Comments: Joyce (2007) coded an ordered multistate character for the absence/presence and contacts of the cleithrum in turtles (present, in contact with the carapace/present, contact with carapace absent/absent). According to the coding strategy followed herein (see above) and in order to allow the scoring of non-chelonian outgroups which do not have shells, the present analysis codes two separate binary characters for the cleithrum (characters 162 and 163). Here, I follow the proposal of Joyce *et al.* (2006) that the epiplastral processes of turtles are indeed cleithra (see Chapter 2). The arguments expressed by Joyce *et al.* (2006) are based on good evidence and it appears reasonable to assume they are accurate. However, these arguments are considered ambiguous by others (e.g., Rieppel, 2008). Whether the so-called 'epiplastral process' of turtles indeed corresponds to the cleithrum of other amniotes or to a mere dorsal expansion of the epiplastron (i.e., of the clavicle) is not important for the purpose of the present analysis. This question would be important however in the context of an analysis of the relationships of turtles within amniotes, notably because the cleithrum is undoubtedly lost in crown-group diapsids (Sauria) and because an inaccurate primary homology assessment might support false relationships for turtles.

Character 163

Osseous contact of cleithrum with carapace: 0 = present; 1 = absent (modified from Joyce, 2007, ch. 120; and references therein).

Comments: See character 162 for a discussion. Li *et al.* (2008) scored *Odontochelys semitestacea* as having a contact of the cleithrum with the carapace, but this contact cannot exist in a form in which the carapace is almost non-existent. Consequently, *Odontochelys semitestacea* is scored inapplicable in the present analysis. Taxa that have lost the cleithrum are scored inapplicable for this character.

SCAPULA

Character 164

Length of acromial process: 0 = less than one half the length of scapular process; 1 = more than one half the length of scapular process (Joyce, 2007, ch. 121; and references therein).

Comments: Following Joyce & Sterli (pers. comm., 2007), the scoring of *Kayentachelys aprix* has been changed from unknown to state 0.

Character 165

Shape of acromial process: 0 = triradiate in section, acromial ridge present; 1 = rod-like (Joyce, 2007, ch. 122; Sterli *et al.*, 2007, ch. 75; and references therein).

Character 166

Glenoid neck on scapula: 0 = absent; 1 = present (Joyce, 2007, ch. 123; and references therein).

CORACOID

Character 167

Coracoid foramen: 0 = present; 1 = absent (Joyce, 2007, ch. 124; and references therein).

PELVIS

Character 168

Sutural articulation of pelvis to shell: 0 = absent; 1 = present (Joyce, 2007, ch. 125; and references therein).

Comments: Following the publication of Joyce (2007), Sterli *et al.* (2007) have confirmed that the pelvis of *Palaeochersis talampayensis* is sutured to the shell, so this species is scored state 1 in the present analysis. As suggested by Joyce (2007: 48), the condition in *Proterochersis robusta* remains ambiguous and this species is scored unknown for this character.

ILIUM

Character 169

Elongated iliac neck: 0 = absent; 1 = present (Joyce, 2007, ch. 126; and references therein).

Character 170

Shape of the ilium articular site on the visceral surface of the carapace: 0 = narrow and pointed posteriorly; 1 = oval (Joyce, 2007, ch. 128; and references therein).

Character 171

Posterior notch in acetabulum: 0 = absent; 1 = present (Joyce, 2007, ch. 129; and references therein).

ISCHIUM

Character 172

Ischial contacts with plastron: 0 = contact via a large central tubercle; 1 = contact via two separate ischial processes (Joyce, 2007, ch. 130; and references therein).

Comments: The morphology of *Odontochelys semitestacea* regarding this character is unclear. Li *et al.* (2008) described a posterior ischial tubercle in this species, but they also stated that the ischium is located behind the plastron so that a contact between the ischium and plastron is absent. This morphology may be the result of *post-mortem* deformation (Li *et al.*, 2008: fig. 2a, b). *Odontochelys semitestacea* is scored unknown in the present analysis. The ischial morphology in *Palaeochersis talampayensis* appears to be different from that of other turtles: the posteromedian part of the ischium is sutured to the xiphiplastron, but no central tubercle is present and the lateral ischial processes do not appear to contact the plastron (see Sterli *et al.*, 2007: 40). Consequently, this species is scored unknown in the present analysis.

HYPOISCHIUM

Character 173

Hypoischium: 0 = present; 1 = absent (Joyce, 2007, ch. 131; and references therein).

Comments: *Odontochelys semitestacea*, *Proganochelys quenstedti* and *Palaeochersis talampayensis* are the only turtles known to have hypoischia, i.e. single or paired postpelvic ossifications that articulate with the ischia anteriorly. The homology between these chelonian postpelvic ossifications and the structures termed hypoischia in some other reptiles, especially lizards, is not well established (Romer, 1956; Gaffney, 1990). Consequently, all of the outgroups are scored unknown for the present character.

LIMBS

FIBULA

Character 174

Fibula: 0 = bowed away from tibia; 1 = straight, not bowed away from tibia (deBraga & Rieppel, 1997, ch. 145; Müller, 2004, ch. 149; Hill, 2005, ch. 281).

Comments: This character is included for outgroup comparison. The plesiomorphic condition among amniotes is a fibula that is bowed away from the tibia (deBraga & Rieppel, 1997: 311). In turtles, Araeoscelidia and Neodiapsida, the fibula is straight and not bowed away from the tibia.

AUTOPODIUM

Character 175

Phalangeal formula of the manus: 0 = 2-3-4-4-3 or more; 1 = digits 2 to 5 with three phalanges or less (modified from Joyce, 2007, ch. 132; and references therein).

Comments: Character 132 of Joyce (2007) originally coded the phalangeal formula as a binary character (most digits with three elongate phalanges/most digits with two short phalanges). In the context of the present analysis, which includes *Odontochelys semitestacea* and non-chelonian outgroups, this character is not appropriate. The plesiomorphic reptilian condition is a phalangeal formula of 2-3-4-5-3, or exceptionally of 2-3-4-4-3 (Romer, 1956). *Odontochelys semitestacea* is unique among turtles in having a manual phalangeal formula of 2-3-4-4-3 (Li *et al.*, 2008). Within remaining turtles, the phalangeal formula of the manus varies greatly but generally does not exceed 2-3-3-3-3 and is even reduced to 2-2-2-2-1 in the most extreme case of terrestrial adaptation (Romer, 1956: 407). In the present analysis, the phalangeal formula of the manus has been separated into two binary characters. Character 175 codes for the acquisition of the reduced phalangeal formula consisting of most digits having three phalanges or less, which unites all turtles with the exception of *Odontochelys semitestacea*. Character 176 (see below) concerns the acquisition of an even more reduced phalangeal formula of the manus where most digits have only two short phalanges, which is interpreted to be a terrestrial adaptation (Joyce & Gauthier, 2004).

Character 176
Reduced phalangeal formula of the manus, all digits with only one or two short phalanges: 0 = absent; 1 = present (modified from Joyce, 2007, ch. 132; and references therein).
Comments: See character 175 for a discussion.

Character 177
Paddles: 0 = absent; 1 = present (modified from Joyce, 2007, ch. 133; and references therein).
Comments: Joyce (2007) coded the development of paddles as an ordered multistate character (absent/short paddles/elongate paddles). However, Joyce (2007) was not explicit regarding the boundary between short and elongate paddles and this is a distinction that is not always easy to make for fossil taxa. For these reasons, only the absence/presence of paddles is considered here. If future workers want to code the relative development of the paddles, it should be coded as a separate character (see Coding strategy, above). Paddles are characterised by immobile digits bound together by connective tissue (Joyce, 2007: 52). Hirayama (1998: 705) clearly stated that *Santanachelys gaffneyi* retains movable digits, as in freshwater turtles, so that paddles, strictly speaking, are absent. This departs from Joyce (2007) who scored *Santanachelys gaffneyi* as possessing short paddles.

Character 178
Claw of the fifth digit of the pes: 0 = present; 1 = absent (Joyce, 2007, ch. 135).

Rejected characters

Eight characters from both Joyce (2007) and Sterli (2008) have been omitted from the present analysis. These characters were either uninformative, redundant, non-discrete, impossible to score for fossil taxa, or their scoring was not reproducible. A specific rationale is provided for each of these characters in Appendix 6.

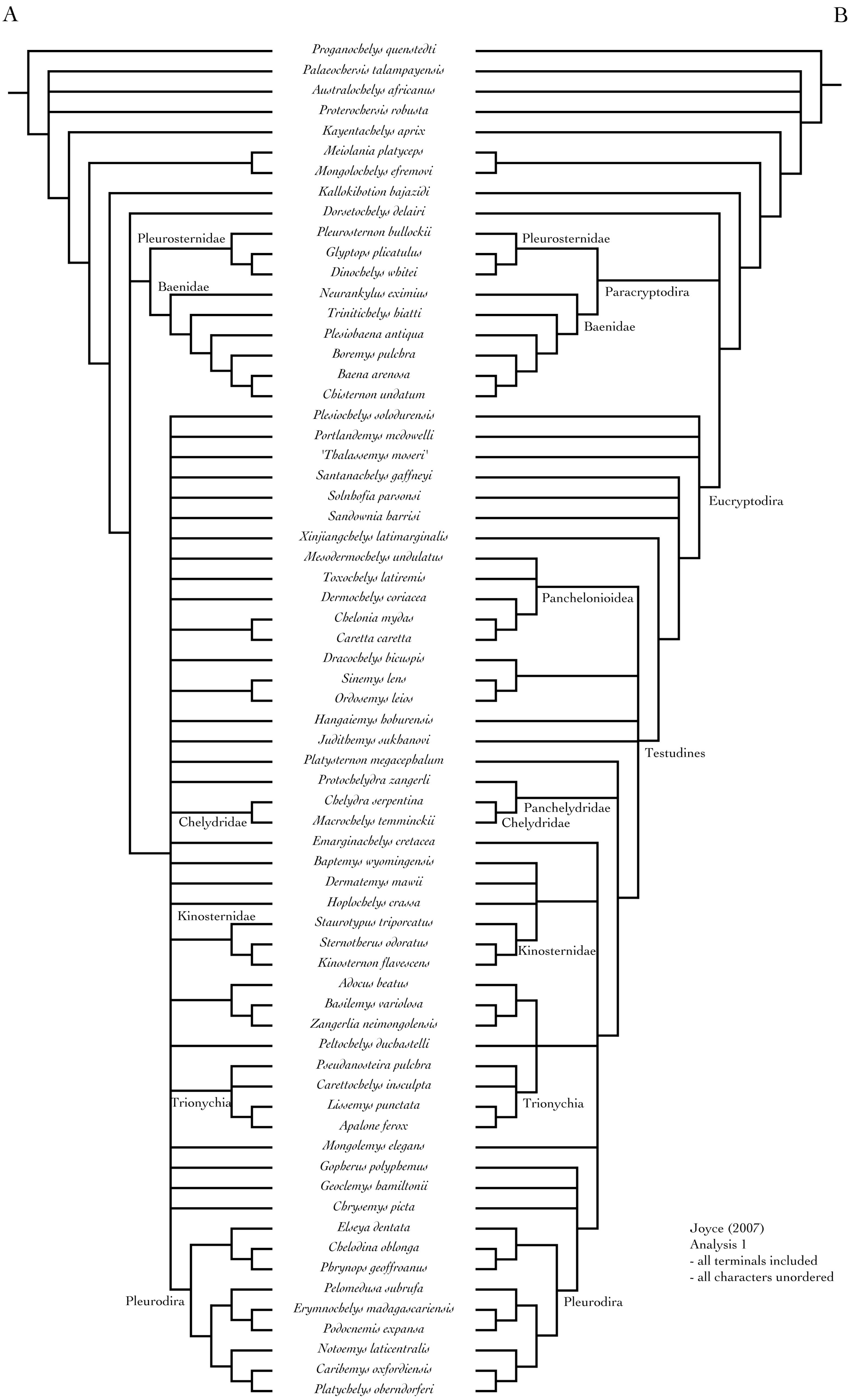


Figure 5.2—Phylogenetic interrelationships of turtles according to Joyce (2007) - all terminal taxa included and all characters treated unordered (analysis 1). A, strict consensus tree; B, Adams consensus tree.

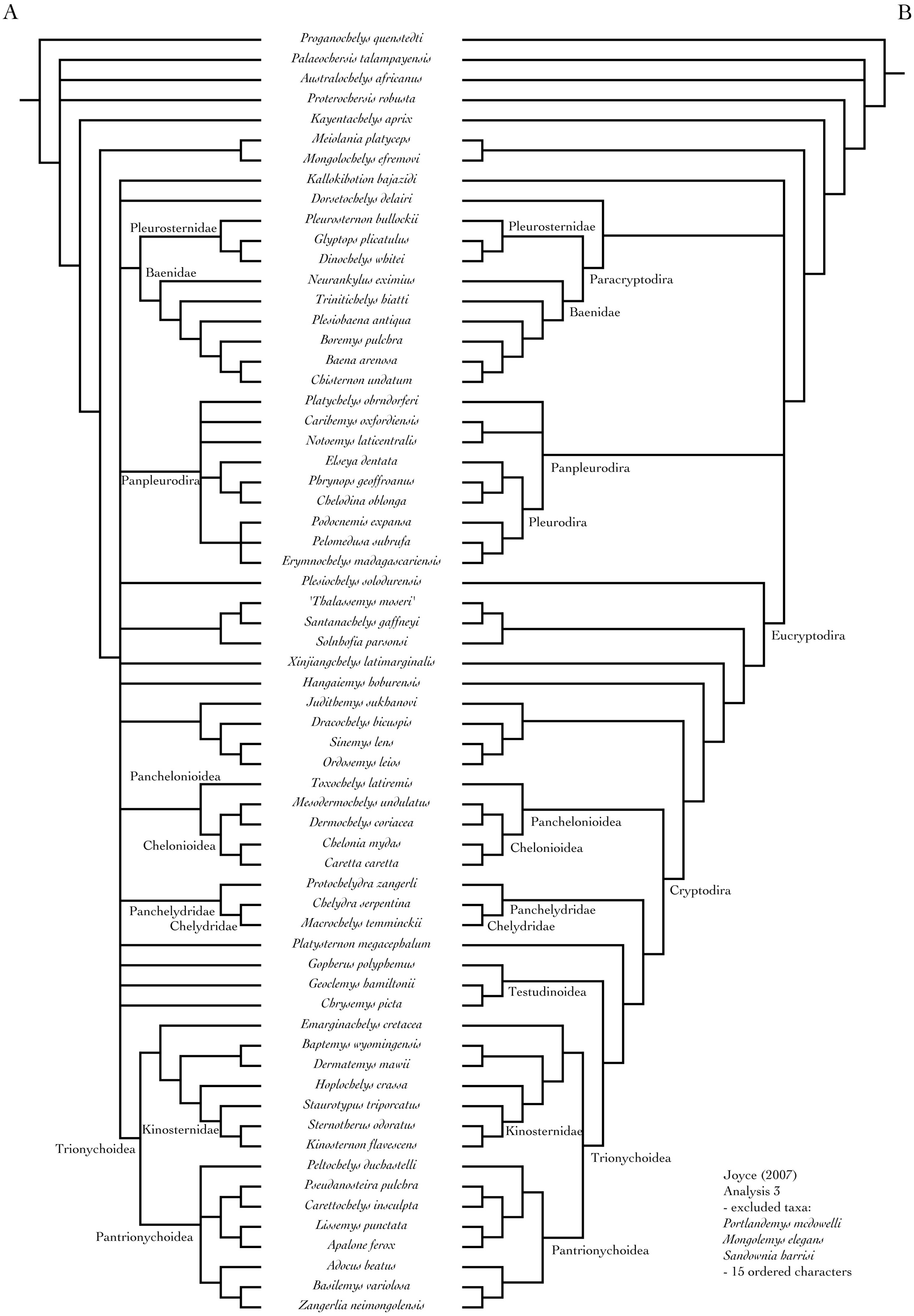


Figure 5.3—Phylogenetic interrelationships of turtles according to Joyce (2007) - rogue taxa (*Portlandemys mcdowelli*, *Mongolemys elegans* and *Sandownia harrisi*) excluded and 15 characters ordered (analysis 3). A, strict consensus tree; B, Adams consensus tree.

CLADISTIC ANALYSIS

Methods

The data matrix (Appendix 5) of 178 binary characters scored for 93 taxa (including 64 fossil and 22 living species of turtles and 7 fossil outgroups) was assembled with MacClade 4.01 (Maddison & Maddison, 2001). The parsimony analyses were performed using PAUP 4.0b10 (Swofford, 2002). Trees were rooted on the seven outgroups (see Choice of the outgroups, above). Characters were considered reversible and equally-weighted. Branches were set to collapse if their minimal length was zero. Due to computational limitations, non-strategic heuristic searches with PAUP failed to find the shortest trees before the memory limit was hit. Consequently, two distinct strategic searches were implemented in order to analyse this data matrix. The first analysis consisted of a two-step process: a heuristic search with 100 randomly seeded replicates, saving 20 trees per replicate, was performed in order to obtain a set of shortest trees, and subsequently these trees were used as the starting point for a tree bisection-reconnection (TBR) branch-swapping algorithm in order to fully explore 'tree space'. The second analysis used the parsimony ratchet method (Nixon, 1999). This method, originally designed for the analysis of large data sets, uses TBR branch-swapping and an algorithm that alternatively reweighs a randomly selected percentage of the characters, allowing the search to 'jump' between 'tree islands' and consequently to explore tree space more thoroughly. In the present analysis, the parsimony ratchet was implemented using PAUPRat (Sikes & Lewis, 2001) and set to perform 200 iterations and reweight 15% of characters. Nixon (1999) and Goloboff (1999) argue that the consensus of the combined results of a sufficient number of parsimony ratchet searches (i.e., between 10 and 20) should be identical to the consensus of all the shortest trees for a given matrix. In the present analysis, 20 independent parsimony ratchet searches were performed. Bremer support values (= decay indices) were calculated with PRAP 2.0b3 (Müller, 2004, 2007), which also uses the parsimony ratchet method (200 iterations, 15% reweighting, 20 independent searches).

The following discussion of the results (see below) is based mostly on strict and Adams consensus trees, which retain only those components that are unambiguously supported by the data set. In contrast, the majority-rule consensus tree retains all components that are found in more than a preset proportion (usually 50%) of the most parsimonious trees (MPT). Interrogations could be raised regarding the legitimacy of those components only supported by 60 or 70% of the MPT. More importantly, concerns have been raised regarding the interpretation of majority-rule consensus trees (Wilkinson, 1995a; Wilkinson & Benton, 1996; Sharkey & Leathers, 2001; Sumrall *et al.*, 2001). Sharkey & Leathers (2001) and especially Sumrall *et al.* (2001) demonstrated that, when ambiguity is rampant within a data matrix because of missing data, biases in the majority-rule consensus method may drive the tree toward the most ambiguous set of topologies. In the case of taxa that can assume various, regionally distinct positions within the MPT, the more these taxa have ambiguous relationships within one set of topologies, the more this set is likely to be the one selected to figure in the majority-rule consensus tree (Sumrall *et al.*, 2001). This problem is particularly relevant for palaeontological studies because of the high proportion of missing data that results from the use of fossil taxa. The interpretation of Adams consensus trees can also be delicate because taxa with ambiguous relationships are relocated to the most inclusive node they have in common. This can produce components that do not occur in any of the MPT (e.g., Kitching *et al.*, 1998) and it may be difficult to identify those spurious components. The safe taxonomic reduction (Wilkinson, 1995c) and strict reduced consensus (Wilkinson, 1994, 1995b) methods were used to identify all strictly supported relationships and taxa with ambiguous relationships. Safe taxonomic reduction (STR) is a simple method to identify those taxa which exclusion prior to the analysis does not alter the relationships among remaining taxa (Wilkinson, 2003). The strict reduced consensus (SRC) method identifies all strictly supported relationships for a given data set by overcoming the insensitivity of the strict reduced consensus method and the sometimes ambiguous interpretation of the Adams consensus tree (Wilkinson, 2003). Safe taxonomic reduction was implemented using TAXEQ3 (Wilkinson, 2001), whereas strict reduced consensus trees were computed using RadCon 1.1.6 (Thorley & Page, 2000).

Results

The analysis of the complete data matrix following the first search methodology (heuristic search with 100 replicates, saving 20 trees per replicate, following by TBR branch-swapping using these trees as starting point; see above) resulted in 73,020 equally parsimonious trees after filtering. The second search methodology (combined results of 20 independent parsimony ratchet searches; see above) resulted in 228 equally parsimonious trees after filtering. The trees from both searches are 433 steps long and they have a Consistency Index (CI) of 0.4111 and a Retention Index (RI) of 0.8176. The low CI accounts for the high level of homoplasy within the data matrix, but the rather high RI indicates that a significant part of this similarity can be interpreted as synapomorphy (i.e., it is phylogenetically informative). These indices are very similar to those obtained by Joyce (2007) for his three analyses, the main divergence rests in the slightly lower CI of the present study (0.4111 against 0.46-0.47). This can be at least partly explained by the increased number of characters and taxa (Kitching *et al.*, 1998). In the interest of comparison, the strict and Adams consensus trees computed by Joyce (2007) in his first and third analyses are reproduced here (Figs. 5.2 and 5.3). The two search methodologies produce exactly the same strict and Adams consensus tree, which confirms the effectiveness of each strategy. The strict consensus tree is 557 steps long and has a CI of 0.3196 and a RI of 0.7289 (Fig. 5.4A). Joyce (2007) did not provide either the length or the indices of any of his consensus trees, but, as a matter of comparison, the indices of the strict consensus trees computed by Anquetin *et al.* (2009) following the protocol of the third analysis of Joyce (2007) were as follows: for their first analysis (data matrix of Joyce, 2007 plus *Eileanchelys waldmani*), CI = 0.360 and RI = 0.713; for their second analysis (inclusion of

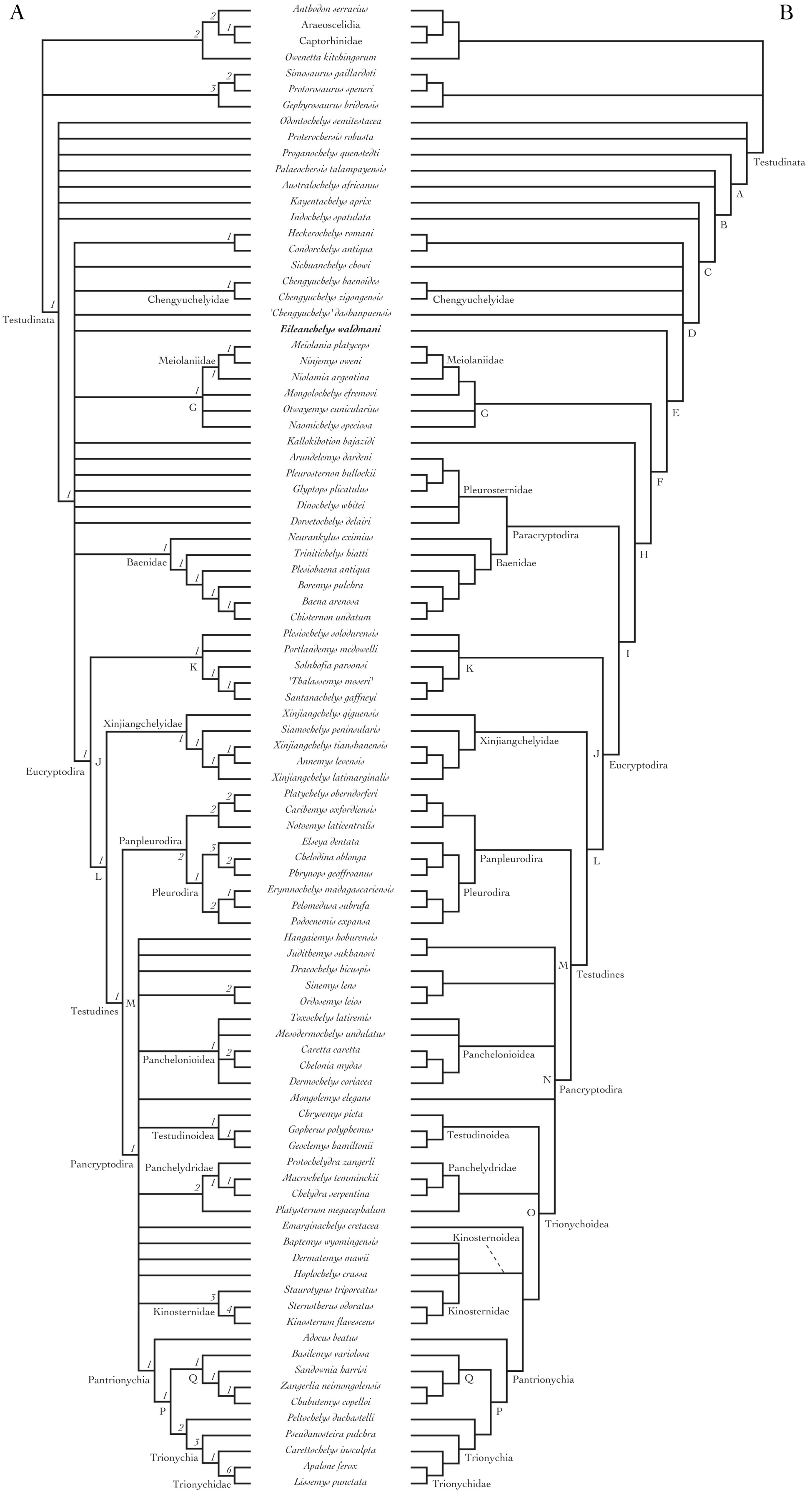
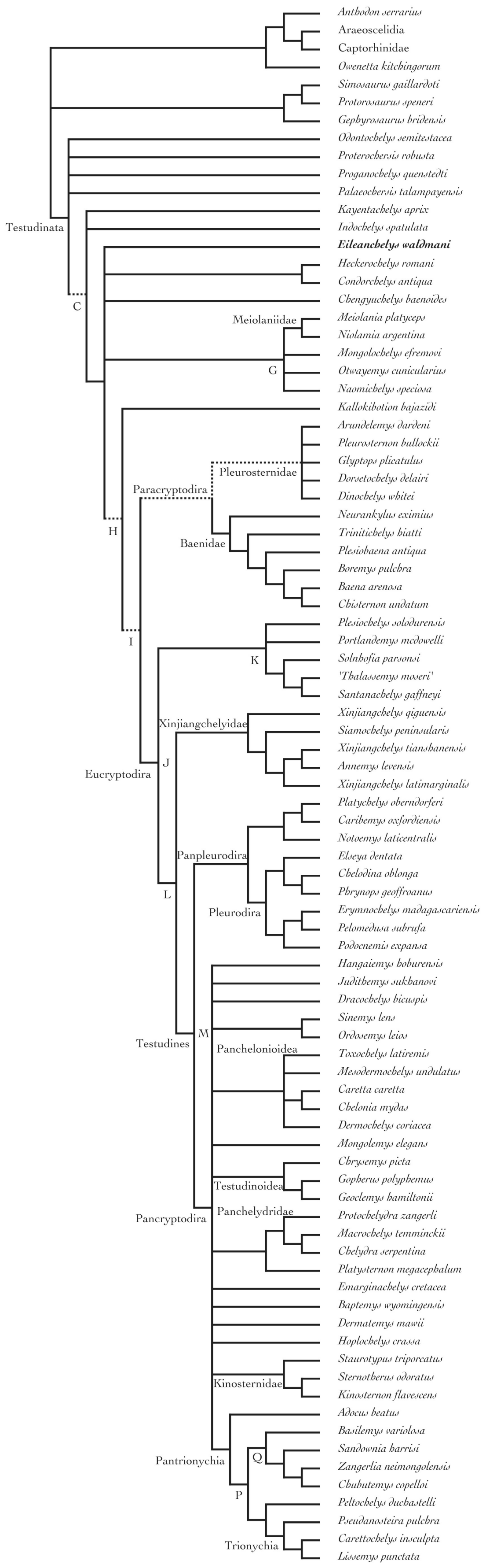

A
B
Anthodon serrarius
Araeoscelidia
Captorhinidae
Owenetta kitchingorum
Simosaurus gaillardoti
Protorosaurus speneri
Gephyrosaurus bridensis
Odontochelys semitestacea
Proterochersis robusta
Proganochelys quenstedti
Palaeochersis talampayensis
Australochelys africanus
Kayentachelys aprix
Indochelys spatulata
Heckerochelys romani
Condorchelys antiqua
Sichuanchelys chowi
Chengyuchelys baenoides
Chengyuchelys zigongensis
'Chengyuchelys' dashanpuensis
Eileanchelys waldmani
Meiolania platyceps
Ninjemys oweni
Niolamia argentina
Mongolochelys efremovi
Otwayemys cunicularius
Naomichelys speciosa
Kallokibotion bajazidi
Arundelemys dardeni
Pleurosternon bullockii
Glyptops plicatulus
Dinochelys whitei
Dorsetochelys delairi
Neurankylus eximius
Trinitichelys hiatti
Plesiobaena antiqua
Boremys pulchra
Baena arenosa
Chisternon undatum
Plesiochelys solodurensis
Portlandemys mcdowelli
Solnhofia parsonsi
'Thalassemys moseri'
Santanachelys gaffneyi
Xinjiangchelys qiguensis
Siamochelys peninsularis
Xinjiangchelys tianshanensis
Annemys levensis
Xinjiangchelys latimarginalis
Platychelys oberndorferi
Caribemys oxfordiensis
Notoemys laticentralis
Elseya dentata
Chelodina oblonga
Phrynops geoffroanus
Erymnochelys madagascariensis
Pelomedusa subrufa
Podocnemis expansa
Hangaiemys hoburensis
Judithemys sukhanovi
Dracochelys bicuspis
Sinemys lens
Ordosemys leios
Toxochelys latiremis
Mesodermochelys undulatus
Caretta caretta
Chelonia mydas
Dermochelys coriacea
Mongolemys elegans
Chrysemys picta
Gopherus polyphemus
Geoclemys hamiltonii
Protochelydra zangerli
Macrochelys temminckii
Chelydra serpentina
Platysternon megacephalum
Emarginachelys cretacea
Baptemys wyomingensis
Dermatemys mawii
Hoplochelys crassa
Staurotypus triporcatus
Sternotherus odoratus
Kinosternon flavescens
Adocus beatus
Basilemys variolosa
Sandownia harrisi
Zangerlia neimongolensis
Chubutemys copelloi
Peltochelys duchastelli
Pseudanosteira pulchra
Carettochelys insculpta
Apalone ferox
Lissemys punctata
Testudinata
Chengyuchelyidae
Meiolaniidae
G
Baenidae
K
Xinjiangchelyidae
Eucryptodira
J
Panpleurodira
L
Pleurodira
Testudines
M
Panchelonioidea
Testudinoidea
Pancryptodira
Panchelydridae
Kinosternidae
Pantrionychia
Q
P
Trionychia
Trionychidae
Testudinata
A
B
C
D
Chengyuchelyidae
Meiolaniidae
G
E
F
Pleurosternidae
Paracryptodira
H
Baenidae
I
K
Xinjiangchelyidae
J
Eucryptodira
Panpleurodira
L
Pleurodira
M
Testudines
Panchelonioidea
N
Pancryptodira
Testudinoidea
Panchelydridae
O
Trionychoidea
Kinosternoidea
Kinosternidae
Pantrionychia
Q
P
Trionychia
Trionychidae

Figure 5.4—(previous page) Phylogenetic interrelationships of turtles resulting from the analysis of the complete data set. A, strict consensus tree (557 steps; CI=0.3196; RI=0.7289) of 73,020 MPT; B, Adams consensus tree (450 steps; CI=0.3956; RI=0.8054) of 73,020 MPT. Capital letters label unnamed clades, whereas numbers on the strict consensus tree correspond to Bremer support values.

Heckerochelys romani and *Condorchelys antiqua*), CI = 0.333 and RI = 0.683. These indices are broadly similar to those of the present study and the slightly lower CI found herein is probably the consequence of the increase number of characters and taxa (Kitching *et al.*, 1998). Overall, Bremer support values are relatively low (i.e., 1 or 2), with the exception of some extant clades (i.e., chelids, kinosternids and Trionychia; see Fig. 5.4A). The Adams consensus tree is 450 steps long and has a CI of 0.3956 and a RI of 0.8054 (Fig. 5.4B).

The analysis of the data matrix with TAXEQ3 (Wilkinson, 2001) revealed that *Australochelys africanus*, *Ninjemys oweni*, *Chengyuchelys zigongensis* and *Apalone ferox* could be discarded without altering the relationships among remaining taxa. Furthermore, this analysis indicated that these four species would arise from the same node as their index taxon (i.e., *Palaeochersis talampayensis*, *Meiolania platyceps*, *Chengyuchelys baenoides* and *Lissemys punctata*, respectively) in any MPT. If the four taxa identified by STR are pruned *a posteriori* from the 73,020 MPT obtained above, 29,304 trees remain after condensing (i.e., collapse branches if minimal branch-length is zero) and filtering. Additionally, *Sichuanchelys chowi* and *'Chengyuchelys' dashanpuensis*, two poorly scored species from the Middle Jurassic of China, have been identified as very unstable taxa within the present analysis. If these two species are pruned *a posteriori* from the 29,304 MPT, only 1998 trees (432 steps, CI = 0.4120, RI = 0.8107) remain after condensing and filtering, which confirms the unstable nature of these taxa. The strict consensus tree of these 1998 MPT (498 steps, CI = 0.3574, RI = 0.7615; Fig. 5.5) presents a slightly better resolution of basal turtle relationships compared to the strict consensus tree of the 73,020 MPT (Fig. 5.4A). However, the Adams consensus tree is identical to that computed with the 73,020 MPT (Fig. 5.4B), minus pruned taxa. Strict reduced consensus (SRC) were computed for these 1998 MPT in order to identify remaining taxa with ambiguous relationships. The SRC analysis can be summarised by ten SRC trees in which ambiguous taxa are alternatively pruned to reveal unambiguous relationships (Fig. 5.6). As usual (Wilkinson, 2003), the first SRC tree corresponds to the strict consensus tree (Fig. 5.5). These results are discussed below.

Figure 5.5—(next page) Strict consensus tree (498 steps; CI=0.3574; RI=0.7615) of 1998 MPT remaining after pruning of STR taxa (*Australochelys africanus*, *Ninjemys oweni*, *Chengyuchelys zigongensis* and *Apalone ferox*, see text), *Sichuanchelys chowi* and *'Chengyuchelys' dashanpuensis*. The Adams consensus of these 1998 MPT is identical to that computed from the 73,020 MPT (see Fig. 5.4B), minus pruned taxa. Dashed branches correspond to gain of resolution.


Anthodon serrarius
Araeoscelidia
Captorhinidae
Owenetta kitchingorum
Simosaurus gaillardoti
Protorosaurus speneri
Gephyrosaurus bridensis
Odontochelys semitestacea
Proterochersis robusta
Proganochelys quenstedti
Palaeochersis talampayensis
Kayentachelys aprix
Testudinata
Indochelys spatulata
Eileanchelys waldmani
Heckerochelys romani
Condorchelys antiqua
Chengyuchelys baenoides
C
Meiolaniidae
Meiolania platyceps
Niolamia argentina
Mongolochelys efremovi
G
Otwayemys cunicularius
Naomichelys speciosa
Kallokibotion bajazidi
Arundelemys dardeni
Pleurosternon bullockii
Glyptops plicatulus
Pleurosternidae
Dorsetochelys delairi
Paracryptodira
Dinochelys whitei
Neurankylus eximius
H
Trinitichelys hiatti
Baenidae
Plesiobaena antiqua
Boremys pulchra
Baena arenosa
Chisternon undatum
Plesiochelys solodurensis
Portlandemys mcdowelli
I
K
Solnhofia parsonsi
'Thalassemys moseri'
Santanachelys gaffneyi
Xinjiangchelys qiguensis
Xinjiangchelyidae
Siamochelys peninsularis
Xinjiangchelys tianshanensis
J
Annemys levensis
Eucryptodira
Xinjiangchelys latimarginalis
Platychelys oberndorferi
Caribemys oxfordiensis
Notoemys laticentralis
Panpleurodira
Elseya dentata
Chelodina oblonga
L
Phrynops geoffroanus
Erymnochelys madagascariensis
Pleurodira
Pelomedusa subrufa
Podocnemis expansa
Hangaiemys hoburensis
Judithemys sukhanovi
Dracochelys bicuspis
Sinemys lens
M
Ordosemys leios
Testudines
Panchelonioidea
Toxochelys latiremis
Mesodermochelys undulatus
Caretta caretta
Chelonia mydas
Dermochelys coriacea
Mongolemys elegans
Chrysemys picta
Testudinoidea
Gopherus polyphemus
Geoclemys hamiltonii
Panchelydridae
Protochelydra zangerli
Pancryptodira
Macrochelys temminckii
Chelydra serpentina
Platysternon megacephalum
Emarginachelys cretacea
Baptemys wyomingensis
Dermatemys mawii
Hoplochelys crassa
Staurotypus triporcatus
Sternotherus odoratus
Kinosternidae
Kinosternon flavescens
Adocus beatus
Basilemys variolosa
Sandownia harrisi
Q
Pantrionychia
Zangerlia neimongolensis
Chubutemys copelloi
P
Peltochelys duchastelli
Pseudanosteira pulchra
Carettochelys insculpta
Trionychia
Lissemys punctata

DISCUSSION

Unless otherwise stated, the following discussion is based on the Adams consensus tree of the 73,020 MPT obtained from the analysis of the complete matrix (Fig. 5.4B). The results of the SRC analysis are discussed where appropriate. A complete list of unambiguous apomorphies is provided in Appendix 7, but the synapomorphies of the major clades are discussed below. Unnamed clades discussed in the text have been labelled with letters in order to avoid lengthy descriptions. This labelling is reported on relevant illustrations.

***Testudinata* Klein 1760 (*sensu* Joyce et al., 2004)**—The monophyly of Testudinata, the apomorphy-based clade uniting all tetrapods possessing a turtle shell (see character 86, above), is supported by the following unambiguous synapomorphies: postfrontal absent (character/state: 14/1); bony turtle shell present(ch. 86/1); transverse processes of cervical vertebrae in the middle of the centrum (ch. 142/0); and scapulocoracoid triradiate in shape, with development of an acromial process (ch. 161/1). This clade consists of a polytomy between *Odontochelys semitestacea*, *Proterochersis robusta* and a clade uniting all remaining turtles, including *Proganochelys quenstedti* (clade A; Fig. 5.4B). The second SRC tree indicates that *Proterochersis robusta* has ambiguous relationships among basalmost turtles. When this species is pruned from the tree, *Odontochelys semitestacea* is strictly supported as the most basal turtle (Fig. 5.6A). This result agrees with Li *et al.* (2008). The unstable behaviour of *Proterochersis robusta* relative to other basal turtles is probably the consequence of the presence of two pairs of mesoplastra (ch. 121/1) in *Odontochelys semitestacea*, suggesting that this may be the plesiomorphic condition for turtles (see character 121, above). However, other features of *Proterochersis robusta* suggest that this species may be more derived than *Proganochelys quenstedti* and *Palaeochersis talampayensis*, these include: the absence of anterior plastral tuberosities (ch. 132/1) and the presence of an elongated iliac neck (ch. 169/1; see clade C, below).

Clade A—All turtles, with the exception of *Odontochelys semitestacea*, are united by the following unambiguous synapomorphies: marginal teeth absent (ch. 39/1); only one pair of mesoplastra present (ch. 121/0); dorsal ribs in contact with two successive centra (ch. 156/1); and most digits with three phalanges or less (ch. 175/1). Within clade A, *Proganochelys quenstedti* is the sister group to all remaining turtles (i.e., clade B).

Clade B—This clade consists of a polytomy between *Palaeochersis talampayensis*, *Australochelys africanus* and a clade uniting all remaining turtles (i.e., clade C). STR analysis has demonstrated that *Australochelys africanus* is not discernible from *Palaeochersis talampayensis* in the present data set and can be consequently pruned from the tree (see Results, above). Clade B is unambiguously supported by the following synapomorphies: jugal-squamosal contact absent (ch. 20/1); vomerine and palatine teeth absent (ch. 45/1); cavum tympani present (ch. 49/1); incisura columellea auris present (ch. 52/1); basipterygoid articulation fused (ch. 58/1); and processus paroccipitalis of opisthotic tightly sutured to squamosal and quadrate (ch. 71/1).

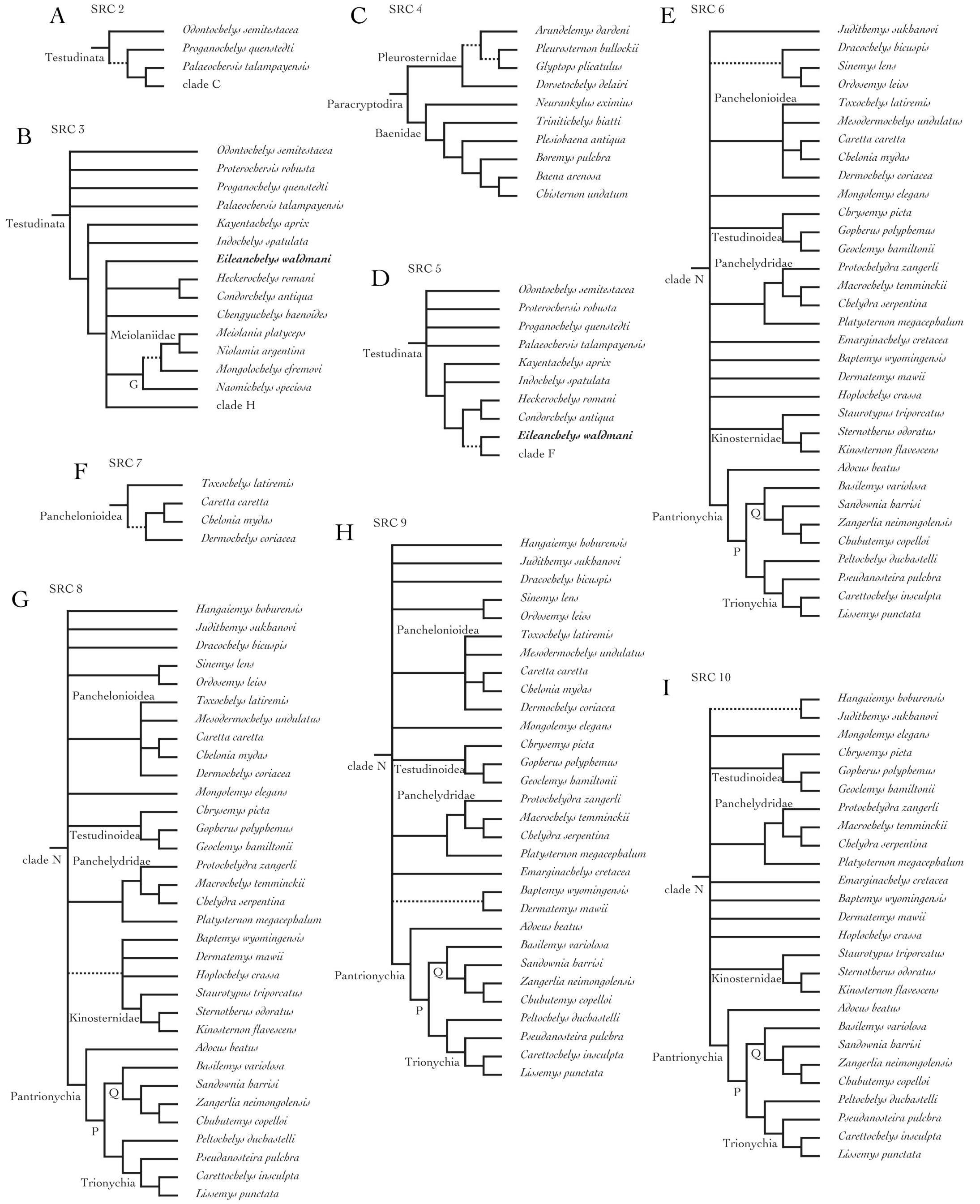


Figure 5.6—Strict reduced consensus (SRC) trees of 1998 MPT (see text). SRC 1 is identical to the strict consensus tree (Fig. 5.5). Pruned taxa: A, *Proterochersis robusta*; B, *Otwayemys cunicularius*; C, *Dinochelys whitei*; D, *Chengyuchelys baenoides*; E, *Hangaiemys hoburensis*; F, *Mesodermochelys undulatus*; G, *Emarginachelys cretacea*; H, *Hoplochelys crassa*, *Staurotypus triporcatus*, *Sternotherus odoratus* and *Kinosternon flavescens*; I, *Dracochelys bicuspis*, *Sinemys lens*, *Ordosemys leios*, *Toxochelys latiremis*, *Mesodermochelys undulatus*, *Dermochelys coriacea*, *Chelonia mydas* and *Caretta caretta*. Dashed lines correspond to the gain in resolution resulting from the pruning of relevant taxa. Only those parts of the SRC trees where relationships are modified are represented in this figure.

Clade C—This clade consists of a polytomy between *Kayentachelys aprix*, *Indochelys spatulata* and a clade uniting all remaining turtles (i.e., clade D). In the context of the present analysis, the exact relationships between *Kayentachelys aprix* and *Indochelys spatulata* are not resolved. This result is similar to that obtained by Sterli (2008). However, the present work and the latter study both support the conclusions of Datta *et al.* (2000) who suggested a close relationships between these two Early Jurassic species. Clade C is supported by numerous unambiguous synapomorphies: dorsal exposure of nasals greatly reduced relative to that of frontals (ch. 3/1); lacrimal absent (ch. 11/1); supratemporal absent (ch. 30/1); internarial process of premaxilla absent (ch. 31/1); anteroventral edge of the orbit formed mostly by maxilla (ch. 40/1); vomer single (ch. 42/1); central constriction of the middle ear by quadrate present (ch. 48/1); antrum postoticum present (ch. 51/1); supramarginals absent (ch. 105/1); anterior plastral tuberosities absent (ch. 132/1); osseous contact of cleithrum with carapace absent (ch. 163/1); coracoid foramen absent (ch. 167/1); elogated iliac neck present (ch. 169/1); and hypoischium absent (ch. 173/1).

Clade D**—**This clade consists of a broad polytomy between chengyuchelyids, *Sichuanchelys chowi*, *'Chengyuchelys' dashanpuensis*, *Heckerochelys romani* + *Condorchelys antiqua* and a clade uniting all remaining turtles (i.e., clade E). Within this analysis, *Sichuanchelys chowi* and *'Chengyuchelys' dashanpuensis* have been observed to be very unstable taxa and their pruning from the MPT dramatically reduces the number of trees (see Results, above). Additionally, STR analysis indicates that *Chengyuchelys zigongensis* could be safely deleted or pruned and would arise from the same node as *C. baenoides* in any MPT (see Results, above). However, even when the three aforementioned species are pruned from the MPT, the relationships between *Chengyuchelys baenoides*, *Heckerochelys romani* + *Condorchelys antiqua* and clade E remain ambiguous (Fig. 5.5). The fifth SRC tree indicates that *Chengyuchelys baenoides* has ambiguous relationships and that the data set strictly supports a topology where *Heckerochelys romani* and *Condorchelys antiqua* are more basal than *Eileanchelys waldmani* (Fig. 5.6D). Clade D is supported by the following unambiguous synapomorphies: pterygoid teeth absent (ch. 57/1); and anterior entoplastral process absent (ch. 113/1). This analysis differs from Danilov & Parham (2008), the only published analysis that investigated the phylogenetic position of the genus *Chengyuchelys*, in finding the chengyuchelyids to be stem turtles less derived than meiolaniids, *Mongolochelys efremovi* and *Kallokibotion bajazidi*. According to Danilov & Parham (2008), *Chengyuchelys* and *Xinjiangchelys latimarginalis* form a clade that is the sister group of Cryptodira.

Heckerochelys romani **+** ***Condorchelys antiqua*****—**This clade is unambiguously supported only by the retention of a central plastral fontanelle in adult individuals (ch. 111/1). Because of the concerns expressed about this feature (see character 111, above), this grouping (Bremer support: 1) should be considered doubtful until further evidence is available (e.g., a thorough description of the *Condorchelys antiqua* material). When extant pleurodires are excluded from the analysis (see Panpleurodira, below), the clade formed by *Heckerochelys romani* and *Condorchelys antiqua* is no longer supported (Fig. 5.7).

Chengyuchelyidae Ye 1990**—***Chengyuchelys baenoides* + *C. zigongensis* are united by the following unambiguous synapomorphies: vertebrals 2 to 4 as narrow as, or narrower than, pleurals (ch. 106/1); medial embayment of vertebral 3-4 sulcus present (ch. 108/1); dagger-shaped entoplastron present (ch. 116/1); and anal scales overlap anteromedially onto hypoplastra (ch. 138/1).

Clade E**—**This clade consists of a sister group relationship between *Eileanchelys waldmani* and a clade uniting all remaining turtles (i.e., clade F). It is supported by a single unambiguous synapomorphy: lateral contact of suprapygal 1 with peripherals present (ch. 95/1). This synapomorphy may not withstand further investigation. State 1 is only known in *Eileanchelys waldmani*, *Naomichelys speciosa*, *Kallokibotion bajazidi*, *Plesiochelys solodurensis* and *Xinjiangchelys latimarginalis*, whereas many early turtles (including meiolaniids, *Mongolochelys efremovi*, *Portlandemys mcdowelli*, *Solnhofia parsonsi*, and *Santanachelys gaffneyi*) are scored as unknown for this character (see Appendix 5).

Clade F**—**This clade unites meiolaniids plus related species (see clade G, below) and a clade consisting of all remaining turtles (i.e., clade H). Clade F is unambiguously supported by the following synapomorphies: vomer with a ventral median septum that separates the meatus choanae (ch. 43/1); posterior process of the pterygoid that floors the cavum acustico-jugulare present (ch. 60/1); and foramen jugulare posterius defined by bone (ch. 78/1).

Clade G**—**This clade, which unites meiolaniids, *Mongolochelys efremovi*, *Otwayemys cunicularius* and *Naomichelys speciosa*, is supported by the following unambiguous synapomorphies: vertebral 5 does not overlap onto peripherals and pygal (ch. 109/1); central plastral fontanelle retained in adult individuals (ch. 111/1); central cervical articulations formed, cervical vertebrae procoelous or opisthocoelous (ch. 145/1); and caudal centra procoelous or opisthocoelous (ch. 160/1). Hirayama *et al.* (2000) were the first to propose a sister group relationships between meiolaniids and *Mongolochelys efremovi* (Fig. 1.1D), followed by Joyce (2007; see Figs. 5.2 and 5.3) and subsequent analyses based on the latter study (e.g., Danilov & Parham, 2008; Sterli, 2008). Hirayama *et al.* (2000) also proposed that *Otwayemys cunicularius* was closely related to meiolaniids and *Mongolochelys efremovi*. Gaffney *et al.* (1998) indeed described *Otwayemys cunicularius* as closely related to meiolaniids, but Gaffney *et al.* (2007) did not find *Mongolochelys efremovi* to be closely related to meiolaniids. The present analysis agrees with Hirayama *et al.* (2000) in finding a close relationship between *Otwayemys cunicularius* and both meiolaniids and *Mongolochelys efremovi*. The relationships of *Naomichelys speciosa* have never been properly investigated in a phylogenetic context. This species is thought to be closely related to *Helochelydra*, which is probably a pancryptodire genus (e.g., Hirayama *et al.*, 2000; Milner, 2004). Although it is not clearly stated, it seems that Hirayama *et al.* (2000) at least partly used FMNH PR273, an undescribed complete individual of *Naomichelys speciosa* (see Taxon sampling, above), to score *Helochelydra* (= *Treutosternon* in Hirayama *et al.*, 2000; but Milner, 2004 concluded that *Treutosternon* is a *nomen dubium*). Hirayama *et al.* (2000) found *Helochelydra* to be the sister group of *Kallokibotion bajazidi*. The present analysis is the first to score *Naomichelys speciosa* as a separate terminal. The third SRC tree indicates that *Otwayemys cunicularius* has ambiguous relationships relative to *Naomichelys speciosa* and *Mongolochelys efremovi* (Fig. 5.6B). The data set strictly supports *Naomichelys speciosa* to be more basal than *Mongolochelys efremovi*, which is congruent with the stratigraphic record.

***Meiolaniidae + Mongolochelys efremovi*—**The clade uniting meiolaniids and *Mongolochelys efremovi* is unambiguously supported by the following synapomorphies: squamosal-supraoccipital contact present (ch. 25/1); crista supraoccipitalis protruding posterior to foramen magnum (ch. 68/1); and ligamentous connexion between carapace and plastron (ch. 110/1).

***Meiolaniidae Lydekker 1889*—**Meiolaniids are unambiguously supported by the following synapomorphies: meiolaniid 'horns' present (ch. 26/1); and intrapterygoid slit present (ch. 67/1). Within meiolaniids, the clade formed by *Meiolania platyceps* and *Ninjemys oweni* is unambiguously supported by the presence of an internarial process dividing the apertura narium externa formed by the nasal and premaxilla (ch. 32/1).

***Clade H*—**This clade consists of a sister group relationship between *Kallokibotion bajazidi* and a clade uniting all remaining turtles (i.e., clade I). Clade H is supported by the following unambiguous synapomorphies: parietal-pterygoid contact present, foramen nervi trigemini defined by the processus inferior parietalis anteriorly (ch. 17/1); epipterygoid laminar (ch. 56/1); pterygoid-basioccipital contact present (ch. 61/1); axillary buttress contacts peripherals and first costal (ch. 119/1); and inguinal buttress contacts peripherals and costals (ch. 123/1).

***Clade I*—**This clade consists of Paracryptodira plus a clade uniting all remaining turtles (i.e., clade J). Clade I is unambiguously supported by the following synapomorphies: articulation of nuchal with neural spine of eighth cervical vertebra absent (ch. 89/1); and glenoid neck on scapula present (ch. 166/1). Because of the unusual position of panpleurodires in the present analysis (see Panpleurodira, below), the paracryptodires are found to be stem Testudines, i.e. they are outside the turtle crown-group (Fig. 5.4B).

***Paracryptodira Gaffney 1975a*—**Paracryptodires (i.e., pleurosternids + baenids) are united by the following unambiguous synapomorphies: dorsal prefrontal exposure reduced to small lappet (ch. 10/1); and foramen posterius canalis carotici interni positioned halfway along the suture between the basisphenoid and the pterygoid (ch. 80/1).

Pleurosternidae Cope 1868*—Dorsetochelys delairi* belongs to pleurosternids in the present analysis. This contrasts with Joyce (2007) for which *D. delairi* was the sister group of paracryptodires. Similarly, *Arundelemys dardeni* is nested within pleurosternids in the present study, whereas it was considered to be the sister group of paracryptodires (or the most basal member of paracryptodires, depending on the interpretation of this name, which is not phylogenetically defined) by Lipka *et al.* (2006). Pleurosternids are supported by the following unambiguous synapomorphies: medial contact of nasals partly or fully prevented by an anterior process of the frontals (ch. 2/1); and marginal scales overlap onto costal plates (ch. 104/1). *Dorsetochelys delairi* and *Dinochelys whitei* form a polytomy at the base of the pleurosternid clade. The fourth SRC tree indicates that *Dinochelys whitei* has ambiguous relationships within pleurosternids. When this species is pruned from the MPT, the relationships within pleurosternids are resolved (Fig. 5.6C): *Dorsetochelys delairi* appears to be the most basal pleurosternid, whereas *Arundelemys dardeni* is the sister group of a clade composed of *Pleurosternon bullockii* and *Glyptops plicatulus* based on the shared presence of a postorbital-maxilla contact preventing the jugal from entering the orbital margin (ch. 28/1, unambiguous). The clade *Pleurosternon bullockii* + *Glyptops plicatulus* is unambiguously supported by the presence of a contact between basisphenoid and vomer (ch. 65/1) and the reacquisition of basipterygoid processes (ch. 74/0). It is interesting to note that the paracryptodire found at Kirtlington (see Chapter 4) would be unambiguously assigned to pleurosternids based on the present analysis.

Baenidae Cope 1882—Baenids are supported by two unambiguous synapomorphies: epipterygoid absent (ch. 55/1); and vertebral scales 2 to 4 as narrow as, or narrower than, pleurals (ch. 106/1). Baenids to the exclusion of *Neurankylus eximius* are unambiguously supported by the absence or near absence of exposure of the prefrontal on the skull roof (ch. 9/1). The present analysis supports the hypothesis that the reduced prefrontal lappets found in *Neurankylus eximius* are homologous to those found in pleurosternids and that the condition in more derived baenids, in which the dorsal exposure of the prefrontal is absent, evolved from this morphology.

Clade J—With the exception of panpleurodires (see below), the content of clade J corresponds to Eucryptodira, as defined by Gaffney (1975a). It is unambiguously supported by the following synapomorphies: medial contact of prefrontal on the dorsal surface of the skull present (ch. 5/1); mesoplastron absent (ch. 120/1); and transverse processes of cervical vertebrae in the anterior part of the centra (ch. 142/1). Within clade J, a small clade consisting of species usually recognised as the most basal eucryptodires (see clade K below) is the sister group of a clade uniting all remaining turtles (i.e., clade L).

Clade K—This clade unites *Santanachelys gaffneyi* with four species usually considered to be the most basal members of eucryptodires (e.g., Gaffney & Meylan, 1988; Joyce, 2007): *Plesiochelys solodurensis*, *Portlandemys mcdowelli*, *Solnhofia parsonsi*, and '*Thalassemys moseri*'. Clade K is supported by the following unambiguous synapomorphies: short anterior extension of the lateral braincase wall (ch. 18/0; reversed in '*Thalassemys moseri*'); and foramen posterius canalis carotici interni formed by the pterygoid and positioned near the posterior edge of this bone (ch. 81/1). Gaffney & Meylan (1988) proposed that numerous Late Jurassic turtles from western Europe formed a clade at the base of Eucryptodira, which they referred to as 'Plesiochelyidae'. This differs from Joyce (2007) who regards 'plesiochelyids' *sensu* Gaffney & Meylan (1988) as paraphyletic, with '*Thalassemys moseri*' and *Solnhofia parsonsi* being more closely related to Cryptodira than to *Plesiochelys solodurensis* (Figs. 5.2 and 5.3). The present analysis is more in agreement with Gaffney

& Meylan (1988), but it is evident that the relationships of these early eucryptodires are poorly understood: for example, when extant pleurodires are excluded prior to the analysis (see below), clade K is no longer supported and 'plesiochelyids' become paraphyletic (Fig. 5.7B). In the context of the present analysis, *Plesiochelys solodurensis* and *Portlandemys mcdowelli* form a true polytomy at the base of clade K (no matter which taxa are pruned from the MPT, this relationship would remain unresolved). As in Joyce (2007), *Solnhofia parsonsi* is optimised to be the sister group of a clade uniting '*Thalassemys moseri*' and *Santanachelys gaffneyi* based on the absence of pterygoid-vomer contact (ch. 44/1) and the retention of a central plastral fontanelle in adult individuals (ch. 111/1). The clade '*Thalassemys moseri*' + *Santanachelys gaffneyi* is unambiguously supported by the absence of medial contact of prefrontals on the dorsal surface of the skull (ch. 5/0) and the presence of a laterally open foramen palatinum posterius (ch. 64/1; independently acquired in *Plesiochelys solodurensis*). These results are identical to those obtained by Joyce (2007), who first suggested the placement of *Santanachelys gaffneyi* as a basal eucryptodire rather than as a panchelonioid. Protostegids like *Santanachelys gaffneyi* are usually considered to be the sister group of Dermochelyidae, the clade that contains the extant leatherback turtle *Dermochelys coriacea* (Hirayama, 1998; Kear & Lee, 2006). More protostegids should be included in future studies in order to confirm this relationship with basal eucryptodires (see also character 81, above).

Clade L — This clade consists of a sister group relationship between Xinjiangchelyidae and a clade uniting all remaining turtles (i.e., clade M). It is supported by the following unambiguous synapomorphies: parietal-squamosal contact absent (ch. 16/1); vertebral scales 2 to 4 as narrow as, or narrower than, pleurals (ch. 106/1); first dorsal rib extending less than halfway across first costal plate (ch. 153/1); and caudal centra procoelous or opisthocoelous (ch. 160/1).

Xinjianchelyidae Ye 1986 — Xinjiangchelyids are supported by the following unambiguous synapomorphies: distinctly sinuous midline sulcus of plastral scales (ch. 127/1); and gular scales restricted to epiplastra only (ch. 129/1). Relationships within xinjiangchelyids are fully resolved by the present data set. One of the most interesting results of this study is the placement of *Siamochelys peninsularis* within xinjiangchelyids. The phylogenetic relationships of this species from the Middle Jurassic of Thailand have been investigated for the first time herein. In their original description, Tong *et al.* (2002) considered *Siamochelys peninsuralis* to be closely related to the genera *Chengyuchelys* and *Xinjiangchelys*. *Xinjiangchelys qiguensis* is found to be the most basal xinjiangchelyid. Xinjiangchelyids to the exclusion of *X. qiguensis* are united by the following unambiguous synapomorphies: vertebral 5 not overlapping onto peripherals and pygal (ch. 109/1; ci = 0.167); and inguinal buttress contacting peripherals only (ch. 123/0; ci = 0.125). Within this clade, *Siamochelys peninsularis* is optimised as the sister group of a clade uniting *X. latimarginalis*, *X. tianshanensis* and *Annemys levensis*. The latter clade is unambiguously supported by the shared presence of anal scales that overlap onto the hypoplastra (ch. 138/1; ci = 0.125), whereas the clade *X. tianshanensis* + *A. levensis* is supported by the partial reduction of posterior neurals allowing the median contact of posterior costals (ch. 94/1; ci = 0.125). The low consistency indices (ci; see above) indicate that characters supporting relationships within xinjiangchelyids are very homoplastic, which suggests that these relationships would be prone to change with the discovery of additional material (especially cranial). The pattern of relationships recovered in the present study is generally congruent with that of Matzke *et al.* (2004), the only other study that investigated the interrelationships of xinjiangchelyids, with the exception that *X. latimarginalis* and *X. tianshanensis* were found to be more closely related to one another than to *Annemys latiens* (the type species of the genus; see Taxon sampling, above) in the latter study. Both Matzke *et al.* (2004) and the present study indicate that the genus *Xinjiangchelys* is paraphyletic: either *X. qiguensis* should be referred to a new genus, or *A. levensis* and *S. peninsularis* should be referred to *Xinjiangchelys*. *Annemys levensis* is the only xinjiangchelyid for which cranial material is found. According to the published description and illustrations (Sukhanov, 2000), the fpcci opens within the basisphenoid (plesiomorphic amniote condition) in this species. Consequently, a fpcci formed by the pterygoid and positioned near the posterior edge of this bone (ch. 81/1) evolved three times within the context of the present study: first, as an ambiguous autapomorphy of *Meiolania platyceps* (DELTRAN optimisation; condition unknown in other meiolaniids); second, as an unambiguous synapomorphy of clade K ('plesiochelyids'; see above); and third, as an unambiguous synapomorphy of clade N (Cryptodira + 'macrobaenids' and 'sinemydids'; see below).

Clade M—This clade unites Panpleurodira to a clade that includes crown-group cryptodires (here clade N). So clade M corresponds to crown-group turtles, or Testudines (Fig. 5.4B). Clade M is supported by the following unambiguous synapomorphies: central cervical articulation procoelous or opisthocoelous (ch. 145/1); chevrons absent or poorly developed (ch. 158/1); and cleithrum absent (ch. 162/1).

Panpleurodira Joyce et al. 2004—The phylogenetic placement of panpleurodires within Eucryptodira is counterintuitive as regards to the available evidence. Joyce (2007) obtained similar results in his first analysis (Fig. 5.2) and explained them by a phenomenon of 'morphological long-branch attraction' (ibid.: 53). Inappropriate taxon sampling is believed to be a possible explanation for this situation. Whereas paracryptodires and eucryptodires are represented by numerous Mesozoic forms, panpleurodires are only represented by three relatively poorly known basal species from the Late Jurassic (*Platychelys oberndorferi*, *Caribemys oxfordiensis* and *Notoemys laticentralis*) and six derived extant species (see Appendices 2 and 4). The morphological gap between these extant pleurodires and their basal relatives or with potential sister groups of panpleurodires is very important. Moreover, these extant pleurodires appear to be convergent with some groups of pancryptodires in numerous characters (e.g., 1, 2, 16, 44, 50, 51, 68, 106, 107 and 120). Most of these characters are scored unknown in the three basal panpleurodire species that are considered, so that panpleurodires may exhibit relationships with various pancryptodire clades due to ambiguous character state optimisation of basal species. In this context, the

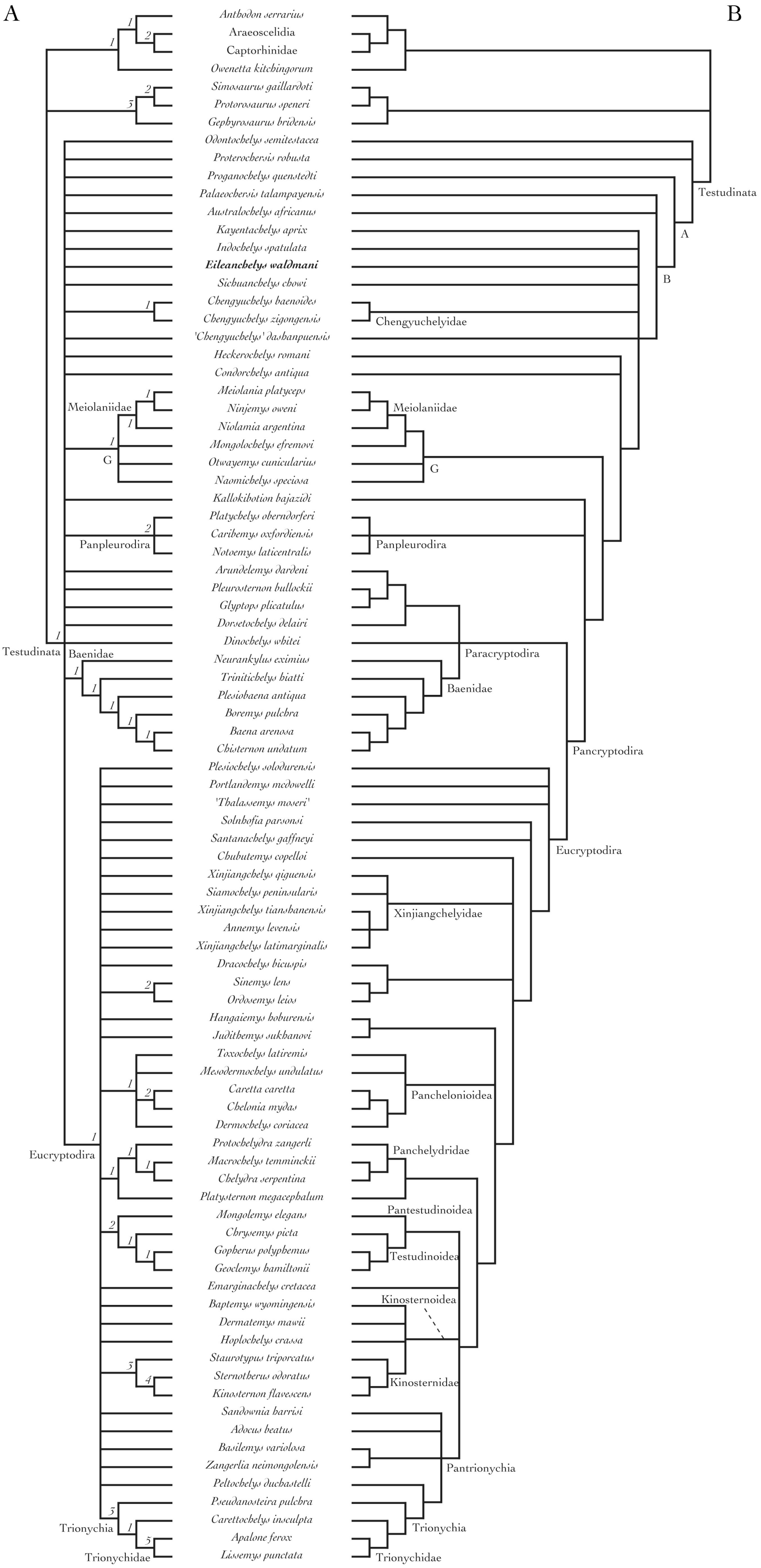

A
B
Anthodon serrarius
Araeoscelidia
Captorhinidae
Owenetta kitchingorum
Simosaurus gaillardoti
Protorosaurus speneri
Gephyrosaurus bridensis
Odontochelys semitestacea
Proterochersis robusta
Proganochelys quenstedti
Palaeochersis talampayensis
Australochelys africanus
Kayentachelys aprix
Indochelys spatulata
Eileanchelys waldmani
Sichuanchelys chowi
Chengyuchelys baenoides
Chengyuchelys zigongensis
'Chengyuchelys' dashanpuensis
Heckerochelys romani
Condorchelys antiqua
Meiolania platyceps
Ninjemys oweni
Niolamia argentina
Mongolochelys efremovi
Otwayemys cunicularius
Naomichelys speciosa
Kallokibotion bajazidi
Platychelys oberndorferi
Caribemys oxfordiensis
Notoemys laticentralis
Arundelemys dardeni
Pleurosternon bullockii
Glyptops plicatulus
Dorsetochelys delairi
Dinochelys whitei
Neurankylus eximius
Trinitichelys biatti
Plesiobaena antiqua
Boremys pulchra
Baena arenosa
Chisternon undatum
Plesiochelys solodurensis
Portlandemys mcdowelli
'Thalassemys moseri'
Solnhofia parsonsi
Santanachelys gaffneyi
Chubutemys copelloi
Xinjiangchelys qiguensis
Siamochelys peninsularis
Xinjiangchelys tianshanensis
Annemys levensis
Xinjiangchelys latimarginalis
Dracochelys bicuspis
Sinemys lens
Ordosemys leios
Hangaiemys hoburensis
Judithemys sukhanovi
Toxochelys latiremis
Mesodermochelys undulatus
Caretta caretta
Chelonia mydas
Dermochelys coriacea
Protochelydra zangerli
Macrochelys temminckii
Chelydra serpentina
Platysternon megacephalum
Mongolemys elegans
Chrysemys picta
Gopherus polyphemus
Geoclemys hamiltonii
Emarginachelys cretacea
Baptemys wyomingensis
Dermatemys mawii
Hoplochelys crassa
Staurotypus triporcatus
Sternotherus odoratus
Kinosternon flavescens
Sandownia harrisi
Adocus beatus
Basilemys variolosa
Zangerlia neimongolensis
Peltochelys duchastelli
Pseudanosteira pulchra
Carettochelys insculpta
Apalone ferox
Lissemys punctata
Testudinata
Meiolaniidae
G
Panpleurodira
Baenidae
Eucryptodira
Trionychia
Trionychidae
Testudinata
A
B
Chengyuchelyidae
Meiolaniidae
G
Panpleurodira
Paracryptodira
Baenidae
Pancryptodira
Eucryptodira
Xinjiangchelyidae
Panchelonioidea
Panchelydridae
Pantestudinoidea
Testudinoidea
Kinosternoidea
Kinosternidae
Pantrionychia
Trionychia
Trionychidae

Figure 5.7—(previous page) Phylogenetic interrelationships of turtles after exclusion of extant pleurodires prior to analysis. A, strict consensus tree (677 steps; CI=0.2511; RI=0.5834) of 975 MPT; B, Adams consensus tree (417 steps; CI=0.4077; RI=0.7970) of 975 MPT. Capital letters label unnamed clades, whereas numbers on the strict consensus tree correspond to Bremer support values.

symplesiomorphies found in *Platychelys oberndorferi*, *Caribemys oxfordiensis* and *Notoemys laticentralis* appear as independently reacquired in the present analysis (see below). The effects of this partial convergence between extant pleurodires and some pancryptodires on the phylogenetic placement of panpleurodires become evident when the analysis is run without the six extant pleurodire species. This analysis (parsimony ratchet; 200 iterations; 15% reweighting; 20 replicates; branches set to collapse if minimum length is zero; ch. 22, 27, 41, 47, 54, 62, 70, 79, 93, 146 and 170 are uninformative) resulted in 975 MPT after filtering (393 steps; CI = 0.4326; RI = 0.8168). In the Adams consensus tree of these 975 MPT (417 steps; CI = 0.4077; RI = 0.7970), the panpleurodires are found in a more traditional position outside the clade uniting Paracryptodira and Eucryptodira (Fig. 5.7B). Future analyses should focus on the scoring of additional early taxa and basal pleurodires in order to properly assess the phylogenetic position of panpleurodires within turtles. In the context of the present analysis (complete matrix; Fig. 5.4B), panpleurodires are unambiguously supported by the following synapomorphies: loss of the posterior process of the pterygoid that floors the cavum acustico-jugulare (ch. 60/0); distinct anal notch on plastron present (ch. 124/1); one single gular scale present (ch. 128/1); inframarginal scales absent (ch. 139/1); transverse process of cervical vertebrae in the middle of centra (ch. 142/0; reacquisition of plesiomorphic state); and sutural articulation of pelvis to shell present (ch. 168/1). Although the reduction of the posterior process of the pterygoid bracing the braincase (ch. 60/0) may seem counterintuitive (see character 47, above), Joyce (2007: 72) already suggested that the pleurodire condition (braincase braced by the quadrate and prootic; ch. 47, see below) probably evolved from the 'cryptodire' condition (braincase braced by the pterygoid), which is also found in some stem turtles (e.g., *Meiolania platyceps*, *Mongolochelys efremovi* and *Kallokibotion bajazidi*). Within panpleurodires, *Platychelys oberndorferi*, *Caribemys oxfordiensis* and *Notoemys laticentralis* form a clade which is the sister group of Pleurodira (crown-group). The former group is unambiguously supported by the following synapomorphies: vertebral scales 2 to 4 significantly broader than pleurals (ch. 106/0; reacquisition of plesiomorphic state); vertebral scale 3-4 sulcus positioned on neural 6 (ch. 107/0; reacquisition of plesiomorphic state); and retention of a central plastral fontanelle in adult individuals (ch. 111/1). Within this clade, *Platychelys oberndorferi* and *Caribemys oxfordiensis* share the presence of a narrow and posteriorly pointed articular site of the ilium with the carapace (ch. 170/0). Pleurodires are supported by the following unambiguous synapomorphies: ventromedial process of the quadrate and/or prootic that floors the cavum acustico-jugulare present (ch. 47/1); and incisura columellae auris closed by the quadrate (ch. 53/1).

Clade N—Within the context of the present analysis (i.e., with respect to the position of panpleurodires), clade N corresponds to Pancryptodira. It consists of a polytomy that unites taxa usually referred to as 'macrobaenids' and 'sinemydids', and Cryptodira (i.e., crown-group cryptodires). Clade N is unambiguously supported by the following synapomorphies: Eustachian tube not contained within incisura columellae auris alongside stapes (ch. 54/0); foramen posterius canalis carotici interni formed by the pterygoid and positioned near the posterior edge of this bone (ch. 81/1); axillary buttress contacting peripherals only (ch. 119/0); inguinal buttress contacting peripherals only (ch. 123/0); loss of extragular scales (ch. 130/1); and posterior cervicals with strongly developed ventral keels (ch. 143/1). In the present analysis, the closure of the incisura columellae auris is coded separately from the position of the Eustachian tube relative to the incisura (see characters 53 and 54, above). This allows these two features to be tested independently by congruence. In Joyce (2007, ch. 36), these features were coded as a single unordered multistate character with the absence/presence of the incisura columellae auris. According to Joyce (2007), a closed incisura appeared twice (in *Sinemys lens* and the clade formed by chelydrids, testudinoids and trionychoids) and was lost three times (in *Adocus beatus*, kinosternoids, and the clade formed by *Chrysemys picta* and *Geoclemys hamiltonii*), while a closed incisura including the Eustachian tube evolved three times (in *Meiolania platyceps*, *Kallokibotion bajazidi*, and pleurodires). In the present analysis, a closed incisura (including the Eustachian tube or not) appears to be a rather homoplastic character with six independent acquisitions: in *Kallokibotion bajazidi*, Pleurodira, *Sinemys lens*, *Gopherus polyphemus*, panchelydrids + *Platysternon megacephalum*, and pantrionychians more derived than *Adocus beatus*. The present analysis also supports the hypothesis that the Eustachian tube is contained within the incisura columellae auris (closed or not) as a plesiomorphic condition for turtles and that this condition is lost only once as an unambiguous synapomorphy of clade N (i.e., Cryptodira + 'macrobaenids' and 'sinemydids').

Hangaiemys hoburensis* + *Judithemys sukhanovi—This relationship is unambiguously supported by the presence of paired pits on the ventral surface of the basisphenoid (ch. 73/1) and the elongate shape of epiplastra (ch. 118/1). This is consistent with Gaffney *et al.* (2007) and Parham & Hutchison (2003), but not with Joyce (2007) in which *Judithemys sukhanovi* was more closely related to *Sinemys lens*, *Ordosemys leios* and *Dracochelys bicuspis* than to *Hangaiemys hoburensis*. The tenth SRC tree indicates that *Dracochelys bicuspis*, *Sinemys lens*, *Ordosemys leios* and panchelonioids have ambiguous relationships with respect to the clade formed by *Hangaiemys hoburensis* and *Judithemys sukhanovi* (Fig. 5.6I).

Dracochelys bicuspis* + *Sinemys lens* + *Ordosemys leios—This clade is unambiguously supported by the shared presence of a precolumellar fossa (ch. 50/1). The sixth SRC tree indicates that *Hangaiemys hoburensis* has ambiguous relationships relative to *Dracochelys bicuspis* (Fig. 5.6E). The latter is the sister group of a clade formed by *Sinemys lens* and *Ordosemys leios*, which is unambiguously supported by the absence of a medial contact between prefrontals on the dorsal surface of skull roof (ch. 5/0) and the presence of a dorsal exposure of prefrontals reduced to small lappets (ch. 10/1).

Panchelonioidea Joyce et al. 2004—Panchelonioids are supported by six unambiguous synapomorphies: raised pedestal on the visceral surface of the nuchal for the articulation with the neural spine of the eighth cervical vertebra present (ch. 90/1); reduction of costal ossifications, costal fontanelles well-developed (ch. 101/1); central plastral fontanelle retained in adult individuals (ch. 111/1); epiplastra elongate in shape (ch. 118/1); xiphiplastra reduced to narrow struts that frame a xiphiplastral fontanelle (ch. 125/1); and paddles present (ch. 177/1). *Toxochelys latiremis* and *Mesodermochelys undulatus* form a polytomy at the base of panchelonioids (Fig. 5.4B). The seventh SRC tree indicates that *Mesodermochelys undulatus* has ambiguous relationships within panchelonioids (Fig. 5.6F). *Mesodermochelys undulatus* is usually considered to be a close relative of *Dermochelys coriacea* (e.g., Hirayama & Chitoku, 1996; Kear & Lee, 2006). In Joyce (2007), this relationship was only supported by the partial loss of carapacial scales, an ordered multistate character (see character 87, above). When characters were run unordered (first analysis of Joyce, 2007; see Fig. 5.2), the relationship between *M. undulatus* and *D. coriacea* was no longer supported, as in the present analysis. The present data set strictly supports *Toxochelys latiremis* as the most basal panchelonioids. Chelonioids (*Dermochelys coriacea*, *Chelonia mydas* and *Caretta caretta*) are supported by the following synapomorphies: nasal absent (ch. 1/1); parietal-squamosal contact present, temporal emargination poorly developed (ch. 16/0); foramen palatinum posterius absent (ch. 63/1); and rostrum basisphenoidale rod-like, thick and rounded (ch. 72/1). According to the present analysis, the loss of the foramen palatinum posterius (fpp) in chelonioids derived from a condition where the fpp is entirely surrounded by bone, which justifies *a posteriori* the coding of two independent characters for the loss of the fpp and the presence of a laterally open fpp in some 'plesiochelyids' (see characters 63 and 64, above). Among chelonioids, *Chelonia mydas* and *Caretta caretta* share the following unambiguous synapomorphies: foramen praepalatinum absent (ch. 34/1); and anterior articulation of first dorsal centrum facing strongly anteroventrally (ch. 157/1).

Clade O—This clade consists of a polytomy between testudinoids, panchelydrids + *Platysternon megacephalum* and trionychoids (Fig. 5.4B). Clade O is supported by the following unambiguous synapomorphies: nasal absent (ch. 1/1); pterygoid contribution to foramen palatinum posterius absent (ch. 66/1); anterior articulation of first dorsal centrum facing strongly anteroventrally (ch. 157/1); and glenoid neck on scapula absent (ch. 166/0).

Testudinoidea Fitzinger 1826 (sensu Joyce et al., 2004)—Testudinoidea are unambiguously supported by the following synapomorphies: axillary buttress contacts peripherals and first costal (ch. 119/1); inguinal buttress contacts peripherals and costals (ch. 123/1); and only two pairs of inframarginal scales present (ch. 140/1). According to Sukhanov (2000), *Mongolemys elegans* is a representative of pantestudinoids but neither the present study nor that of Joyce (2007; Fig. 5.2) successfully resolved the relationships of this species. *Mongolemys elegans* was considered to be a rogue taxon by Joyce (2007) and excluded from his third analysis (Fig. 5.3). In the present study, *M. elegans* arises from clade O (Fig. 5.4B). However, it is interesting to note that when extant pleurodires are excluded prior to the analysis *Mongolemys elegans* is strictly supported as the sister group of testudinoids (Fig. 5.7A,B), which tends to confirm the conclusions of Sukhanov (2000).

***Panchelydridae* + *Platysternon megacephalum*—**The present analysis unambiguously supports the placement of *Platysternon megacephalum* as the sister group of panchelydrids (Fig. 5.4A,B). This clade is relatively well supported with a Bremer support value of 2 (i.e., greater support than for baenids or panchelonioids). Such a relationship has been proposed many times in the past (see Gaffney, 1975b), but *Platysternon megacephalum* was generally considered to be a derived member of Chelydridae (e.g., Gaffney, 1975b; Gaffney & Meylan, 1988). However, Shaffer *et al.* (1997) and Brinkman & Wu (1999) have suggested a sister group relationship between these two taxa. These results are in contradiction with the most recent molecular studies which optimised *Platysternon megacephalum* to be a member of testudinoids (Parham *et al.*, 2006), as well as with Joyce (2007) for which *P. megacephalum* is more closely related to testudinoids and trionychoids than panchelydrids (Fig. 5.3B). The clade uniting panchelydrids and *P. megacephalum* is supported by the following unambiguous synapomorphies: frontal excluded from the orbital margin (ch. 13/0); incisura columellae auris closed by quadrate (ch. 53/1); epiplastra elongate in shape (ch. 118/1); and chevrons present (ch. 158/0).

***Panchelydridae* Joyce et al. 2004—**Panchelydrids are supported by the following unambiguous synapomorphies: medial contact of abdominal scales absent (ch. 137/1); and anal scales overlap medially onto hypoplastra (ch. 138/1). In the context of the present analysis, chelydrids (i.e., *Chelydra serpentina* + *Macrochelys temminckii*) are supported unambiguously only by the retention of a central plastral fontanelle in adult individuals (ch. 111/1).

***Trionychoidea* Fitzinger 1826 (sensu Joyce et al., 2004)—**Trionychoids are unambiguously supported only by the presence of a palatine contribution to the anterior extension of the lateral braincase wall (ch. 46/1). The basal relationships within trionychoids are not well resolved in the present analysis (Fig. 5.4B). The eighth SRC tree indicates that *Emarginachelys cretacea* has ambiguous relationships with respect to kinosternoids (Fig. 5.6G).

***Kinosternoidea* Joyce et al. 2004—**kinosternoids are supported by the following unambiguous synapomorphies: pectoral scales absent (ch. 135/1); and articulation between cervical vertebrae 3 and 4 concave anteriorly (i.e., 3)4; ch. 147/1). Within kinosternoids, relationships between *Hoplochelys crassa*, *Dermatemys mawii* and *Baptemys wyomingensis* are ambiguous (Fig. 5.4B). The ninth SRC tree indicates that a sister group relationship between *Dermatemys mawii* and *Baptemys wyomingensis* is strictly supported by the data set, but that other kinosternoids prevent its representation in the Adams consensus tree (Fig. 5.6H).

Pantrionychia Joyce et al. 2004— Relationships within pantrionychians are fully resolved by the present data set (Fig. 5.4). This clade is supported by the following unambiguous synapomorphies: distincly sinuous midline sulcus of plastral scales (ch. 127/1); reacquisition of extragulars (ch. 130/0); and central articulations between cervical vertebrae 4-5, 5-6 and 6-7 convex anteriorly (ch. 148/0, 149/0 and 150/0). *Adocus beatus* is found to be the most basal member of the group and to be the sister taxon of a clade uniting the remaining pantrionychians (i.e., clade P).

Clade P— This clade is supported by the following unambiguous synapomorphies: vomer-pterygoid contact in palatal view absent (ch. 44/1); and incisura columellae auris closed by the quadrate (ch. 53/1). Clade P splits basally into two clades: clade Q, containing *Basilemys variolosa* and *Zangerlia neimongolensis*, and a clade uniting *Peltochelys duchastelli* and Trionychia.

Trionychia + Peltochelys duchastelli— This clade is unambiguously supported by a reduction of the number of peripherals to 10 pairs (ch. 98/1).

Trionychia Hummel 1929 (sensu Joyce et al., 2004)— Trionychians are supported by the following unambiguous synapomorphies: reduction of posterior neurals allowing partial contact of posterior costals (ch. 94/1); ligamentous connection between carapace and plastron (ch. 110/1); and plastral scales absent (ch. 126/1). In contrast to Joyce (2007), *Pseudanosteira pulchra* is optimised to be a basal member of Trionychia rather than a carettochelyid. In Joyce (2007), the clade formed by *Carettochelys insculpta* and *P. pulchra* was only supported by the development of elongate flippers, a character that is not considered in the present analysis (see rationale in Appendix 6). More characters supporting the carettochelyids should be included in future analyses.

Clade Q— The content of this clade constitutes one of the most unexpected results of this study: the placement of *Chubutemys copelloi* within pantrionychians. *Chubutemys copelloi* is known from relatively poorly preserved material from the Early Cretaceous of Argentina. It was interpreted by Gaffney *et al.* (2007) as closely related to meiolaniids. This species is poorly scored in the present analysis (approximately 70% missing data) and its relationships are likely to change in future analyses. The exclusion of extant pleurodires from the analysis is enough to take *C. copelloi* out of pantrionychians and place it among basal eucryptodires (Fig. 5.7B). The present analysis agrees with Meylan *et al.* (2000) in the placement of *Sandownia harrisi* as a member of Trionychoidea. In contrast, Joyce (2007: 66) tentatively reconstructed *Sandownia harrisi* as the sister taxon of '*Thalassemys moseri*' because this hypothesis only required one additional step compared to its placement as a basal trionychoid. In the present analysis, *Sandownia harrisi* is unambiguously supported as a member of pantrionychians (see below), although its phylogenetic relationships are prone to change with future discoveries as this species is only known from cranial material while most characters supporting relationships within pantrionychians concern shell or postcranial morphology. Clade Q is supported by the following unambiguous synapomorphies: extragular scales contacting one another posterior to gulars (ch. 131/1); and most digits with two short phalanges (ch. 176/1). The sister group relationship between *Sandownia harrisi* and a clade formed by *Zangerlia neimongolensis* and *Chubutemys copelloi* is supported by the presence of a parietal-squamosal contact (ch. 16/0). The clade *Zangerlia neimongolensis* + *Chubutemys copelloi* is supported by the absence of a frontal contribution to the orbital margin (ch. 13/0).

CONCLUSIONS

The present study modified the data set of Joyce (2007) to limit the effects of *a priori* assumptions on the recovered pattern of relationships, and 19 turtle species have been added to the taxon sample in order to achieve a more thorough representation of basal turtle taxa. The recovered topology generally agrees with that of Joyce (2007), and the analysis attains similar levels of resolution (see Figs. 5.2 and 5.3). The phylogenetic relationships of most newly added taxa have been resolved or at least constrained by this analysis. *Odontochelys semitestacea* is unambiguously supported as the most basal turtle, which agrees with the conclusions of Li *et al.* (2008). The phylogenetic placement of *Heckerochelys romani*, *Condorchelys antiqua* and *Eileanchelys waldmani* as stem turtles less derived than meiolaniids and *Mongolochelys efremovi* is confirmed. The present analysis weakly supports a sister group relationship between *H. romani* and *C. antiqua* based on the retention of a central plastral fontanelle in adult individuals. This differs from Anquetin *et al.* (2009) who suggested a close relationship between *E. waldmani* and *H. romani*. In the present analysis, *Eileanchelys waldmani* is found to be more closely related to Testudines than to *H. romani* and *C. antiqua*. The relationships of *Sichuanchelys chowi*, chengyuchelyids and *'Chengyuchelys' dashanpuensis* are not entirely resolved by the present data set. However, the analysis suggests that these Middle Jurassic Chinese turtles could be stem turtles more basal than meiolaniids and *Kallokibotion bajazidi*. This differs from Danilov & Parham (2008) who found the genus *Chengyuchelys* to be closely related to *Xinjiangchelys*. As in Hirayama *et al.* (2000) and Joyce (2007), a sister group relationship between meiolaniids and *Mongolochelys efremovi* is unambiguously supported. The present analysis goes further in proposing that *Naomichelys speciosa* and *Otwayemys cunicularius* are stem turtles that are more closely related to meiolaniids and *M. efremovi* than to any other species. This clade constitutes a side branch of stem turtles that existed alongside crown-group turtles up until the Pleistocene and was spread worldwide (i.e., South America, North America, Mongolia and Australia) during the Mesozoic and early Cenozoic. *Arundelemys dardeni* and *Dorsetochelys delairi*, which were previously considered to be sister taxa of the clade uniting pleurosternids and baenids (i.e., Paracryptodira; Lipka *et al.*, 2006; Joyce, 2007), are here found to be nested within pleurosternids. This is more in agreement with available data: e.g., presence of a maxilla-postorbital contact in *Arundelemys dardeni*, and presence of an anterior process of the frontals that partly separates the nasals posteromedially in *Dorsetochelys delairi*. A clade uniting species generally referred to as 'plesiochelyids' and *Santanachelys gaffneyi* at the base of Eucryptodira is supported by the analysis of the complete data set, but this clade is no longer supported if the analysis is run without extant pleurodire species. The relationships of these basal eucryptodires should be further investigated. *Siamochelys peninsularis*, which is included in a phylogenetic analysis for the first time, is found to be nested within xinjiangchelyids. The exact phylogenetic placement of panpleurodires remains uncertain. Convergence between extant pleurodires and certain pancryptodires appears to draw panpleurodires into eucryptodires. When extant pleurodires are excluded from the data set, a more conventional topology emerges and panpleurodires are found to be basal to a clade uniting paracryptodires and eucryptodires. Only the scoring of more panpleurodires and basal pleurodires could help to resolve the relationships of this clade among other turtles. In contrast to Joyce (2007), but in agreement with Parham & Hutchison (2003) and Gaffney *et al.* (2007), *Hangaiemys hoburensis* and *Judithemys sukhanovi* are unambiguously supported to form a clade, although their relationships with other eucryptodires are ambiguous. *Sandownia harrisi* and *Chubutemys copelloi* are found to be closely related to *Basilemys variolosa* and *Zangerlia neimongolensis*. This placement of *Chubutemys copelloi* is unexpected, but it is probably the consequence of the sparse scoring of this poorly known species.

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CHAPTER 6: CONCLUSIONS AND PERSPECTIVES

CONCLUSIONS

- *Eileanchelys waldmani*, a basal turtle from the Kilmaluag Formation (Bathonian) at Cladach a'Ghlinne, Isle of Skye, Scotland, is described in detail and its anatomy is compared to that of other basal species. With cranial and postcranial remains of several individuals, this is the most comprehensive Middle Jurassic turtle material known to date. *Eileanchelys waldmani* exhibits a mosaic of plesiomorphic and derived characters. This new taxon also documents an intermediate stage between the most basal turtles (e.g., *Proganochelys quenstedti*) and the crown-group regarding the evolution of several features. This is especially the case with respect to the morphology and contacts of the vomer, as well as the migration of the aditus canalis stapedio-temporalis and of the posterior opening of the canalis cavernosus. The slender processus interfenestralis of the opisthotic in *Eileanchelys waldmani* is also intermediate in development between that of *Proganochelys quenstedti* or *Kayentachelys aprix* and that of crown-group turtles.

- The palaeoecology of basal turtles has been debated regularly over the past two decades in the context of discussions on turtle origins. With the exception of *Odontochelys semitestacea*, most stem turtles are interpreted to be terrestrial taxa. Based on taphonomical arguments, *Eileanchelys waldmani* can be interpreted as an aquatic turtle, which confirms that stem turtles are ecologically more diverse than previously thought.

- The UK is one of the few places in the world where Middle Jurassic turtle remains are found. A brief review shows that most of this material is very fragmentary and not particularly useful taxonomically, with the exception of the material from Kirtlington and Stonesfield.

- A morphological reassessment of the fragmentary turtle material from Kirtlington, Oxfordshire, supports the presence of paracryptodires at this locality. This reassessment fails to entirely confirm the results of an associated histological study of the remains (conducted by T. Scheyer) that suggested the presence of a pleurosternid and an indeterminate cryptodire in this fauna. By supporting the presence of paracryptodires in the Bathonian, this study reduces the ghost lineage of this clade by fourteen million years.

- The material from the Stonesfield Slate represents the earliest British turtle, but it had been completely overlooked since the end of the 19th century. This material is properly described and compared for the first time. *Protochelys blakii* is considered to be a *nomen dubium* because the remains are not diagnosable. The Stonesfield turtle has a plesiomorphic carapacial scale pattern with vertebrals that are twice as wide as long, pleurals that are reduced in width and a fifth vertebral with an anterior margin as long as the posterior margin. These features are commonly found in stem turtles and some basal crown-group turtles. Any phylogenetic assignment of the Stonesfield turtle is difficult to achieve due to the paucity of the material. With the exception of a coracoid and a small plastron fragment, all turtle remains from Stonesfield consist of isolated epidermal scales from the carapace, which is a unique example of fossil preservation. A review of the taphonomical literature suggests that these isolated scales result from *post-mortem* disarticulation rather than shedding.

- A cladistic analysis, based on a revised and updated version of a previously published data matrix, proposes a reassessment of the relationships among basal turtles. All sufficiently well-known pre-Late Jurassic turtles are included as well as several younger species whose relationships were uncertain. Some of these newly added species have been included in a phylogenetic analysis for the first time. *Odontochelys semitestacea* is confirmed to be the most basal turtle. *Heckerochelys romani* and *Condorchelys antiqua* are found to be more basal than *Eileanchelys waldmani*. The relationships of chengyuchelyids (i.e., *Chengyuchelys baenoides* and *C. zigongensis*), *Sichuanchelys chowi* and '*Chengyuchelys*' *dashanpuensis*, from the Middle Jurassic of China, are not entirely resolved but the present study suggests that they may be stem turtles more basal than meiolaniids and *Kallokibotion bajazidi*. *Naomichelys speciosa*, whose individual relationships are investigated for the first time, and *Otwayemys cunicularius* are found to be stem turtles and to have close relationships with *Mongolochelys efremovi* and meiolaniids. This clade constitutes a side branch of stem turtles which existed alongside crown-group turtles up until the Pleistocene. The Middle Jurassic *Siamochelys peninsularis*, which is also included in a phylogenetic analysis for the first time, is found to be a xinjiangchelyid. A phenomenon of 'morphological long-branch attraction' resulting from the inclusion of relatively convergent extant pleurodires draw panpleurodires into eucryptodires. When extant pleurodires are removed from the data matrix, the panpleurodires form a polytomy with *Kallokibotion bajazidi* and pancryptodires (including eucryptodires and paracryptodires). This agrees with the commonly accepted pattern of relationships. *Arundelemys dardeni* and *Dorsetochelys delairi* are found to be pleurosternids and the characters supporting this clade agree retrospectively with the attribution of the Kirtlington material to pleurosternids.

FUTURE WORK

- *Reassessment of the Late Jurassic and Early Cretaceous European turtle fauna* — The systematics and relationships of the turtles generally referred to the plesiochelyids, thalassemydids, and eurysternids are unclear. According to most available phylogenetic analyses, these turtles appear to be the most basal members of Eucryptodira and are consequently important for the resolution of the relationships of this clade with the paracryptodires and panpleurodires. More generally, these species are known mainly from shell material and their inclusion in a phylogenetic framework requires a necessary reassessment of the shell characters used for cladistic analyses.

- *Multiple adaptations to marine environment* — Adaptation to marine environment was long thought to have occurred only once within pancryptodires (in panchelonioids), but the recent placement of the protostegid *Santanachelys gaffneyi* along the base of the phylogenetic stem of crown-group cryptodires and the marine isotopic signature recovered from plesiochelyid shell bones suggest a more complex scenario involving multiple adaptations to marine environment. A thorough and reliable phylogeny of basal pancryptodires is a prerequisite for understanding these multiple events.

- *Improving current phylogenetic hypotheses* — The grounds on which are based current phylogenetic analyses of turtle interrelationships are partly unstable. This is mainly due to a relatively low number of available characters and a high level of homoplasy. An intensive search for new characters and a reassessment of primary homology statements are needed to improve these results. Future analyses would also need to include representatives of basal pleurodires in order to prevent the phenomenon of 'morphological long-branch attraction' caused by the inclusion of relatively convergent extant pleurodires.

APPENDIX 1: GLOSSARY OF TURTLE SKULL NOMENCLATURE

Following Parsons & Williams (1961), Gaffney (1972) proposed a glossary of turtle skull nomenclature in order to standardise the multitude of synonymous anatomical terms used to describe the turtle skull. This glossary was subsequently updated by Gaffney (1979) and most fossil turtle specialists now follow this terminology. In order to simplify the reading of the present dissertation, this glossary is reproduced, and slightly updated, below.

ADITUS CANALIS STAPEDIO-TEMPORALIS—The posteroventral opening of the canalis stapedio-temporalis into the roof of the cavum acustico-jugulare; in most cases formed by the quadrate and prootic. The arteria stapedialis passes through it.

ANTRUM POSTOTICUM—Generally a cone-shaped cavity with apex pointing posteriorly and base opening into the posterodorsal region of the cavum tympani into which it grades gradually in most genera. The incisura columellae auris in most cases marks the anteroventral limits of the antrum. The antrum is formed by the squamosal and quadrate.

APERTURA NARIUM EXTERNA—The external bony openings of the nares; formed by the prefrontals, maxillae, premaxillae and nasals, when present.

APERTURA NARIUM INTERNA—The internal bony opening of the nares, in most cases on the palate. The bones involved vary somewhat. In most turtles (*Chelydra*, for example) the vomer, maxilla, and palatine bones outline the apertura. In most pelomedusids the vomer is lost, whereas in many chelonioids (particularly living cheloniids) the development of a secondary palate excludes the maxillae; the palatines and vomer are the principal elements.

AREA ARTICULARIS MANDIBULARIS—The area on the lower jaw that articulates with the condylus mandibularis of the quadrate; consists primarily of the articular bone.

BASIS COLUMELLAE—The medial, expanded end of the columella auris, fits into the fenestra ovalis. See columella auris.

BASIS TUBERCULI BASALIS—An oval tubercle generally situated on the midline of the skull at the union of the basisphenoid and basioccipital on the floor of the cavum cranii. Most of the tubercle is generally on the latter bone. "Gives attachment to the bifid ligament of the medulla" (Kesteven, 1910, p. 376).

CANALIS ALVEOLARIS INFERIOR—A canal extending anteriorly for most of the length of the dentary, beginning at the foramen alveolare inferius. Soliman (1964, figs. 11-13) indicated that the ramus alveolaris inferior (V_3), the ramus cutaneus externus (V_3), and small blood vessels traverse the canalis.

CANALIS ALVEOLARIS SUPERIOR—This canal roughly parallels the lateral edge of the outer maxillary surface on the floor of the fossa orbitalis; has connections to the foramen alveolare superius and the canalis infraorbitalis. "The superior alveolar artery goes through the foramen alveolare superius and into the canalis alveolaris superior" (Albrecht, 1967, p. 90).

CANALIS CAROTICO-PHARYNGEALIS—A canal formed in the pterygoid bone, directed and opening ventrally, and communicating dorsally with the canalis caroticus lateralis. Albrecht (1967, pp. 85, 86) reported it in *Chrysemys* and *Sternotherus*. The arteria carotico-pharyngealis is transmitted by this canal.

CANALIS CAROTICUS INTERNUS—A pair of canals curving anteromedially, from the posterior region of the skull through the basicranium to an opening in the basisphenoid at the posterior end of the sella turcica; in most cases formed at least in part by the pterygoid, basisphenoid and sometimes the prootic; contains the arteria carotica interna.

CANALIS CAROTICUS LATERALIS—"In *Chrysemys*, *Sternotherus*, and *Trionyx*, the canalis caroticus on each side of the skull gives off an anterior canal in the pterygoid bone which opens into the sulcus cavernosus directly lateral to the basisphenoid" (Albrecht, 1967, p. 84). The "anterior canal" is the canalis caroticus lateralis and carries the arteria palatina in the first two genera and the arteria pseudopalatina in *Trionyx*.

CANALIS CARTILAGINIS MECKELII—Any part of the sulcus cartilaginis meckelii that is roofed over by bone to form a canal.

CANALIS CAVERNOSUS—The canal that is continuous posteriorly with the sulcus cavernosus (and is essentially the sulcus closed over); runs on the floor of the cavum cranii on either side of the basisphenoid posterolaterally beneath the aditus canalis stapedio-temporalis and into the cavum acustico-jugulare. The canalis and sulcus contain the vena capitis lateralis and represent the cranio-quadrate space of other vertebrates.

CANALIS CHORDA TYMPANI MANDIBULARIS—The canal in the lower jaw that contains the chorda tympani branch of the facial (VII) nerve; formed in most cases by the articular and prearticular bones.

CANALIS CHORDA TYMPANI QUADRATI—The canal in the quadrate bone between the foramen chorda tympani superius and the foramen chorda tympani inferius. The chorda tympani branch of the facial (VII) nerve exits from the skull via this canal.

CANALIS INFRAORBITALIS—A canal beginning medially at the foramen supramaxillare and extending anterolaterally to the canalis alveolaris superior; contains the arteria supramaxillaris in *Chrysemys*, *Sternotherus*, and *Trionyx* (Albrecht, 1967); is in most cases contained in the maxilla.

CANALIS INTRAPALATINUS—A canal found in *Trionyx* (but not in *Sternotherus* or *Chrysemys*) that connects the foramen palatinum accessorium with the foramen palatinum posterius and is formed by the palatine bone (Albrecht, 1967, p. 88); transmits a small branch of the arteria inframaxillaris.

CANALIS NERVI ABDUCENTIS—A paired canal in the lateral part of the dorsum sellae in the basisphenoid. The abducent (VI) nerve traverses this canal.

CANALIS NERVI VIDIANI—A canal that extends anteriorly along the side of the basicranium in the pterygoid and/or palatine bones; in most cases begins in the foramen pro ramo nervi vidiani and ends in the foramen palatinum posterius in cryptodires. The palatine branch (vidian nerve) of the facial (VII) nerve and in some cases, small arteries (Albrecht, 1967) traverse the canalis.

CANALIS SEMICIRCULARIS ANTERIOR—Strictly speaking the term canalis semicircularis should refer only to the membranous endolymphatic canals of the inner ear and not to the bony canals which contain them. The bony canals are variable in their enclosure of the membranous canals which tend to be rather consistent in vertebrates. However, it is common practice to use the term canalis as I do here for the bony canals; canalis semicircularis anterior extends from the recessus labyrinthicus supraoccipitalis to the recessus labyrinthicus prooticus; formed by the supraoccipital and prootic.

CANALIS SEMICIRCULARIS HORIZONTALIS—Extends from the recessus labyrinthicus prooticus to the recessus labyrinthicus opisthoticus; is in most cases formed by the prootic and opisthotic.

CANALIS SEMICIRCULARIS POSTERIOR—Extends from the recessus labyrinthicus supraoccipitalis to the recessus labyrinthicus opisthoticus; formed by the supraoccipital and opisthotic.

CANALIS STAPEDIO-TEMPORALIS—The passage of the arteria stapedialis from the aditus canalis stapedio-temporalis in the cavum acustico-jugulare to the fossa temporalis superior; formed between the quadrate and prootic.

CARTILAGO TRANSILIENS—The sliding sesamoid cartilage at the site of contact between the external tendon (the main adductor aponeurosis or "Bodenaponeurosis") on either the processus trochlearis oticum (cryptodires) or the processus trochlearis pterygoidei (pleurodires). This cartilage may ossify; is generally meniscus-shaped.

CAVUM ACUSTICO-JUGULARE—A large cavity in the posteroventral region of the skull approximately between the cavum tympani and the cavum labyrinthicum; contains the columella auris, the arteria stapedialis, the vena capitis lateralis, the glossopharyngeal (IX) nerve, the hyomandibular (posterior) branch of the facial (VII) nerve, and the vena cerebralis posterior. The processus interfenestralis tends to separate a small area including the recessus scalae tympani, which is posteromedial to the main part of the cavum. The posterior wall of the cavum acustico-jugulare is in most cases unossified and named the fenestra postotica. The cavum acustico-jugulare is bound anteriorly and laterally by the quadrate, medially by the prootic and opisthotic, ventrally by the pterygoid, and dorsally by the quadrate and opisthotic.

CAVUM CRANII—The large central space occupying the area from the fossa nasalis to the foramen magnum; is defined by bone, and an endocranial cast would be a replica of it. The brain and dura mater are the principal occupants of the cavum in life. Most of the median bones in the skull participate in the formation of the cavum cranii.

CAVUM LABYRINTHICUM—The bony inner ear cavity, formed by the prootic anteriorly, the opisthotic posteriorly, and the supraoccipital dorsally. In life, the bony capsule is usually completed by cartilage medially (the hiatus acusticus) and ventrally. The cavum contains the membranous labyrinth of the inner ear.

CAVUM TYMPANI—A large concavity, opening laterally, in the posterior region of the skull; houses the tympanic organ (middle ear) and distalmost portion of the columellae auris. The incisura columellae auris lies in the centre of the cavum tympani and is in most cases the most medial portion of the cavum. Most of the cavum is formed by the quadrate with some contribution from the squamosal. The antrum postoticum is continuous with, and lies posterodorsal to, the cavum.

COLUMELLA AURIS—The bony rod (stapes) extending from the fenestra ovalis laterally across the cavum acustico-jugulare and through the incisura columellae auris into the cavum tympani. In most cases the lateral end is finished in cartilage, the extrastapes or extracolumella. This structure transmits sounds from the tympanic organ to the inner ear.

CONDYLUS MANDIBULARIS—The distal end of the processus articularis of the quadrate that articulates with the area articularis mandibularis of the lower jaw.

CONDYLUS OCCIPITALIS—The posteriorly projecting end of the occiput that articulates with the axis-atlas complex.

CRISTA DORSALIS BASIOCCIPITALIS—The sagittal crest on the dorsal surface of the basioccipital just posterior to the basis tuberculi basalis.

CRISTA PTERYGOIDEA—A vertical plate rising from the main body of the pterygoid, and sutured to the parietal dorsally. Together with the processus inferior parietalis it forms a lateral wall between the cavum cranii and the fossa temporalis inferior.

CRISTA SUPRAOCCIPITALIS—The sagittal crest of the supraoccipital in the posterodorsal part of the skull. The parietal may contribute to this crest in some cases. The adductor mandibulae externus musculature attaches along the crista. The crista may develop a posteriorly projecting spine and/or horizontal plate in some genera.

DORSUM SELLAE—A raised area in the centre of the dorsal surface of the basisphenoid just posterior to the sella turcica. A processus clinoideus extends anteriorly from each side.

FENESTRA OVALIS—The lateral opening of the cavum labyrinthicum into the cavum acustico-jugulare. The prootic forms the anterior border and the opisthotic the posterior border, whereas the ventral limits are formed by cartilage in life, but in the dried skull the fenestra is incomplete ventrally. In life, the basis columellae fits into and fills the fenestra ovalis and there is no free communication here between the cavum labyrinthicum and the cavum acustico-jugulare.

FENESTRA PERILYMPHATICA—An opening between the cavum labyrinthicum and the recessus scalae tympani of the cavum acustico-jugulare, formed mostly by the processus interfenestralis of the opisthotic; may be completely contained within the opisthotic or may have a ventromedial contribution from the basioccipital. Baird (1960, fig. 49) indicated that the periotic sac of the inner ear extends posteriorly through this opening.

FENESTRA POSTOTICA—The posterior opening of the cavum acustico-jugulare; may be continuous laterally with the incisura columellae auris or medially with the foramen jugulare posterius, partially filled with cartilage in life; usually bordered by the exoccipital, quadrate, pterygoid, opisthotic, and sometimes the basioccipital. The following structures usually traverse the fenestra postotica: the stapedial artery, the lateral head vein, the vena cerebralis posterior, the glossopharyngeal (IX) nerve, the vagus (X) nerve, the accessory (XI) nerve and the hyomandibular branch of the facial (VII) nerve. The fenestra may be subdivided to a variable extent so that some or all of the above structures have their own foramen.

FENESTRA SUBTEMPORALIS—The ventral opening of the fossa temporalis inferior. The adductor jaw musculature, mandibular artery, and V_3 branch of the trigeminal nerve descend through this opening to the lower jaw. The quadrate, pterygoid, maxilla, jugal and quadratojugal form the margins of the fenestra subtemporalis in most cases.

FISSURA ETHMOIDALIS—A fissure developed in the midline of the posterior wall of the fossa nasalis above, and confluent with, the sulcus vomeri below; transmits the olfactory (I) nerves dorsally, ventrally filled with cartilage to form a canal for the nerves in life. Usually formed by prefrontals.

FORAMEN ALVEOLARE INFERIUS—The posterior opening into the canalis alveolaris inferior in the dentary; is in most cases in the posterior portion of the sulcus cartilaginis meckelii on the medial (internal) face of the mandible.

FORAMEN ALVEOLARE SUPERIUS—The medial opening of the canalis alveolaris superius into the fossa nasalis; contains the arteria alveolaris superior (Albrecht, 1967); is in most cases formed by the maxilla.

FORAMEN ANTERIUS CANALIS CAROTICI INTERNI—Paired foramina in the dorsal surface of the basisphenoid in most cases opening at the posterior margin of the sella turcica. These foramina are the anterior openings of the canalis caroticus internus. The medialmost branch of the arteria carotica internus enters into the cavum cranii here.

FORAMEN ANTERIUS CHORDA TYMPANI—The anterior opening of the canalis chorda tympani mandibularis in the lower jaw; contains the chorda tympani branch of the facial (VII) nerve; opens into the fossa meckelli in *Chelydra* and is formed by the articular and prearticular bones. In *Podocnemis*, however, it opens on the medial face of the prearticular (Fuchs, 1931, pl. 2, fig. 5b).

FORAMEN AQUADUCTI VESTIBULI—A notch or foramen in the medioventral wall of the cavum labyrinthicum in the supraoccipital bone; opens into the cavum cranii and transmits the endolymphatic duct from the sacculus to the endolymphatic sac.

FORAMEN ARTERIAE ANTERIOVIDIANAE—A small opening on the dorsal surface of the pterygoid anterior to the anterior end of the crista pterygoidea, posteromedial to the dorsal foramen palatinum posterius in *Sternotherus* (Albrecht, 1967, p. 87), contains the anterior vidian artery in *Sternotherus*.

FORAMEN ARTERIAEVIDIANAE—A series of "very small canals opening in the ventral surface of the palatine bone medial to the ventral foramen palatinum posterius..." (Albrecht, 1967, p. 87) in *Sternotherus*. A variable number of branches of the arteria anterior vidianae exit through these foramina to the roof of the mouth.

FORAMEN CAROTICO-PHARYNGEALE—A ventral opening (or series of openings) in the pterygoid connecting with the canalis caroticus lateralis. The arteria carotico-pharyngealis exits from the skull through this foramen.

FORAMEN CAROTICUM LATERALE—"In *Chrysemys*, *Sternotherus*, and *Trionyx*, the canalis caroticus internus on each side of the skull gives off an anterior canal (the canalis caroticus lateralis) in the pterygoid bone which opens into the sulcus cavernosus directly lateral to the basisphenoid" (Albrecht, 1967, p. 84). This opening is the foramen caroticum laterale, and in *Chrysemys* and *Sternotherus* (and most cryptodires) it carries the arteria palatina, whereas in *Trionyx* the arteria mandibularis passes through it.

FORAMEN CAVERNOSUM—The anterior opening of the canalis cavernosus into the cavum cranii proper; is thus placed between the canalis cavernosus and the sulcus cavernosus; traversed by the lateral head vein and, in most cryptodires, by the mandibular artery; usually formed by the pterygoid ventrally and the prootic dorsally. The posterior margin of the foramen nervi trigemini may also be the lateral margin of the foramen cavernosum. Thus, the foramen cavernosum is usually visible in anterolateral view through the foramen nervi trigemini.

FORAMEN CHORDA TYMPANI INFERIUS—The ventral and lateral opening of the canalis chorda tympani quadrati; contains the chorda tympani branch of the facial (VII) nerve and usually occurs on the posterior face of the quadrate just below the incisura columellae auris.

FORAMEN CHORDA TYMPANI SUPERIUS—The dorsal and medial opening of the canalis chorda tympani quadrati containing the chorda tympani branch of the facial (VII) nervi; is formed on the medial face of the quadrate near the incisura columellae auris.

FORAMEN DENTOFACIALE MAJUS—An opening on the lateral surface of the lower jaw within the posterodorsal margin of the dentary; opens into a short canal (not named here) that extends anteroventromedially into the canalis alveolaris inferior.

FORAMEN EXTERNUM NERVI GLOSSOPHARYNGEI—The opening containing the glossopharyngeal (IX) nerve as it enters the cavum acustico-jugulare in the dorsal portion of the processus interfenestralis of the opisthotic.

FORAMEN INTERMANDIBULARIS CAUDALIS—A small opening between the ventral region of the fossa meckelii and the medial surface of the lower jaw. The ramus intermandibularis caudalis of the mandibular of the mandibular (V3) nerve passes through this structure. The foramen is in most cases on the angular-prearticular suture but may not be completely surrounded by bone.

FORAMEN INTERMANDIBULARIS MEDIUS—The large anterior opening of the fossa meckelii on the medial surface of the lower; is in most cases bounded posteriorly by the prearticular and anteriorly by the dentary. The ramus intermandibularis medius of the mandibular (V3) nerve and in some cases (as in *Chelydra*) the meckelian cartilage are contained in the foramen.

FORAMEN INTERMANDIBULARIS ORALIS—A small opening or notch communicating between the anterior region of the fossa meckelii and the medial surface of the lower jaw. The ramus intermandibularis oralis of the mandibular (V_3) nerve passes through this structure. The foramen is formed by the prearticular and angular in *Chelydra* but may be present only as a notch or indentation in the angular or prearticular.

FORAMEN INTERMAXILLARIS—An unpaired median opening found in the anterior region of the palate in *Carettochelys* and most trionychids. Formed primarily by the maxillae with contributions from the vomer and/or premaxillae in some forms. In *Carettochelys* the foramen intermaxillaris is apparently confluent with the apertura narium interna.

FORAMEN INTERNUM NERVI GLOSSOPHARYNGEI—The opening at the point of exit of the glossopharyngeal (IX) nerve from the cavum labyrinthicum into a canal leading to the foramen externum nervi glossopharyngei. Both foramina are in the opisthotic. The foramen internum is absent when the glossopharyngeal passes to the outside without actually entering the cavum labyrinthicum.

FORAMEN INTERORBITALE—The paired openings between the orbits filled in life with cartilage; traversed by the optic nerves (II), portion of the eye muscles and the oculomotor (III), trochlearis (IV), a branch of the trigeminal (V) cranial nerves. Dorsally, the ridge defining the sulcus olfactorius forms a border for the foramen interorbitale. The following bones may take part in the formation of the foramen interorbitale: prefrontal, frontal, parietal, epipterygoid, pterygoid, palatine, and vomer.

FORAMEN JUGULARE ANTERIUS—The opening between the cavum cranii and the recessus scalae tympani portion of the cavum acustico-jugulare through which pass the vagus (X) and accessory (XI) nerves and the vena cerebralis posterior (or vena jugularis of mammals). The foramen is usually bounded anteriorly by the opisthotic and posteriorly by the exoccipital.

FORAMEN JUGULARE INTERMEDIUM—[This anatomical term has been subsequently coined by Sterli & Joyce (2007)] In basalmost turtles (e.g., *Proganochelys quenstedti*, *Kayentachelys aprix*, and *Eileanchelys waldmani*), there are no proper recessus scalae tympani or ossified posterior wall to the cavum acustico-jugulare developed by the exoccipital and opisthotic. Consequently, there is no foramen jugulare posterius (see below). Instead, there is a large foramen formed by the exoccipital and the posteromedial border of the processus interfenestralis of the opisthotic. This foramen, called foramen jugulare intermedium, splits into two channels, the foramen jugulare anterius medially and the fenestra perilymphatica laterally.

FORAMEN JUGULARE POSTERIUS—An opening formed mostly by the exoccipital communicating between the recessus scalae tympani (a part of the cavum acustico-jugulare) and the outside of the skull; faces posteriorly and may be confluent with the fenestra postotica or completely absent; is traversed by the vena cerebralis posterior and in some cases by the vagus (X) and accessory (XI) nerves.

FORAMEN MAGNUM—The large medial opening at the posterior end of the skull, opening posteriorly and placed just above the condylus occipitalis; transmits the spinal cord from the cavum cranii to the outside of the skull. The following bones may be involved in the formation of the foramen magnum: supraoccipital, exoccipital, and basioccipital.

FORAMEN MEDIALIS NERVI GLOSSOPHARYNGEI—The exit of the glossopharyngeal (IX) nerve from the cavum cranii occurs either in cartilage (the hiatus acusticus) or in bone; when ossified, this structure is usually found in the opisthotic.

FORAMEN NERVI ABDUCENTIS—The anterior and posterior openings of the canalis nervi abducentis. The abducent (VI) nerve enters and exits via these foramina in the basisphenoid.

FORAMEN NERVI ACUSTICI—The foramina, in most cases in the fossa acustico-facialis, through which the branches of the acoustic (VIII) nerve exit from the cavum cranii and enter the cavum labyrinthicum. There are usually two foramina and these are formed by the prootic bone.

FORAMEN NERVI AURICULOTEMPORALIS—An opening (may be more than one) in the posterior portion of the lateral surface of the lower jaw containing the auriculotemporalis nerve of Fuchs (1931) which appears to be the ramus cutaneus recurrens branch of the mandibular (V_3) nerve of Soliman (1964, fig. 15). The foramen or foramina are in most cases formed by the surangular bone.

FORAMEN NERVI FACIALIS—The opening, in most cases in the fossa acustico-facialis in the prootic bone, through which the facial (VII) nerve exits from the cavum cranii and enters the sulcus cavernosus; may communicate with the foramen pro ramo nervi vidiani. This term is used for the opening visible in sagittal view as well as the short canal and more ventral opening into the canalis cavernosus.

FORAMEN NERVI HYPOGLOSSI—The opening by which branches of the hypoglossal (XII) nerve leave the cavum cranii. The foramina nervi hypoglossi are in general formed by the exoccipital bone and in some cases by the basioccipital.

FORAMEN NERVI TRIGEMINI—The opening between the cavum cranii and the fossa temporalis inferior, in most cases bordered, at least in part, by the prootic posteriorly, the pterygoid (and sometimes the epipterygoid) ventrally, and the parietal dorsally. Two branches (V_2, V_3)

of the trigeminal (V) nerve exit here along with the arteria mandibularis in most cryptodires (Soliman, 1964; Albrecht, 1967). Only the nerves exit in pleurodires.

FORAMEN NERVI VIDIANI—Any opening in the canalis nervi vidiani into the cavum cranii. The palatine branch of the facial (VII) nerve and various small arteries in most cases traverse this foramen. The foramen (or foramina) is usually formed by the pterygoid and/or palatine bones.

FORAMEN ORBITO-NASALE—An opening between the fossa nasalis and the fossa orbitalis generally situated in the posteroventrolateral region of the fossa nasalis, transmits the posterior nasal artery from the fossa orbitalis to the fossa nasalis (Albrecht, 1967). The prefrontal, palatine, and maxilla in most cases participate in the formation of the foramen orbito-nasale.

FORAMEN PALATINUM ACCESSORIUM—In *Trionyx*, the ventral opening (actually a variable number of small foramina) of the canalis intrapalatinus in the palatine bone (Albrecht, 1967, p. 88). A small branch of the inframaxillary artery goes through the canalis intrapalatinus and exits through these foramina to supply tissue on the roof of the mouth (Albrecht, 1967, p. 94).

FORAMEN PALATINUM POSTERIUS—An opening between the palatal surface of the skull and the area just behind the fossa orbitalis (pleurodires) or at the posteriormost limits of the fossa orbitalis (cryptodires); transmits the inframaxillary artery from the skull to the palate (Albrecht, 1967). The maxilla, palatine, and pterygoid may participate in the formation of the foramen palatinum posterius.

FORAMEN POSTERIUS CANALIS CAROTICI INTERNI—The most posterior opening of the canalis caroticus internus. The arteria carotica interna enters the canalis at this foramen; in most cryptodires the pterygoid forms the foramen but in baenoids it is formed by the basisphenoid and pterygoid. In pleurodires the foramen is usually formed by the prootic and sometimes the quadrate.

FORAMEN POSTERIUS CHORDA TYMPANI—The posterior opening of the canalis chorda tympani mandibularis in the lower jaw; contains the chorda tympani branch of the facial (VII) nerve. The foramen is formed by the articular and prearticular and occurs on the medial edge of the area articularis mandibularis in *Chelydra*.

FORAMEN PRAEPALATINUM—Paired foramina in the anterior part of the palate that extend between the palate and fossa nasalis; transmit the anterior nasal artery from the palate into the nasal tissue (Albrecht, 1967, p. 94; Seydel, 1896); in most cases formed by the vomer and premaxilla.

FORAMEN PRO RAMO NERVI VIDIANI—A short canal connecting the canalis caroticus internus with the canalis cavernosus; transmits the vidian nerve (palatine branch of VII) and a small branch of the internal carotid artery (Albrecht, 1967). The foramen is usually just ventral to the opening of the foramen nervi facialis into the canalis cavernosus. The canalis nervi vidiani in most cases extends anteriorly from the foramen pro ramo nervi vidiani and contains branches of the vidian nerve and blood vessels (Albrecht, 1967, p. 87). It is usually formed by the prootic and pterygoid. The foramen is apparently absent in pleurodires.

FORAMEN STAPEDIO-TEMPORALE—The dorsal opening of the canalis stapedio-temporalis into the fossa temporalis. The arteria stapedialis passes through this structure. The prootic and quadrate form the foramen stapedio-temporale.

FORAMEN SUPRAMAXILLARE—An opening in the maxilla in the floor of the fossa orbitalis; the foramen supramaxillare leads into the canalis infraorbitalis and transmits the arteria supramaxillaris (Albrecht, 1967).

FORAMEN SUPRAORBITALE—An "extremely small arterial foramen... located on the prefrontal bone in the anterodorsal part of the orbit, dorsolateral from the dorsal edge of the fissura ethmoidalis" (Albrecht, 1967, p. 88); contains a branch of the arteria supraorbitalis (*ibid.*).

FOSSA ACUSTICO-FACIALIS—A depression in that part of the prootic that forms the lateral wall of the cavum cranii. There are usually three foramina in this fossa: the foramen nervi facialis and two foramina nervi acustici. The fossa contains the ganglion vestibulare (Soliman, 1964).

FOSSA CARTILAGINIS EPIPTERYGOIDEI—The space between the posteroventral process of the epipterygoid (or parietal if epipterygoid is absent) and the processus epipterygoideus of the quadrate which is occupied in life by a remnant of the palatoquadrate cartilage. The limits of the fossa are usually formed by the quadrate, pterygoid, and epipterygoid (or parietal).

FOSSA MECKELII—In the lower jaw, a space behind the processus coronoideus and anterior to the jaw articulation that is open dorsally and communicates anteriorly with the sulcus cartilaginis meckelii.

FOSSA NASALIS—The large, median cavity at the very front of the skull, anterior and median to the fossa orbitalis. This cavity houses the nasal capsules and cavities. The nasal (when present), prefrontal, maxilla, premaxilla, and vomer usually participate in the formation of this fossa.

FOSSA ORBITALIS—The bony socket for the eye, usually poorly defined and open to the fossa temporalis, cavum cranii, and fossa nasalis. The following bones usually form parts of the fossa orbitalis: prefrontal, maxilla, jugal, palatine, postorbital, and parietal.

FOSSA TEMPORALIS INFERIOR—The space below the level of the otic chamber and anterior to it and continuous with the fossa temporalis superior; contains the M. adductor mandibulae internus, part of the M. adductor mandibulae externus, and the M. pterygoideus. Parietal, postorbital, jugal, maxilla, quadratojugal, pterygoid, epipterygoid (when present), prootic, and quadrate in most cases are involved in forming the fossa temporalis inferior.

FOSSA TEMPORALIS SUPERIOR—The space above and behind the otic chamber and below the temporal roof (if present); contains the main mass of the M. adductor mandibulae externus. The following bones usually form the boundaries of the fossa temporalis superior: supraoccipital, parietal, prootic, opisthotic, quadrate, squamosal, postorbital, and exoccipital.

HIATUS ACUSTICUS—The large, irregular opening between the cavum cranii and the cavum labyrinthicum; in life it is occupied by a cartilaginous wall, which in some forms may be ossified. The following bones in most cases form the margins of the hiatus acusticus: supraoccipital, prootic, basisphenoid, basioccipital, and opisthotic. Siebenrock (1897, figs. 1-9) illustrated variable conditions of ossification of the bones surrounding the hiatus acusticus.

HIATUS POSTLAGENUM—An opening connecting the cavum labyrinthicum and the recessus scalae tympani. Dorsally it is formed by the ventral edge of the processus interfenestralis of the opisthotic and ventrally by the basioccipital. The term is modified from "postlagenar hiatus" of McDowell (1964) and is presumably equivalent to the canalis hypoperilymphaticus of Versluys (1936) and the ductus hypoperilymphaticus of Nick (1912) and deBeer (1937).

INCISURA COLUMELLAE AURIS—The groove or canal within the quadrate which contains the columella auris. In some turtles the incisura also contains the eustachian tube.

MEATUS CHOANAE—A tunnel or tube connecting the fossa nasalis and the apertura narium interna, not developed in most turtles.

PROCESSUS ARTICULARIS—The ventral process of the quadrate that bears the actual articulation with the lower jaw; the condylus mandibularis.

PROCESSUS CLINOIDEUS—Paired anterolateral spines on the basisphenoid, generally on either side of the dorsum sellae. The canalis nervi abducentis in most turtles penetrates the base of the processus.

PROCESSUS CORONOIDEUS—A dorsally directed process of the lower jaw generally developed on the coronoid bone; is found between the triturating surface and the fossa meckelii. Fibers of the M. adductor mandibulae externus attach on the processus along with the main external adductor tendon (Schumacher, 1954, 1955a, 1955b).

PROCESSUS EPIPTERYGOIDEUS—An anterior extension of the quadrate, generally found below the foramen nervi trigemini in the fossa subtemporalis; process generally extends toward the epipterygoid or a ventral extension of the parietal is the epipterygoid is absent.

PROCESSUS INFERIOR PARIETALIS—The ventral process of the parietal that forms a lateral wall for the cavum cranii; the processus generally has an extensive ventral contact with the crista pterygoidea and forms part of the lateral wall between the cavum cranii and the fossa temporalis.

PROCESSUS INTERFENESTRALIS—A ventral process of the opisthotic extending into the cavum acustico-jugulare and separating the cavum into two parts, lateral and posterior, the latter being the recessus scalae tympani. The foramen internum nervi glossopharyngei and foramen externum nervi glossopharyngei generally penetrate the dorsal portion of the process. The anterior surface of the processus walls the cavum labyrinthicum.

PROCESSUS PAROCCIPITALIS—The posterolateral process of the opisthotic that contacts the quadrate and squamosal laterally.

PROCESSUS PTERYGOIDEUS EXTERNUS—The lateral process of the pterygoid in cryptodires that extends around the anteromedial edge of the fossa temporalis inferior and may extend into the fossa. The lateral edge is generally produced into a vertical plate that acts as a guide for the lower jaw during adduction.

PROCESSUS TROCHLEARIS OTICUM—The extension or area on the otic chamber developed for an articular facet with the cartilago transiliens; it is generally borne mostly by the quadrate with a smaller contribution from the prootic, and is found only in cryptodires.

PROCESSUS TROCHLEARIS PTERYGOIDEI—A lateral extension of the pterygoid into the fossa temporalis inferior which supports the cartilago transiliens; the processus is generally convex outward and forward and is found only in pleurodires. Bears modified mundplatte.

RECESSUS LABYRINTHICUS OPISTHOTICUS—A hemispherical cavity off the cavum labyrinthicum in the opisthotic that houses the posterior ampulla and the union of the posterior and horizontal semicircular canals.

RECESSUS LABYRINTHICUS PROOTICUS—A hemispherical cavity off the cavum labyrinthicum in the prootic that houses the ampullae of the anterior and horizontal semicircular canals.

RECESSUS LABYRINTHICUS SUPRAOCCIPITALIS—A variously shaped cavity off the cavum labyrinthicum in the supraoccipital that houses the union of the anterior and posterior semicircular canals.

RECESSUS SCALAE TYMPANI—That portion of the cavum acustico-jugulare lying roughly posterior to the processus interfenestralis of the opisthotic. The vagus (X) and accessory (XI) nerves and the vena cerebralis posterior traverse the posterior part of the chamber. Most of the recessus is filled by the periotic sac (Baird, 1960) and it is usually formed by the pterygoid, opisthotic, exoccipital, and basioccipital.

ROSTRUM BASISPHENOIDALE—The anterior elongation of the basisphenoid anterior to the sella turcica.

SELLA TURCICA—The pit or depression in the anterior part of the dorsal surface of the basisphenoid that houses the pituitary.

SULCUS CARTILAGINIS MECKELII—A medially concave groove on the inside of the dentary bone extending anteriorly from the fossa meckelii.

SULCUS CAVERNOSUS—A long trough lying on the floor of the cavum cranii medial to the crista pterygoidea on the pterygoid and lateral to the rostrum basisphenoidale; begins at the anterior opening of the canalis cavernosus and continues anteromedially. The vena capitis lateralis travels along the sulcus.

SULCUS OLFACTORIUS—A ventrally open median trough extending from the cavum cranii into the fossa nasalis; carries the olfactory (I) nerve to the nasal capsule. The sulcus is usually formed by the prefrontal, frontal and parietal.

SULCUS VOMERI—A dorsally open, median groove extending posteriorly from the fossa nasalis and formed by the vomer; supports the cartilaginous septum nasalis (Soliman, 1964, figs. 12, 23).

TUBERCULUM BASIOCCIPITALE—Paired posterolateral processes formed on the ventral surface of the basioccipital.

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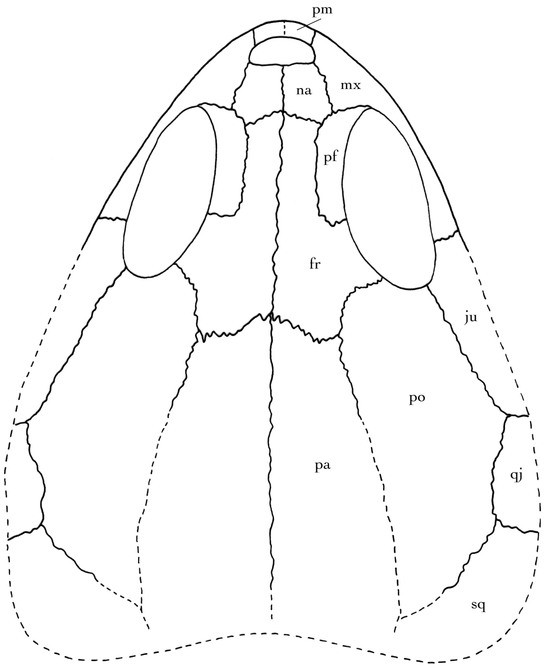
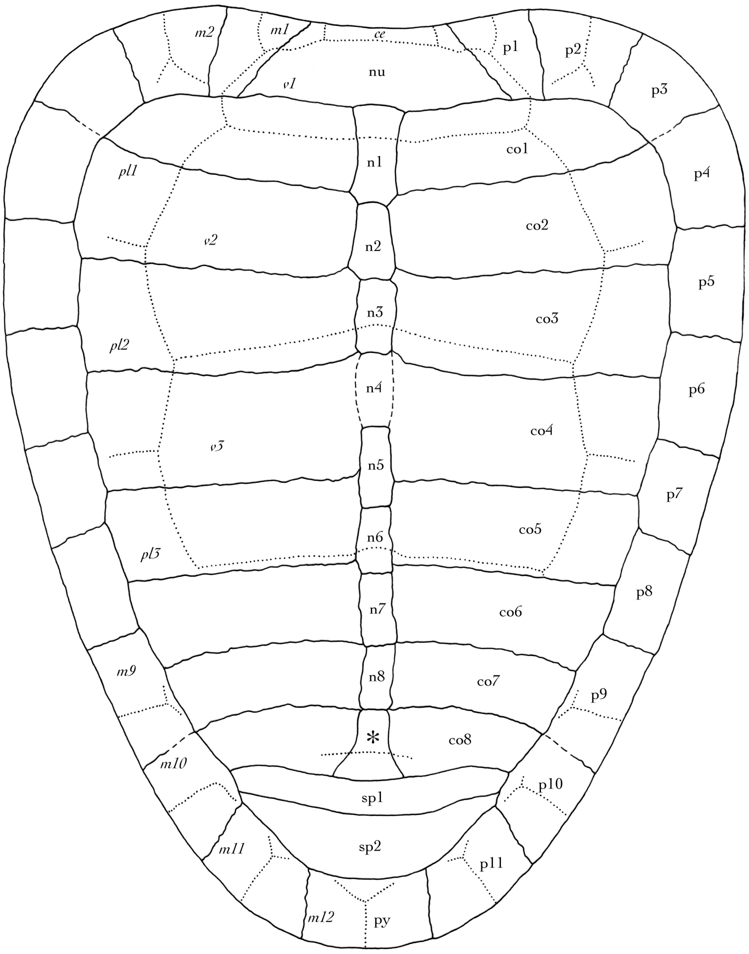
APPENDIX 2: RECONSTRUCTION OF THE SKULL AND CARAPACE OF *EILEANCHELYS WALDMANI*



Supplemental figure 1—Tentative reconstruction of the skull of *Eileanchelys waldmani* in dorsal view. Abbreviations: fr, frontal; ju, jugal; mx, maxilla; na, nasal; pa, parietal; pf, prefrontal; pm, premaxilla; po, postorbital; qj, quadratojugal; sq, squamosal.



Supplemental figure 2—Tentative reconstruction of the carapace of *Eileanchelys waldmani*. Epidermal scales are in italics. Abbreviations: ce, cervical scale; co, costal plate; m, marginal scale; n, neural plate; nu, nuchal plate; p, peripheral plate; pl, pleural scale; v, vertebral scale.

APPENDIX 3: SPECIMENS AND REFERENCES USED FOR THE PHYLOGENETIC ANALYSIS

Anthodon serrarius

Lee (1997)

Owenetta kitchingorum

Reisz & Scott (2002)

Simosaurus gaillardoti

Rieppel (1994)

Gephyrosaurus bridensis

Evans (1980, 1981)

Protorosaurus speneri

Gottmann-Quesada & Sander (2009)

Araeoscelidia

Reisz *et al.* (1984)

Captorhinidae

Fox & Bowman (1966), Heaton (1979) and Müller & Reisz (2005)

Odontochelys semitestacea

Li *et al.* (2008)

Proganochelys quenstedti

Gaffney (1990), personal observation of SMNS 15759, SMNS 16980, SMNS 17204 and MB R. 1854 (previously numbered MB 1910.45.2)

Palaeochersis talampayensis

Rougier *et al.* (1995), Sterli *et al.* (2007) and Sterli (2008)

Australochelys africanus

Gaffney & Kitching (1994, 1995), personal observation of BP/1/4933 (holotype and only known specimen)

Proterochersis robusta (= *Murrhardtia staeschei* Karl & Tichy 2000)

Gaffney (1986, 1990), Karl & Tichy (2000), personal observation of SMNS 16442, SMNS 16603, SMNS 17561, SMNS 17755, SMNS 17757 and SMNS 18440

Kayentachelys aprix

Gaffney *et al.* (1987), Sterli & Joyce (2007), Joyce & Sterli (pers. comm., 2007), personal observation of MCZ 8917, MCZ 8988, MNA V1558 (holotype), MNA V1563, MNA V2664, TMM 43651-1, TMM 43653-1 and TMM 43670-2

Indochelys spatulata

Datta *et al.* (2000)

Eileanchelys waldmani

Personal description of all currently known material (see Anquetin *et al.*, 2009 and present study)

Heckerochelys romani

Sukhanov (2006)

Condorchelys antiqua

Sterli (2008)

Meiolania platyceps

Gaffney (1983, 1985, 1996)

Ninjemys oweni

Gaffney (1992, 1996), personal observation of NHM R391 (holotype)

Niolamia argentina

Woodward (1901) and Gaffney (1996: 72)

Chubutemys copelloi

Gaffney *et al.* (2007)

Otwayemys cunicularius

Gaffney *et al.* (1998)

Mongolochelys efremovi

Khosatzky (1997), Sukhanov (2000) and Joyce (2007)

Kallokibotion bajazidi

Nopcsa (1923), Gaffney & Meylan (1992), personal observation of NHM R4918, NHM R4921 and NHM R4925

Platychelys oberndorferi

Wagner (1853), Bräm (1965), personal observation of BSPG AS I 1438 and MB R. 2424

Caribemys oxfordiensis

Fuente & Iturralde-Vinent (2001) and Cadena Rueda & Gaffney (2005)

Notoemys laticentralis

Fernandez & Fuente (1994) and Lapparent de Broin *et al.* (2007)

Elseya dentata

Scoring of Joyce (2007)

Chelodina oblonga

Gaffney (1979b) and scoring of Joyce (2007)

Phrynops geoffranus

Scoring of Joyce (2007)

Erymnochelys madagascariensis

Gaffney (1979b) and scoring of Joyce (2007)

Pelomedusa subrufa

Gaffney (1979b), scoring of Joyce (2007), personal observation of FMNH 17160 (extant reptile collection)

Podocnemis expansa

Gaffney (1979b), scoring of Joyce (2007), personal observation of FMNH 98958 (extant reptile collection)

Arundelemys dardeni

Lipka *et al.* (2006)

Dorsetochelys delairi

Evans & Kemp (1976)

Pleurosternon bullockii (= *Mesochelys durlstonensis* Evans & Kemp 1975)

Milner (2004), Evans & Kemp (1975), personal observation of all specimens at the NHM

Glyptops plicatulus

Gaffney (1979a), personal observation of AMNH 336

Dinochelys whitei

Gaffney (1979a) and Brinkman *et al.* (2000)

Neurankylus eximius

Gaffney (1972) and Brinkman & Nicholls (1993)

Trinitichelys hiatti

Gaffney (1972)

Plesiobaena antiqua

Gaffney (1972) and Brinkman (2003)

Boremys pulchra

Gaffney (1972), Brinkman & Nicholls (1991) and Lyson & Joyce (2009)

Baena arenosa

Gaffney (1972)

Chisternon undatum

Gaffney (1972)

Naomichelys speciosa

Personal observation of FMNH PR273

Sichuanchelys chowi

Ye & Pi (1997), Peng *et al.* (2005), personal observation of ZDM 3001 and ZDM 3017

Siamochelys peninsularis

Tong *et al.* (2002)

Chengyuchelys baenoides

Young & Chow (1953), Ye (1990a,b, 1994, 1996), Peng *et al.* (2005), Danilov & Parham (2008), personal observation of IVPP V708 (cast), IVPP V6507 and ZDM 3007

Chengyuchelys zigongensis

Ye (1982, 1990a,b, 1994), Fang (1987) and Peng *et al.* (2005)

'Chengyuchelys' dashanpuensis

Fang (1987), Ye (1990a,b, 1994) and Peng *et al.* (2005)

Xinjiangchelys tianshanensis

Nessov (1987, 1995), Kaznyshkin *et al.* (1990), Peng & Brinkman (1993) and Matzke *et al.* (2004)

Xinjiangchelys latimarginalis

Peng & Brinkman (1993), Brinkman & Wu (1999) and Matzke *et al.* (2004)

Xinjiangchelys qiguensis

Matzke *et al.* (2004)

Annemys levensis

Sukhanov (2000) and Sukhanov & Narmandakh (2006)

Portlandemys mcdowelli

Parsons & Williams (1961), Gaffney (1975c, 1976), personal observation of NHM R2914 (holotype), NHM R3163 and NHM R3164

Plesiochelys solodurensis

As described and figured as *Plesiochelys solodurensis* and *Plesiochelys etalloni* by Bräm (1965) and Gaffney (1975c, 1976). This follows the scoring of Joyce (2007).

Solnhofia parsonsi

Parsons & Williams (1961), Gaffney (1975b) and Joyce (2000)

'Thalassemys moseri'

Rieppel (1980)

Sandownia harrisi

Meylan *et al.* (2000)

Santanachelys gaffneyi

Hirayama (1998)

Hangaiemys hoburensis

Sukhanov & Narmandakh (1974), Sukhanov (2000) and Parham & Hutchison (2003)

Judithemys sukhanovi

Parham & Hutchison (2003)

Dracochelys bicuspis

Gaffney & Ye (1992) and Parham & Hutchison (2003)

Sinemys lens

Brinkman & Peng (1993b), personal observation of PMU.R 1500-1506 and PMU.R 1509

Ordosemys leios

Brinkman & Peng (1993a) and Brinkman & Wu (1999)

Toxochelys latiremis

Zangerl (1953), Gaffney (1979b) and Nicholls (1988)

Mesodermochelys undulatus

Hirayama & Chitoku (1996)

Caretta caretta

Gaffney (1979b) and scoring of Joyce (2007)

Chelonia mydas

Gaffney (1979b) and scoring of Joyce (2007)

Dermochelys coriacea

Gaffney (1979b), scoring of Joyce (2007) and personal observation of FMNH 171756

Protochelydra zangerli

Erickson (1973) and Gaffney (1975a)

Macrochelys temminckii

Gaffney (1979b), scoring of Joyce (2007) and personal observation of specimens at the FMNH including FMNH 39296, FMNH 51643, FMNH 211746 and FMNH 215473

Chelydra serpentina

Gaffney (1979b), scoring of Joyce (2007) and personal observation of specimens at the FMNH including FMNH 8717, FMNH 13058, FMNH 22056, FMNH 22337, FMNH 22413, FMNH 35322, FMNH 43908 and FMNH 217067

Platysternon megacephalum

Gaffney (1979b), scoring of Joyce (2007) and personal observation of FMNH 51627 (extant reptile collection)

Mongolemys elegans

Khosatzky & Mlynarski (1971) and Sukhanov (2000)

Gopherus polyphemus

Gaffney (1979b) and scoring of Joyce (2007)

Chrysemys picta

Gaffney (1979b), scoring of Joyce (2007) and personal observation of FMNH 22224 (extant reptile collection)

Geoclemys hamiltonii

Gaffney (1979b) and scoring of Joyce (2007)

Emarginachelys cretacea

Whetstone (1978) and Meylan & Gaffney (1989)

Baptemys wyomingensis

Hay (1908) and Meylan & Gaffney (1989)

Dermatemys mawii

Gaffney (1979b), scoring of Joyce (2007) and personal observation of FMNH 4163 and FMNH 98950 (extant reptile collection)

Hoplochelys crassa

Gilmore (1919)

Staurotypus triporcatus

Scoring of Joyce (2007)

Sternotherus odoratus

Gaffney (1979b), scoring of Joyce (2007) and personal observation of FMNH 211687 and FMNH 692 (extant reptile collection)

Kinosternon flavescens

Scoring of Joyce (2007) and personal observation of FMNH 6849 (extant reptile collection)

Zangerlia neimongolensis

Brinkman & Peng (1996), scoring supplemented using *Z. ukhaachelys* Joyce & Norell 2005 (this follows the scoring of Joyce, 2007)

Basilemys variolosa

Langston (1956), Brinkman (1998) and Hirayama *et al.* (2001)

Adocus beatus

Meylan & Gaffney (1989)

Peltochelys duchastelli

Meylan (1988)

Apalone ferox

Scoring of Joyce (2007)

Lissemys punctata

Gaffney (1979b) and scoring of Joyce (2007)

Pseudanosteira pulchra

Clark (1932) and Gaffney (1979b) as *Pseudanosteira?* for cranial character

Carettochelys insculpta

Gaffney (1979b) and scoring of Joyce (2007)

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APPENDIX 4: LIST OF CHARACTERS

1: Nasals: 0 = present; 1 = absent.

2: Medial contact of nasals: 0 = nasals contact one another medially along their entire length; 1 = medial contact of nasals partly or fully prevented by an anterior process of the frontal.

3: Size of nasals: 0 = dorsal exposure of nasals large, about the same size or larger than that of frontal; 1 = dorsal exposure of nasals greatly reduced relative to that of frontals.

4: Nasomaxillary sinus: 0 = absent; 1 = present.

5: Medial contact of prefrontals on the dorsal skull surface: 0 = absent; 1 = present, absence of contact between the nasal or apertura narium externa and the frontal.

6: Prefrontal-vomer contact: 0 = absent; 1 = present.

7: Prefrontal-palatine contact: 0 = present; 1 = absent.

8: Foramen orbito-nasale: 0 = absent; 1 = present.

9: Dorsal prefrontal exposure: 0 = present; 1 = absent or near absent.

10: Dorsal prefrontal exposure: 0 = large; 1 = reduced to small lappets.

11: Lacrimal: 0 = present; 1 = absent.

12: Lacrimal: 0 = elongate, enters the border of the external nares (apertura narium externa of turtles) and prevents the contact between maxilla and nasal and/or prefrontal; 1 = short, does not enter the border of the external nares and allows extensive contact between maxilla and nasal and/or prefrontal.

13: Frontal contribution to orbit: 0 = absent, contact between prefrontal and postorbital; 1 = present.

14: Postfrontal: 0 = present; 1 = absent.

15: Upper and lower temporal fenestrae: 0 = absent; 1 = present.

16: Parietal-squamosal contact: 0 = present, upper temporal emargination absent or poorly developed; 1 = absent, upper temporal emargination well developed.

17: Parietal contact with the pterygoid, epipterygoid, or palatine: 0 = absent, foramen nervi trigemini usually developed as a notch; 1 = present, foramen nervi trigemini clearly formed by the processus inferior parietalis.

18: Length of anterior extension of the lateral braincase wall: 0 = short, processus inferior parietalis only produces a narrow strut anterior to the foramen nervi trigemini, usually absence of contact with palatine; 1 = elongate, processus inferior parietalis produces an extended process anterior to the foramen nervi trigemini, contact with palatine commonly present.

19: Postparietal: 0 = present; 1 = absent.

20: Jugal-squamosal contact: 0 = present; 1 = absent, contact between postorbital and quadratojugal commonly present.

21: Jugal participation to upper temporal rim: 0 = absent; 1 = present, upper temporal emargination extensive.

22: Deep lower temporal emargination extending above the upper limit of the cavum tympani: 0 = absent; 1 = present, generally associated with a loss of the quadratojugal.

23: Quadratojugal-maxilla contact: 0 = absent; 1 = present.

24: Quadratojugal-squamosal contact below the cavum tympani: 0 = absent; 1 = present.

25: Squamosal-supraoccipital contact: 0 = absent; 1 = present.

26: Meiolaniid 'horns': 0 = absent; 1 = present.

27: Postorbital-palatine contact: 0 = absent; 1 = present, foramen palatinum posterius situated posterior to the orbital wall.

28: Postorbital-maxilla contact preventing the jugal from entering the orbital margin: 0 = absent; 1= present.

29: Postorbital-supratemporal contact: 0 = present; 1 = absent.

30: Supratemporal: 0 = present; 1 = absent.

31: Subdivision of the apertura narium externa by an internarial process of the premaxilla: 0 = present; 1 = absent.

32: Apertura narium externa subdivided by an internarial process formed by the nasal and premaxilla and somewhat recessed within the apertura: 0 = absent; 1 = present.

33: Fusion of the premaxillae: 0 = absent; 1 = present.

34: Foramen praepalatinum: 0 = present; 1 = absent.

35: Foramen intermaxillaris: 0 = absent; 1 = present.

36: Exclusion of the premaxillae from the apertura narium externa: 0 = absent; 1 = present.

37: Distinct medial premaxillary hook along the labial margin of the premaxillae: 0 = absent; 1 = present.

38: Accessory ridge on triturating surface: 0 = absent; 1 = present.

39: Teeth on the upper and lower jaws (maxilla, premaxilla and dentary): 0 = present; 1 = absent.

40: Maxillary contribution to orbital margin: 0 = maxillary entirely or largely excluded from the orbital margin by a lacrimal-jugal contact; 1 = maxillary forms most of the anteroventral edge of the orbit.

41: Vomer: 0 = present; 1 = absent or vestigial.

42: Vomer: 0 = paired; 1 = single.

43: Vomer shape: 0 = flat blade, either convex dorsally or horizontal; 1 = develops a ventral median septum and often a ventral horizontal plate contributing to an incipient secondary palate.

44: Vomer-pterygoid contact in palatal view: 0 = present; 1 = absent, medial contact of palatines present.

45: Vomerine and palatine teeth: 0 = present; 1 = absent.

46: Palatine contribution to the anterior extension of the lateral braincase wall: 0 = absent; 1 = present, well-developed.

47: Ventromedial process of the quadrate and/or ventral expansion of the prootic that partly floors the cavum acustico-jugulare: 0 = absent; 1 = present.

48: Central constriction of the middle ear by the quadrate: 0 = absent; 1 = present.

49: Cavum tympani: 0 = absent; 1 = present.

50: Precolumellar fossa: 0 = absent; 1 = present.

51: Antrum postoticum: 0 = absent; 1 = present.

52: Incisura columellae auris: 0 = absent; 1 = present.

53: Incisura columellae auris: 0 = open posteroventrally; 1 = closed by the quadrate.

54: Eustachian tube contained within the incisura columellae auris alongside the stapes: 0 = absent; 1 = present.

55: Epipterygoid: 0 = present; 1 = absent.

56: Shape of the epipterygoid: 0 = stout and pillar-shaped; 1 = laminar.

57: Pterygoid teeth: 0 = present: 1 = absent.

58: Basipterygoid articulation: 0 = open; 1 = fused.

59: Interpterygoid vacuity: 0 = present; 1 = absent.

60: Posterior process of the pterygoid that floors the cavum acustico-jugulare: 0 = absent; 1 = present.

61: Pterygoid-basioccipital contact: 0 = absent; 1 = present.

62: Processus trochlearis pterygoideus: 0 = absent; 1 = present.

63: Foramen palatinum posterius: 0 = present; 1 = absent.

64: Foramen palatinum posterius open laterally: 0 = absent; 1 = present.

65: Medial contact of pterygoid: 0 = present, pterygoids in medial contact with one another for at least part of their length; 1 = absent, contact of the basisphenoid with the vomer and/or palatines present.

66: Pterygoid contribution to foramen palatinum posterius: 0 = present; 1 = absent.

67: Intrapterygoid slit: 0 = absent; 1 = present.

68: Crista supraoccipitalis: 0 = poorly developed; 1 = protruding significantly posterior to the foramen magnum.

69: Large supraoccipital exposure on dorsal skull roof: 0 = absent; 1 = present.

70: Medial contact of exoccipitals dorsal to foramen magnum: 0 = absent; 1 = present.

71: Processus paroccipitalis: 0 = loosely articulated to squamosal and quadrate; 1 = tightly sutured to squamosal and quadrate.

72: Rostrum basisphenoidale: 0 = flat; 1 = rod-like, thick and rounded.

73: Paired pits on ventral surface of basisphenoid: 0 = absent; 1 = present.

74: Basispterygoid process: 0 = present; 1 = absent.

75: Position of the canalis stapedio-temporalis: 0 = posterior to fenestra ovalis between the paroccipital process of the opisthotic and the quadrate; 1 = anterior to fenestra ovalis between the quadrate and the prootic.

76: Foramen stapedio-temporale: 0 = present; 1 = absent.

77: Size of the foramen stapedio-temporale: 0 = relatively large (the size of a blood foramen); 1 = significantly reduced in size.

78: Foramen jugulare posterius formed by bone: 0 = absent; 1 = present, formed mostly by the exoccipital.

79: Foramen posterius canalis carotici interni formed by the prootic only: 0 = absent; 1 = present.

80: Foramen posterius canalis carotici interni positioned halfway along the suture between the basisphenoid and the pterygoid: 0 = absent; 1 = present.

81: Foramen posterius canalis carotici interni formed by the pterygoid and positioned near the posterior edge of this bone: 0 = absent; 1 = present.

82: Fenestra perilymphatica: 0 = large; 1 = reduced in size to that of a small foramen.

83: Medial contact of dentaries: 0 = fused; 1 = open suture.

84: Splenial: 0 : present; 1 = absent.

85: Lateral exposure of angular: 0 = exposed along one-third of the lateral surface of the posterior part of the mandible; 1 = exposed only as a small sliver (dorventrally short) or absent along the lateral surface of the mandible.

86: Bony turtle shell (i.e., a dorsal carapace, formed by neural bones fused to the neural arches of the underlying vertebra, costal bones fused to the underlying ribs, and generally peripheral elements connected laterally by a bridge to a ventral plastron formed by the clavicles, interclavicles and a series of three to five paired plates; see Zangerl, 1939, 1969; Gaffney & Meylan, 1988: 161): 0 = absent; 1 = present.

87: Carapacial scale sulci: 0 = present; 1 = absent or poorly developed.

88: Tricarinate carapace: 0 = absent; 1 = present.

89: Articulation of nuchal with neural spine of eighth cervical vertebra along a blunt facet: 0 = present; 1 = absent.

90: Raised pedestal on the visceral surface of the nuchal for the articulation with the neural spine of the eighth cervical vertebra: 0 = absent; 1 = present.

91: Elongate costiform processes of the nuchal: 0 = absent; 1 = present, process crosses peripheral 1 to contact peripheral 2 and sometimes peripheral 3.

92: Neural formula 6>4<6<6<6<6: 0 = absent; 1 = present.

93: Neurals: 0 = present; 1 = absent, allowing medial contact of all costals.

94: Partial reduction of the posterior neurals allowing medial contact of up to three posterior costals: 0 = absent; 1 = present.

95: Lateral contact of suprapygal 1 with peripherals: 0 = absent; 1 = present.

96: Peripherals: 0 = present; 1 = absent.

97: Number of peripherals: 0 = more than 11 pairs; 1 = 11 pairs or less.

98: Number of peripherals: 0 = 11 pairs or more; 1 = reduced to 10 pairs.

99: Anterior peripherals incised by musk ducts: 0 = absent; 1 = present.

100: Medial contact of the first pair of costal: 0 = absent; 1 = present, but complete set of neurals present.

101: Reduction of costal ossification: 0 = absent, costals fully or almost fully ossified, costal fontanelles small or absent; 1 = present, costals ossified only two thirds the length of the costal ribs, costal fontanelles well developed.

102: Cervical: 0 = present; 1 = absent, carapacial scales otherwise present.

103: Number of cervical scales: 0 = one cervical scale; 1 = more than one cervical scale present.

104: Marginal scales overlap onto costal plates: 0 = absent, marginals restricted to peripheral plates; 1 = present.

105: Supramarginals: 0 = present; 1 = absent.

106: Shape of vertebrals: 0 = vertebrals 2 to 4 significantly broader than pleurals; 1 = vertebrals 2 to 4 as narrow as, or narrower than, pleurals.

107: Position of vertebral 3-4 sulcus in taxa with five vertebrals: 0 = sulcus positioned on neural 6; 1 = sulcus positioned on neural 5.

108: Vertebral 3-4 sulcus with a distinct medial embayment: 0 = absent; 1 = present.

109: Vertebral 5: 0 = overlaps onto peripherals and often pygal posteriorly; 1 = does not overlap onto peripherals and pygal.

110: Connection between carapace and plastron: 0 = osseous; 1 = ligamentous.

111: Central plastral fontanelle: 0 = absent in adult individuals; 1 = present, even in adult individuals.

112: Plastral kinesis: 0 = absent, scale sulci and bony sutures do not overlap; 1 = present, scale sulci coincide with epiplastral-hyoplastral contact.

113: Anterior entoplastral process: 0 = present, medial contact of epiplastra absent; 1 = absent, medial contact of epiplastra present.

114: Size of the posterior entoplastral process: 0 = posterior process long, reaching as posteriorly as the mesoplastra; 1 = posterior process reduced in length.

115: Entoplastron: 0 = massive and cross- to diamond-shaped; 1 = strap like and V-shaped.

116: Dagger-shaped entoplastron: 0 = absent; 1 = present.

117: Entoplastron: 0 = present; 1 = absent.

118: Shape and contact of epiplastra: 0 = epiplastra sub-square in outline, minor posterior contact with hyoplastra; 1 = epiplastra elongate in shape, long posteromedial contact with hyoplastra.

119: Contacts of axillary buttresses: 0 = peripherals only; 1 = peripherals and first costal.

120: Mesoplastron: 0 = present; 1 = absent.

121: Mesoplastron: 0 = one pair present; 1 = two pairs present.

122: Medial contact of mesoplastra: 0 = present, or virtually present when a central plastral fontanelle is present, absence of contact between hyoplastron and hypoplastron; 1 = absent, partial contact between hyoplastron and hypoplastron present.

123: Contacts of inguinal buttresses: 0 = peripherals only; 1 = peripherals and costals.

124: Distinct anal notch: 0 = absent; 1 = present.

125: Shape of xiphiplastra: 0 = elongate rectangles; 1 = narrow struts that frame a xiphiplastral fontanelle.

126: Plastral scales: 0 = present; 1 = absent.

127: Midline sulcus of plastral scales: 0 = straight; 1 = distinctly sinuous, at least for part of its length.

128: Plastral scale set 1, gulars: 0 = one medially situated pair of scales present; 1 = one medially situated single scale present.

129: Plastral scale set 1, gulars: 0 = extending posteriorly onto entoplastron; 1 = limited to epiplastra only.

130: Plastral scale set 2, extragulars: 0 = present; 1 = absent.

131: Medial contact of plastral scale set 2, extragulars: 0 = absent; 1 = present, extragulars contacting one another posterior to gulars.

132: Anterior plastral tuberosities: 0 = present; 1 = absent.

133: Plastral scale set 8, intergulars: 0 = absent; 1 = present.

134: Plastral scale set 3, humerals: 0 = one pair present; 1 = two pairs present, subdivided by a plastral hinge.

135: Plastral scale set 4, pectorals: 0 = present; 1 = absent.

136: Plastral scale set 5, abdominals: 0 = present; 1 = absent.

137: Plastral scale set 5, abdominals: 0 = contact one another medially; 1 = absence of medial contact between abdominals.

138: Plastral scale set 7, anals: 0 = only cover parts of the xiphiplastra; 1 = overlap anteromedially onto the hypoplastra.

139: Inframarginal scales: 0 = present; 1 = absent.

140: Inframarginals scales: 0 = complete row present; 1 = only two pairs present (axillary and inguinal), limited contact between plastral scales and marginals present.

141: Cervical ribs: 0 = large cervical ribs present; 1 = cervical ribs reduced or absent.

142: Position of the transverse processes: 0 = middle of the centrum; 1 = anterior end of the centrum.

143: Posterior cervicals with strongly developed ventral keels: 0 = absent; 1 = present.

144: Eighth cervical centrum significantly shorter than seventh: 0 = absent; 1 = present.

145: Central articulations of cervical vertebrae: 0 = articulations not formed, cervical vertabrae amphicoelous or platycoelous; 1 = articulations formed, cervical vertebrae procoelous or opisthocoelous.

146: Articulation between second and third cervicals: 0 = 2(3; 1 = 2)3.

147: Articulation between third and fourth cervicals: 0 = 3(4; 1 = 3)4.

148: Articulation between fourth and fifth cervicals: 0 = 4(5; 1 = 4)5.

149: Articulation between fifth and sixth cervicals: 0 = 5(6; 1 = 5)6.

150: Articulation between sixth and seventh cervicals: 0 = 6(7; 1 = 6)7.

151: Articulation between seventh and eighth cervicals: 0 = 7(8; 1 = 7)8.

152: Articulation between the eighth cervical and the first dorsal vertebrae: 0 = along the vertebral centra and zygapophyses; 1 = along zygapophyses only.

153: Length of the first dorsal rib: 0 = long, extends full length of the first costal and may even contact the peripherals distally; 1 = short, extends less than halfway across the first costal.

154: Contact of dorsal ribs 9 and 10 with costals: 0 = present; 1 = absent.

155: Dorsal rib 10: 0 = long, spanning full length of costals and contacting peripherals distally; 1 = short, not spanning farther distally than pelvis.

156: Contact between dorsal vertebrae and dorsal ribs: 0 = transverse processes of all dorsal vertebrae in the middle or anterior part of the vertebral centra; 1 = dorsal ribs in contact with two successive vertebral centra.

157: Anterior articulation of the first dorsal centrum: 0 = faces at most slightly anteroventrally; 1 = faces strongly anteroventrally.

158: Chevrons: 0 = present on nearly all caudal vertebrae; 1 = absent, or only poorly developed, along the posterior caudal vertebrae.

159: Tail club: 0 = present; 1 = absent.

160: Caudal centra : 0 = amphicoelous; 1 = procoelous or opisthocoelous.

161: Morphology of the scapulocoracoid: 0 = horizontal blade with a dorsal process, not triradiate; 1 = triradiate in shape, with the development of an acromial process.

162: Cleithrum: 0 = present; 1 = absent.

163: Osseous contact of cleithrum with carapace: 0 = present; 1 = absent.

164: Length of acromial process: 0 = less than one half the length of scapular process; 1 = more than one half the length of scapular process.

165: Shape of acromial process: 0 = triradiate in section, acromial ridge present; 1 = rod-like.

166: Glenoid neck on scapula: 0 = absent; 1 = present.

167: Coracoid foramen: 0 = present; 1 = absent.

168: Sutural articulation of pelvis to shell: 0 = absent; 1 = present.

169: Elongated iliac neck: 0 = absent; 1 = present.

170: Shape of ilium articular site on the visceral surface of the carapace: 0 = narrow and pointed posteriorly; 1 = oval.

171: Posterior notch in acetabulum: 0 = absent; 1 = present.

172: Ischial contacts with plastron: 0 = contact via a large central tubercle; 1 = contact via two separate ischial processes.

173: Hypoischium: 0 = present; 1 = absent.

174: Fibula: 0 = bowed away from tibia; 1 = straight, not bowed away from tibia.

175: Phalangeal formula of the manus: 0 = 2-3-4-4-3 or more; 1 = digits 2 to 5 with three phalanges or less.

176: Reduced phalangeal formula of the manus; all digits with only one or two short phalanges: 0 = absent; 1 = present.

177: Paddles: 0 = absent; 1 = present.

178: Claw of the fifth digit of the pes: 0 = present; 1 = absent.

APPENDIX 5: MATRIX

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**
Anthodon serrarius	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	-	0	0
Owenetta kitchingorum	0	0	0	0	1	0	0	1	0	0	0	1	1	0	0	1	0	-	0	0
Simosaurus gaillardoti	0	1	1	0	0	0	0	0	0	1	1	-	1	0	1	0	0	-	1	1
Gephyrosaurus bridensis	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	-	1	0
Protorosaurus speneri	0	0	0	0	0	0	?	?	0	1	0	1	1	0	1	0	0	-	1	1
Araeoscelidia	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	0	-	0	0
Captorhinidae	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	-	0	0
Odontochelys semitestacea	0	0	0	?	0	?	?	?	0	0	?	?	?	1	0	0	?	?	1	?
Proganochelys quenstedti	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	-	1	0
Palaeochersis talampayensis	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	-	1	1
Australochelys africanus	?	?	?	?	?	?	?	?	?	?	0	?	?	?	0	0	?	?	?	?
Proterochersis robusta	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Kayentachelys aprix	0	0	1	0	0	?	0	?	0	1	1	-	1	1	0	0	?	?	1	1
Indochelys spatulata	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Eileanchelys waldmani	0	0	1	0	0	1	?	?	0	1	1	-	1	1	0	0	?	?	1	1
Heckerochelys romani	0	?	?	?	0	1	?	?	0	?	1	-	1	1	0	0	?	?	1	1
Condorchelys antiqua	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?
Meiolania platyceps	0	0	0	1	0	1	0	1	0	0	1	-	0	1	0	0	0	-	1	1
Ninjemys oweni	0	?	?	1	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?
Niolamia argentina	?	?	?	?	?	?	0	?	?	?	?	?	?	?	0	?	?	?	?	?
Chubutemys copelloi	?	?	?	?	1	?	?	?	0	0	1	-	0	1	0	0	?	?	1	?
Otwayemys cunicularius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Mongolochelys efremovi	0	0	1	0	0	1	0	1	0	0	1	-	0	1	0	0	?	?	1	1
Kallokibotion bajazidi	0	0	1	?	0	?	?	?	0	0	1	-	?	1	0	0	1	?	1	1
Platychelys oberndorferi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Caribemys oxfordiensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Notoemys laticentralis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Elseya dentata	0	1	1	0	0	0	1	1	0	1	1	-	1	1	0	0	1	1	1	1
Chelodina oblonga	0	1	1	0	0	0	1	1	0	1	1	-	1	1	0	1	1	1	1	1
Phrynops geoffranus	0	1	1	0	0	0	1	1	0	1	1	-	1	1	0	0	1	1	1	1
Erymnochelys madagascariensis	1	-	-	0	1	0	1	1	0	0	1	-	1	1	0	1	1	1	1	1
Pelomedusa subrufa	1	-	-	0	1	0	1	1	0	0	1	-	1	1	0	1	1	1	1	1
Podocnemis expansa	1	-	-	0	1	0	1	1	0	0	1	-	1	1	0	1	1	1	1	1
Arundelemys dardeni	0	1	1	0	0	1	0	?	0	1	1	-	1	?	?	?	1	1	?	?
Dorsetochelys delairi	0	1	1	0	0	1	0	1	0	1	1	-	1	1	0	0	1	?	1	1
Pleurosternon bullockii	0	1	1	0	0	?	?	?	0	1	1	-	1	1	0	0	1	1	1	1
Glyptops plicatulus	0	1	1	0	0	1	?	?	0	1	1	-	1	1	0	?	1	1	1	1
Dinochelys whitei	0	?	1	0	0	?	?	?	0	1	1	-	1	?	0	?	?	?	?	1
Neurankylus eximius	?	?	?	?	0	?	?	?	0	1	?	?	1	?	?	?	1	1	?	?
Trinitichelys hiatti	0	0	1	0	0	1	0	1	1	-	1	-	1	1	0	1	1	1	1	1
Plesiobaena antiqua	0	0	1	0	0	1	0	1	1	-	1	-	1	1	0	1	1	1	1	1
Boremys pulchra	0	0	1	0	0	1	0	?	1	-	1	-	1	1	0	1	1	1	1	1
Baena arenosa	1	-	-	0	0	1	0	1	1	-	1	-	1	1	0	0	1	1	1	1
Chisternon undatum	0	0	1	0	0	1	0	1	1	-	1	-	1	1	0	0	1	1	1	1
Naomichelys speciosa	0	0	1	0	?	?	?	?	?	?	1	-	?	1	0	0	?	?	1	?
Sichuanchelys chowi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Siamochelys peninsularis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Chengyuchelys baenoides	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Chengyuchelys zigongensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
'Chengyuchelys' dashanpuensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Xinjiangchelys tianshanensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Xinjiangchelys latimarginalis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Xinjiangchelys qiguensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Annemys levensis	0	0	1	0	1	?	?	?	0	0	1	-	1	1	0	1	?	?	1	1

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**
Portlandemys mcdowelli	0	0	1	0	1	1	0	1	0	0	1	-	1	?	?	?	1	0	?	?
Plesiochelys solodurensis	0	0	1	0	1	1	0	1	0	0	1	-	1	1	0	0	1	0	1	1
Solnhofia parsonsi	0	0	1	0	1	1	0	1	0	0	1	-	1	1	0	?	1	0	1	1
'Thalassemys moseri'	0	0	1	0	0	1	0	1	0	0	1	-	1	1	0	0	1	1	1	1
Sandownia harrisi	1	-	-	0	1	1	0	1	0	0	1	-	1	1	0	0	1	1	1	1
Santanachelys gaffneyi	0	0	1	0	0	1	0	1	0	0	1	-	1	1	0	1	1	0	1	1
Hangaiemys hoburensis	0	0	1	0	1	1	0	1	0	0	1	-	1	1	0	0	1	1	1	1
Judithemys sukhanovi	?	?	?	?	1	?	?	?	0	0	1	-	1	1	0	?	1	1	1	1
Dracochelys bicuspis	?	?	?	0	1	1	?	1	0	0	1	-	1	1	0	1	1	1	1	1
Sinemys lens	0	0	1	?	0	?	?	?	0	1	1	-	1	1	0	1	1	1	1	1
Ordosemys leios	0	0	1	0	0	1	0	1	0	1	1	-	1	1	0	?	1	1	1	1
Toxochelys latiremis	0	0	1	0	1	1	0	1	0	0	1	-	1	1	0	1	1	?	1	1
Mesodermochelys undulatus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Caretta caretta	1	-	-	0	1	1	0	1	0	0	1	-	?	1	0	0	1	0	1	1
Chelonia mydas	1	-	-	0	1	?	0	1	0	0	1	-	1	1	0	0	1	0	1	1
Dermochelys coriacea	1	-	-	0	1	1	1	1	0	0	1	-	0	1	0	0	0	-	1	0
Protochelydra zangerli	1	-	-	0	1	1	?	1	0	0	1	-	0	1	0	1	1	1	1	1
Macrochelys temminckii	1	-	-	0	1	1	0	1	0	0	1	-	0	1	0	1	1	1	1	1
Chelydra serpentina	1	-	-	0	1	1	0	1	0	0	1	-	0	1	0	1	1	1	1	1
Platysternon megacephalum	1	-	-	0	1	1	0	1	0	0	1	-	0	1	0	1	1	1	1	1
Mongolemys elegans	1	-	-	0	1	1	0	1	0	0	1	-	1	1	0	1	1	1	1	1
Gopherus polyphemus	1	-	-	0	1	1	0	1	0	0	1	-	1	1	0	1	1	1	1	1
Chrysemys picta	1	-	-	0	1	1	0	1	0	0	1	-	1	1	0	1	1	1	1	1
Geoclemys hamiltonii	1	-	-	0	1	1	0	1	0	0	1	-	0	1	0	1	1	1	1	1
Emarginachelys cretacea	1	-	-	0	1	1	0	1	0	0	1	-	1	1	0	1	1	1	1	1
Baptemys wyomingensis	1	-	-	0	1	1	0	1	0	0	1	-	1	1	0	1	1	1	1	1
Dermatemys mawii	1	-	-	0	1	1	0	1	0	0	1	-	1	1	0	1	1	1	1	1
Hoplochelys crassa	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Staurotypus triporcatus	1	-	-	0	1	1	0	1	0	0	1	-	0	1	0	1	1	1	1	1
Sternotherus odoratus	1	-	-	0	1	1	0	1	0	0	1	-	0	1	0	1	1	1	1	1
Kinosternon flavescens	1	-	-	0	1	1	0	1	0	0	1	-	0	1	0	1	1	1	1	1
Zangerlia neimongolensis	1	-	-	0	1	1	?	?	0	0	1	-	0	1	0	?	1	?	1	1
Basilemys variolosa	1	-	-	0	1	?	?	?	0	0	1	-	1	1	0	1	?	?	1	1
Adocus beatus	1	-	-	0	1	1	0	1	0	0	1	-	1	1	0	1	1	1	1	1
Peltochelys duchastelli	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Apalone ferox	1	-	-	0	1	1	1	1	0	0	1	-	1	1	0	1	1	1	1	1
Lissemys punctata	1	-	-	0	1	1	1	1	0	0	1	-	1	1	0	1	1	1	1	1
Pseudanosteira pulchra	1	-	-	0	1	?	?	?	0	0	1	-	1	1	0	1	?	?	1	1
Carettochelys insculpta	1	-	-	0	1	1	1	1	0	0	1	-	1	1	0	1	1	1	1	1

	21	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**
Anthodon serrarius	0	0	0	-	0	0	0	0	0	0	0	0	0	?	0	0	0	-	0	0
Owenetta kitchingorum	0	0	0	-	0	0	0	0	0	0	0	0	0	?	0	0	0	-	0	0
Simosaurus gaillardoti	0	0	0	-	1	0	0	0	-	1	0	0	0	?	0	0	0	-	0	0
Gephyrosaurus bridensis	0	0	0	-	0	0	0	0	-	1	0	0	0	?	0	0	0	-	0	1
Protorosaurus speneri	0	0	0	-	0	0	0	0	-	1	0	0	0	?	0	0	0	-	0	0
Araeoscelidia	0	0	0	-	0	0	0	0	1	0	0	0	0	?	0	0	0	-	0	0
Captorhinidae	0	0	0	-	0	0	0	0	1	0	0	0	0	?	0	0	0	-	0	0
Odontochelys semitestacea	0	0	?	?	0	0	?	?	1	0	0	0	?	?	?	?	?	?	0	?
Proganochelys quenstedti	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0
Palaeochersis talampayensis	0	0	0	0	0	0	0	0	1	0	0	0	0	?	?	0	?	0	1	0
Australochelys africanus	0	0	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	0	1	?
Proterochersis robusta	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Kayentachelys aprix	0	0	0	0	0	0	0	0	-	1	1	0	0	?	?	0	0	0	1	1
Indochelys spatulata	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Eileanchelys waldmani	0	0	0	0	?	0	0	0	-	1	1	0	?	?	0	0	0	0	1	1
Heckerochelys romani	0	0	?	?	?	?	?	?	-	1	1	0	?	?	?	?	?	?	?	?
Condorchelys antiqua	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Meiolania platyceps	0	0	0	1	1	1	0	0	-	1	1	1	0	0	0	0	0	1	1	1
Ninjemys oweni	0	0	?	1	1	1	?	?	?	?	1	1	?	?	?	?	0	1	1	?
Niolamia argentina	0	0	?	?	1	1	?	?	?	?	1	0	?	?	0	?	0	0	1	?
Chubutemys copelloi	0	0	0	?	0	0	?	0	-	1	?	?	?	?	?	?	?	0	1	1
Otwayemys cunicularius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	1
Mongolochelys efremovi	0	0	0	0	1	0	0	0	-	1	1	0	0	0	0	0	0	1	1	1
Kallokibotion bajazidi	0	0	0	0	0	0	0	0	-	1	1	?	0	0	0	0	0	0	1	1
Platychelys oberndorferi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Caribemys oxfordiensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Notoemys laticentralis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Elseya dentata	0	1	-	-	0	0	1	0	-	1	1	0	0	0	0	0	0	0	1	1
Chelodina oblonga	0	1	-	-	0	0	1	0	-	1	1	0	0	0	0	0	0	0	1	1
Phrynops geoffranus	0	1	-	-	0	0	1	0	-	1	1	0	0	0	0	0	0	0	1	1
Erymnochelys madagascariensis	0	0	0	0	0	0	1	0	-	1	1	0	0	0	0	0	0	0	1	1
Pelomedusa subrufa	0	0	0	0	0	0	1	0	-	1	1	0	0	0	0	0	0	0	1	1
Podocnemis expansa	0	0	0	0	0	0	1	0	-	1	1	0	0	0	0	0	0	0	1	1
Arundelemys dardeni	?	?	?	?	?	?	0	1	?	?	1	0	0	0	0	0	0	0	1	1
Dorsetochelys delairi	0	0	0	0	0	0	0	0	-	1	1	0	0	0	0	0	0	0	1	1
Pleurosternon bullockii	0	0	0	0	0	0	?	1	-	1	1	0	0	0	0	0	0	0	1	1
Glyptops plicatulus	0	0	?	?	?	0	?	1	?	?	1	0	0	?	?	0	1	0	1	1
Dinochelys whitei	0	0	0	?	?	?	?	?	?	?	1	0	0	?	?	0	1	?	1	1
Neurankylus eximius	?	?	?	?	0	?	0	?	-	1	?	?	?	?	?	?	?	?	?	?
Trinitichelys hiatti	0	0	0	0	0	0	0	0	-	1	1	0	0	0	0	0	0	0	1	1
Plesiobaena antiqua	0	0	0	0	0	0	0	1	-	1	1	0	0	0	0	0	0	0	1	1
Boremys pulchra	0	0	0	0	0	0	0	?	-	1	1	0	0	0	0	0	0	0	1	1
Baena arenosa	0	0	0	0	0	0	0	0	-	1	1	0	0	0	0	0	0	0	1	1
Chisternon undatum	0	0	0	0	0	0	0	0	-	1	1	0	0	0	0	0	0	0	1	1
Naomichelys speciosa	0	0	0	0	0	0	?	0	-	1	1	?	0	?	?	0	0	?	1	1
Sichuanchelys chowi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Siamochelys peninsularis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Chengyuchelys baenoides	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Chengyuchelys zigongensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
'Chengyuchelys' dashanpuensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Xinjiangchelys tianshanensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Xinjiangchelys latimarginalis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Xinjiangchelys qiguensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Annemys levensis	0	0	0	0	0	0	?	0	-	1	1	0	0	?	?	0	0	0	1	1
Portlandemys mcdowelli	?	?	?	?	?	?	0	?	?	?	1	0	0	0	0	0	0	0	1	1
Plesiochelys solodurensis	0	0	0	0	0	0	0	0	-	1	1	0	0	0	0	0	0	0	1	1
Solnhofia parsonsi	0	0	0	0	0	0	0	0	-	1	1	0	0	0	0	0	0	0	1	1

	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
'Thalassemys moseri'	0	0	0	0	0	0	0	0	-	1	1	0	0	0	0	0	0	0	1	1
Sandownia harrisi	0	0	0	0	0	0	0	0	-	1	1	0	0	?	?	0	0	0	1	1
Santanachelys gaffneyi	0	0	0	0	0	0	0	0	-	1	1	0	0	?	?	0	0	?	1	1
Hangaiemys hoburensis	0	0	0	0	0	0	0	0	-	1	1	0	0	0	0	0	0	0	1	1
Judithemys sukhanovi	0	0	0	0	0	0	0	?	-	1	1	0	?	?	?	?	0	0	1	1
Dracochelys bicuspis	0	0	0	0	0	0	?	0	-	1	1	0	0	0	0	0	0	0	1	1
Sinemys lens	0	0	0	0	0	0	?	0	-	1	1	0	?	?	?	0	0	?	1	1
Ordosemys leios	0	0	0	0	0	0	0	0	-	1	1	0	0	0	0	0	0	0	1	1
Toxochelys latiremis	0	0	0	0	0	0	0	0	-	1	1	0	0	0	0	0	0	0	1	1
Mesodermochelys undulatus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Caretta caretta	0	0	0	0	0	0	0	0	-	1	1	0	0	1	0	0	0	0	1	1
Chelonia mydas	0	0	0	0	0	0	0	0	-	1	1	0	0	1	0	0	1	0	1	1
Dermochelys coriacea	0	0	0	0	0	0	0	0	-	1	1	0	0	0	0	0	0	0	1	1
Protochelydra zangerli	0	0	0	0	0	0	0	0	-	1	1	0	0	0	0	0	0	0	1	1
Macrochelys temminckii	0	0	0	0	0	0	0	0	-	1	1	0	0	0	0	0	1	0	1	1
Chelydra serpentina	0	0	0	0	0	0	0	0	-	1	1	0	0	0	0	0	1	0	1	1
Platysternon megacephalum	0	0	1	0	0	0	0	1	-	1	1	0	0	0	0	0	1	0	1	1
Mongolemys elegans	0	0	0	0	0	0	0	0	-	1	1	0	0	0	0	0	0	0	1	1
Gopherus polyphemus	0	0	0	0	0	0	0	0	-	1	1	0	0	0	0	0	0	0	1	1
Chrysemys picta	0	0	0	0	0	0	0	?	-	1	1	0	0	0	0	0	0	0	1	1
Geoclemys hamiltonii	1	0	0	0	0	0	0	0	-	1	1	0	0	0	0	0	0	0	1	1
Emarginachelys cretacea	0	0	0	0	0	0	0	0	-	1	1	0	0	0	0	0	0	0	1	1
Baptemys wyomingensis	0	0	0	0	0	0	0	0	-	1	1	0	0	0	0	0	0	0	1	1
Dermatemys mawii	0	0	0	0	0	0	0	0	-	1	1	0	0	0	0	0	0	0	1	1
Hoplochelys crassa	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Staurotypus triporcatus	1	0	1	0	0	0	0	0	-	1	1	0	0	0	0	0	1	0	1	1
Sternotherus odoratus	0	0	1	0	0	0	0	0	-	1	1	0	0	0	0	0	0	0	1	1
Kinosternon flavescens	0	0	1	0	0	0	0	0	-	1	1	0	0	0	0	0	0	0	1	1
Zangerlia neimongolensis	?	0	0	0	0	0	0	?	-	1	1	0	0	0	0	0	0	0	1	1
Basilemys variolosa	0	0	0	0	0	0	0	0	-	1	1	0	0	?	?	0	0	0	1	1
Adocus beatus	?	0	0	0	0	0	0	0	-	1	1	0	0	0	0	0	0	0	1	1
Peltochelys duchastelli	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Apalone ferox	1	0	0	0	0	0	0	?	-	1	1	0	1	-	1	1	0	0	1	1
Lissemys punctata	1	0	0	0	0	0	0	0	-	1	1	0	1	-	1	1	0	0	1	1
Pseudanosteira pulchra	0	0	0	0	0	0	0	0	-	1	1	0	?	-	1	0	0	0	1	1
Carettochelys insculpta	0	0	1	0	0	0	0	0	-	1	1	0	1	-	1	0	0	0	1	1

	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Anthodon serrarius	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	1	0	0
Owenetta kitchingorum	0	0	0	0	0	0	0	0	0	0	0	0	-	-	?	?	0	0	0	0
Simosaurus gaillardoti	0	0	0	0	1	0	0	0	0	0	0	0	-	-	?	?	1	1	1	0
Gephyrosaurus bridensis	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	0	0
Protorosaurus speneri	0	?	?	?	?	0	0	0	0	0	0	0	-	-	?	?	?	?	?	?
Araeoscelidia	0	0	0	?	0	0	0	0	0	0	0	0	-	-	0	0	0	0	0	0
Captorhinidae	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	0	0	0
Odontochelys semitestacea	0	?	?	?	?	?	0	?	0	?	0	?	?	?	?	?	0	0	0	0
Proganochelys quenstedti	0	0	0	0	0	0	0	0	0	0	0	0	-	-	?	?	0	0	0	0
Palaeochersis talampayensis	0	0	0	?	1	?	0	0	1	0	0	1	0	?	?	?	?	1	0	0
Australochelys africanus	0	?	0	?	?	?	0	0	1	0	0	1	0	?	?	?	?	1	0	0
Proterochersis robusta	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Kayentachelys aprix	0	1	0	0	1	0	0	1	1	0	1	1	0	?	0	0	0	1	0	0
Indochelys spatulata	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Eileanchelys waldmani	0	1	0	?	1	?	0	1	1	0	1	1	0	?	?	?	?	1	?	0
Heckerochelys romani	0	1	0	?	1	?	0	1	1	0	1	1	0	?	?	?	1	1	0	0
Condorchelys antiqua	?	?	?	?	?	?	0	1	1	0	1	1	0	?	?	?	1	1	0	0
Meiolania platyceps	0	1	1	0	1	0	0	1	1	0	1	1	0	?	0	0	1	1	1	1
Ninjemys oweni	0	?	?	?	?	?	?	?	1	?	?	1	?	?	?	?	?	?	?	?
Niolamia argentina	0	?	1	?	1	?	?	1	1	?	?	1	?	?	0	?	1	1	1	?
Chubutemys copelloi	0	1	1	1	1	?	0	1	1	0	1	1	?	?	?	?	1	1	1	?
Otwayemys cunicularius	?	?	?	?	?	?	?	1	1	0	1	1	0	?	?	?	?	?	?	?
Mongolochelys efremovi	0	1	1	0	1	0	0	1	1	0	1	1	0	?	0	?	1	1	1	1
Kallokibotion bajazidi	0	1	1	1	1	0	0	1	1	0	1	1	1	1	0	1	1	1	1	1
Platychelys oberndorferi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Caribemys oxfordiensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Notoemys laticentralis	?	?	?	?	?	?	0	1	1	0	?	1	0	?	?	?	?	1	?	0
Elseya dentata	0	1	1	0	1	0	1	1	1	0	1	1	1	1	1	-	1	1	1	0
Chelodina oblonga	0	1	1	0	1	0	1	1	1	0	1	1	1	1	1	-	1	1	1	0
Phrynops geoffranus	0	1	1	0	1	0	1	1	1	0	1	1	1	1	1	-	1	1	1	0
Erymnochelys madagascariensis	1	-	-	-	1	0	1	1	1	1	1	1	1	1	1	-	1	1	1	0
Pelomedusa subrufa	1	-	-	-	1	0	1	1	1	1	1	1	1	1	1	-	1	1	1	0
Podocnemis expansa	1	-	-	-	1	0	1	1	1	1	1	1	1	1	1	-	1	1	1	0
Arundelemys dardeni	0	1	1	0	1	?	0	1	1	?	1	1	0	?	0	1	1	1	1	1
Dorsetochelys delairi	0	1	1	0	1	?	0	1	1	0	1	1	0	?	0	1	1	1	1	1
Pleurosternon bullockii	0	1	1	?	1	0	0	1	1	0	1	1	0	?	0	1	1	1	1	1
Glyptops plicatulus	0	1	?	?	1	0	0	1	1	0	?	1	0	?	0	1	1	1	1	1
Dinochelys whitei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Neurankylus eximius	?	?	?	?	?	?	0	1	1	0	1	1	0	?	1	-	1	1	1	1
Trinitichelys hiatti	0	1	1	0	1	0	0	1	1	0	1	1	0	?	1	-	1	1	1	1
Plesiobaena antiqua	0	1	1	0	1	0	0	1	1	0	1	1	0	?	1	-	1	1	1	1
Boremys pulchra	0	1	1	0	1	0	0	1	1	0	1	1	0	?	1	-	1	1	1	1
Baena arenosa	0	1	1	0	1	0	0	1	1	0	1	1	0	?	1	-	1	1	1	1
Chisternon undatum	0	1	1	0	1	0	0	1	1	0	1	1	0	?	1	-	1	1	1	1
Naomichelys speciosa	?	?	?	?	?	?	0	1	1	0	1	1	0	?	?	?	?	1	?	1
Sichuanchelys chowi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Siamochelys peninsularis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Chengyuchelys baenoides	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Chengyuchelys zigongensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
'Chengyuchelys' dashanpuensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Xinjiangchelys tianshanensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Xinjiangchelys latimarginalis	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	1	1
Xinjiangchelys qiguensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Annemys levensis	0	1	?	0	1	?	0	1	1	0	1	1	0	?	?	?	1	1	1	1
Portlandemys mcdowelli	0	1	1	0	1	0	0	1	1	0	1	1	0	?	0	1	1	1	1	1
Plesiochelys solodurensis	0	1	1	0	1	0	0	1	1	0	1	1	0	?	0	1	1	1	1	1
Solnhofia parsonsi	0	1	1	1	1	0	0	1	1	0	1	1	0	?	0	1	1	1	1	1

	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
‘Thalassemys moseri’	0	1	1	1	1	0	0	1	1	0	1	1	0	?	0	1	1	1	1	1
Sandownia harrisi	0	1	1	?	1	1	0	1	1	0	1	1	1	0	1	-	1	1	1	1
Santanachelys gaffneyi	0	1	1	1	1	0	0	1	1	0	1	1	0	?	?	?	1	1	1	1
Hangaiemys hoburensis	0	1	1	0	1	0	0	1	1	?	1	1	0	?	?	?	1	1	1	1
Judithemys sukhanovi	0	1	1	0	1	?	0	1	1	0	1	1	0	?	?	?	1	1	1	1
Dracochelys bicuspis	0	1	1	0	1	?	0	1	1	1	1	1	0	?	?	?	1	1	1	1
Sinemys lens	?	?	?	?	1	?	0	1	1	1	1	1	1	0	?	?	1	1	1	1
Ordosemys leios	0	1	1	0	1	0	0	1	1	1	1	1	0	?	0	1	1	1	1	1
Toxochelys latiremis	0	1	1	0	1	0	0	1	1	0	1	1	0	?	?	?	1	1	1	1
Mesodermochelys undulatus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Caretta caretta	0	1	1	0	1	0	0	1	1	0	1	1	0	?	0	1	1	1	1	1
Chelonia mydas	0	1	1	0	1	0	0	1	1	0	1	1	0	?	0	1	1	1	1	1
Dermochelys coriacea	0	1	1	0	1	0	0	1	1	0	1	1	0	?	1	-	1	1	1	1
Protochelydra zangerli	0	1	1	0	1	?	0	1	1	0	1	1	1	0	?	?	1	1	1	1
Macrochelys temminckii	0	1	1	0	1	0	0	1	1	0	1	1	1	0	0	1	1	1	1	1
Chelydra serpentina	0	1	1	0	1	0	0	1	1	0	1	1	1	0	0	1	1	1	1	1
Platysternon megacephalum	0	1	1	0	1	0	0	1	1	0	1	1	1	0	0	1	1	1	1	1
Mongolemys elegans	0	1	1	0	1	0	0	1	1	0	1	1	0	?	0	1	1	1	1	1
Gopherus polyphemus	0	1	1	0	1	0	0	1	1	0	1	1	1	0	0	1	1	1	1	1
Chrysemys picta	0	1	1	0	1	0	0	1	1	0	1	1	0	?	0	1	1	1	1	1
Geoclemys hamiltonii	0	1	1	0	1	0	0	1	1	0	1	1	0	?	0	1	1	1	1	1
Emarginachelys cretacea	0	1	1	0	1	1	0	1	1	0	1	1	0	?	0	1	1	1	1	1
Baptemys wyomingensis	0	1	1	0	1	1	0	1	1	0	1	1	0	?	0	1	1	1	1	1
Dermatemys mawii	0	1	1	0	1	1	0	1	1	0	1	1	0	?	0	1	1	1	1	1
Hoplochelys crassa	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Staurotypus triporcatus	0	1	1	0	1	1	0	1	1	0	1	1	0	?	0	1	1	1	1	1
Sternotherus odoratus	0	1	1	0	1	1	0	1	1	0	1	1	0	?	0	1	1	1	1	1
Kinosternon flavescens	0	1	1	0	1	1	0	1	1	0	1	1	0	?	0	1	1	1	1	1
Zangerlia neimongolensis	0	1	1	?	1	?	0	1	1	0	1	1	1	0	?	?	1	1	1	1
Basilemys variolosa	0	?	?	?	1	?	0	1	1	0	1	1	1	0	?	?	1	1	1	1
Adocus beatus	0	1	1	0	1	1	0	1	1	0	1	1	0	?	0	1	1	1	1	1
Peltochelys duchastelli	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Apalone ferox	0	1	1	1	1	1	0	1	1	0	1	1	1	0	0	1	1	1	1	1
Lissemys punctata	0	1	1	1	1	1	0	1	1	0	1	1	1	0	0	1	1	1	1	1
Pseudanosteira pulchra	0	1	1	1	1	?	0	1	1	0	1	1	1	0	?	?	1	1	1	1
Carettochelys insculpta	0	1	1	1	1	1	0	1	1	0	1	1	1	0	0	1	1	1	1	1

	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
Anthodon serrarius	0	0	0	0	0	1	0	0	0	0	?	0	0	1	?	?	?	0	0	0
Owenetta kitchingorum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	0
Simosaurus gaillardoti	1	0	1	-	0	-	0	0	0	?	?	0	0	?	?	?	?	0	?	?
Gephyrosaurus bridensis	0	0	0	0	0	0	0	0	0	?	?	0	0	0	?	?	?	0	0	0
Protorosaurus speneri	?	?	?	?	?	?	?	?	0	0	?	0	0	?	?	?	?	0	?	?
Araeoscelidia	0	0	0	0	0	?	0	0	0	?	0	0	0	0	?	?	?	0	0	0
Captorhinidae	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	?	?	0	0	0
Odontochelys semitestacea	0	0	?	?	0	?	0	0	0	?	?	?	?	0	?	?	?	?	?	?
Proganochelys quenstedti	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Palaeochersis talampayensis	0	0	0	0	0	0	0	0	0	0	1	?	0	0	?	?	?	0	?	?
Australochelys africanus	0	0	0	0	?	0	0	0	?	?	1	?	0	0	?	?	?	0	?	?
Proterochersis robusta	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Kayentachelys aprix	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0
Indochelys spatulata	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Eileanchelys waldmani	0	?	?	?	?	?	?	?	?	0	1	?	0	?	1	0	0	0	?	?
Heckerochelys romani	0	0	?	?	0	?	0	0	?	?	1	0	0	0	?	?	?	0	0	0
Condorchelys antiqua	0	0	?	?	0	?	0	?	?	?	1	?	1	0	?	?	?	0	0	0
Meiolania platyceps	1	0	0	0	0	0	1	1	1	0	1	0	0	1	1	0	0	1	0	0
Ninjemys oweni	?	?	?	?	?	?	1	1	1	?	?	?	?	?	?	?	?	?	?	?
Niolamia argentina	?	0	?	?	0	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?
Chubutemys copelloi	?	?	0	0	0	0	0	1	0	0	1	?	0	1	?	?	?	?	?	?
Otwayemys cunicularius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	?	?	?
Mongolochelys efremovi	0	0	0	0	0	0	0	1	0	0	1	?	0	1	1	0	0	?	0	0
Kallokibotion bajazidi	1	0	0	?	0	?	0	?	0	0	1	0	0	1	1	0	0	1	0	0
Platychelys oberndorferi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Caribemys oxfordiensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Notoemys laticentralis	0	?	?	?	?	?	?	?	?	0	1	?	0	1	1	0	0	0	0	0
Elseya dentata	0	1	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	1	1	0
Chelodina oblonga	0	1	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	1	1	0
Phrynops geoffranus	0	1	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	1	1	0
Erymnochelys madagascariensis	0	1	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	1	0	0
Pelomedusa subrufa	0	1	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	1	1	0
Podocnemis expansa	0	1	0	0	0	1	0	1	0	0	1	0	0	1	1	0	0	1	0	0
Arundelemys dardeni	1	0	0	0	0	0	0	?	?	0	1	?	0	1	?	0	0	1	0	1
Dorsetochelys delairi	1	0	0	0	0	0	0	0	0	0	1	?	0	1	1	0	0	?	0	1
Pleurosternon bullockii	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1
Glyptops plicatulus	1	0	0	0	1	0	0	0	?	?	1	?	0	0	1	0	0	1	0	1
Dinochelys whitei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Neurankylus eximius	1	0	?	?	0	?	?	0	0	0	1	0	0	1	1	0	0	1	0	1
Trinitichelys hiatti	1	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	1
Plesiobaena antiqua	1	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	1
Boremys pulchra	1	0	0	0	0	1	0	0	0	0	1	0	0	1	1	0	0	1	0	1
Baena arenosa	1	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	1
Chisternon undatum	1	0	0	0	0	1	0	0	0	0	1	0	0	1	1	0	0	1	0	1
Naomichelys speciosa	0	?	?	?	?	?	?	0	0	?	1	?	0	?	1	0	0	?	0	0
Sichuanchelys chowi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Siamochelys peninsularis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Chengyuchelys baenoides	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Chengyuchelys zigongensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
'Chengyuchelys' dashanpuensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Xinjiangchelys tianshanensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Xinjiangchelys latimarginalis	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?
Xinjiangchelys qiguensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Annemys levensis	0	0	0	?	0	0	0	?	0	?	1	?	0	1	1	0	0	?	0	0
Portlandemys mcdowelli	1	0	0	0	0	0	0	?	?	0	1	0	0	1	1	0	0	1	0	0
Plesiochelys solodurensis	1	0	0	1	0	-	0	0	0	0	1	0	0	1	1	0	0	1	0	0
Solnhofia parsonsi	1	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0

	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
‘Thalassemys moseri’	1	0	0	1	0	-	0	0	0	0	1	0	0	1	1	0	0	1	0	0
Sandownia harrisi	1	0	?	?	0	?	0	0	0	0	1	0	0	1	1	0	0	1	0	0
Santanachelys gaffneyi	1	0	0	1	0	-	0	1	0	0	1	?	0	1	1	0	0	1	?	?
Hangaiemys hoburensis	1	0	0	0	0	0	0	1	0	0	1	?	1	1	1	0	0	1	0	0
Judithemys sukhanovi	1	0	0	0	0	0	0	1	0	0	1	0	1	1	1	0	0	1	0	0
Dracochelys bicuspis	1	0	0	0	0	0	0	?	0	0	1	?	?	1	1	0	0	1	?	?
Sinemys lens	0	0	0	0	0	0	0	1	0	0	1	?	1	1	1	0	0	?	0	0
Ordosemys leios	1	0	0	0	0	0	0	?	0	0	1	0	1	1	1	0	0	1	0	0
Toxochelys latiremis	1	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	?	0	0
Mesodermochelys undulatus	?	?	?	?	?	?	?	1	0	?	?	?	?	?	?	?	?	?	?	?
Caretta caretta	1	0	1	-	0	-	0	1	0	0	1	1	0	1	1	0	0	1	0	0
Chelonia mydas	1	0	1	-	0	-	0	1	0	0	1	1	0	1	1	0	0	1	0	0
Dermochelys coriacea	1	0	1	-	0	-	0	1	0	0	1	1	0	1	1	0	0	1	0	0
Protochelydra zangerli	1	0	0	0	0	1	0	1	0	0	1	?	0	1	1	0	0	?	0	0
Macrochelys temminckii	1	0	0	0	0	1	0	1	0	0	1	0	0	1	1	0	0	1	0	0
Chelydra serpentina	1	0	0	0	0	1	0	1	0	0	1	0	0	1	1	0	0	1	0	0
Platysternon megacephalum	1	0	0	0	0	1	0	1	0	0	1	0	0	1	1	0	0	1	0	0
Mongolemys elegans	1	0	0	0	0	0	0	1	0	?	1	?	0	1	1	0	0	?	0	0
Gopherus polyphemus	1	0	0	0	0	1	0	1	0	0	1	0	0	1	1	0	0	1	0	0
Chrysemys picta	0	0	0	0	0	1	0	1	0	0	1	0	0	1	1	0	0	1	0	0
Geoclemys hamiltonii	1	0	0	0	0	1	0	1	0	0	1	0	0	1	1	0	0	1	0	0
Emarginachelys cretacea	1	0	0	0	0	1	0	1	0	0	1	0	0	1	1	0	0	?	0	0
Baptemys wyomingensis	1	0	0	0	0	?	0	1	0	0	1	?	0	1	-	1	-	?	0	0
Dermatemys mawii	1	0	0	0	0	1	0	1	0	0	1	0	0	1	-	1	-	1	0	0
Hoplochelys crassa	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Staurotypus triporcatus	1	0	0	0	0	1	0	1	0	0	1	0	0	1	1	0	1	?	0	0
Sternotherus odoratus	1	0	0	0	0	1	0	1	0	0	1	0	0	1	1	0	1	?	0	0
Kinosternon flavescens	1	0	0	0	0	1	0	1	0	0	1	0	0	1	1	0	1	1	0	0
Zangerlia neimongolensis	1	0	0	0	0	0	0	1	0	0	1	?	0	1	1	0	0	1	0	0
Basilemys variolosa	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Adocus beatus	1	0	0	0	0	1	0	1	0	0	1	0	0	1	1	0	0	1	0	0
Peltochelys duchastelli	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Apalone ferox	1	0	0	0	1	1	0	1	0	0	1	0	0	1	1	0	0	?	0	0
Lissemys punctata	1	0	0	0	1	1	0	1	0	0	1	0	0	1	1	0	0	1	0	0
Pseudanosteira pulchra	1	0	0	0	1	?	0	1	0	0	1	?	0	1	1	0	0	?	0	0
Carettochelys insculpta	1	0	0	0	1	1	0	1	0	0	1	0	0	1	1	0	0	1	0	0

	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100
Anthodon serrarius	0	-	1	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Owenetta kitchingorum	0	-	1	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Simosaurus gaillardoti	?	-	1	0	1	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gephyrosaurus bridensis	0	-	1	0	1	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Protorosaurus speneri	?	-	1	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Araeoscelidia	0	-	1	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Captorhinidae	0	-	1	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Odontochelys semitestacea	?	?	?	?	?	1	?	?	?	?	?	?	0	?	?	?	?	?	?	?
Proganochelys quenstedti	0	-	0	0	1	1	0	0	0	0	0	?	0	?	?	0	0	0	0	?
Palaeochersis talampayensis	?	-	0	0	1	1	0	?	?	?	?	?	?	?	?	0	?	?	0	?
Australochelys africanus	?	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Proterochersis robusta	?	?	?	?	?	1	0	0	?	?	?	?	?	?	?	0	0	0	0	?
Kayentachelys aprix	0	0	0	0	1	1	0	0	0	0	0	0	0	0	?	0	1	0	0	0
Indochelys spatulata	?	?	?	?	?	1	0	0	?	?	?	0	0	0	0	0	?	?	?	0
Eileanchelys waldmani	?	0	0	?	?	1	0	0	?	?	?	0	0	0	1	0	1	0	0	0
Heckerochelys romani	0	?	?	?	?	1	0	0	0	0	?	0	0	0	0	0	1	0	0	0
Condorchelys antiqua	0	?	?	?	?	1	0	0	?	?	?	?	0	0	0	0	?	?	?	?
Meiolania platyceps	1	0	0	0	1	1	0	0	0	0	0	?	0	?	?	0	1	0	0	?
Ninjemys oweni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Niolamia argentina	?	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Chubutemys copelloi	?	?	?	?	?	1	0	?	?	?	?	?	0	?	?	?	?	?	?	0
Otwayemys cunicularius	?	?	?	?	?	1	0	0	0	0	?	?	0	?	?	0	?	?	?	0
Mongolochelys efremovi	0	0	0	0	1	1	0	0	0	0	0	0	0	0	?	0	1	0	0	0
Kallokibotion bajazidi	0	?	0	?	?	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0
Platychelys oberndorferi	?	?	?	?	?	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0
Caribemys oxfordiensis	?	?	?	?	?	1	0	0	1	0	0	0	0	?	?	0	?	?	0	?
Notoemys laticentralis	0	?	?	?	?	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0
Elseya dentata	0	0	0	0	1	1	0	0	1	0	0	0	1	0	?	0	1	0	0	0
Chelodina oblonga	0	0	1	0	1	1	0	0	1	0	0	0	1	0	?	0	1	0	0	0
Phrynops geoffranus	0	0	1	0	1	1	0	0	1	0	0	0	0	1	?	0	1	0	0	0
Erymnochelys madagascariensis	0	0	0	1	1	1	0	0	1	0	0	0	0	1	?	0	1	0	0	0
Pelomedusa subrufa	0	0	0	1	1	1	0	0	1	0	0	0	0	1	?	0	1	0	0	0
Podocnemis expansa	0	0	0	1	1	1	0	0	1	0	0	0	0	1	?	0	1	0	0	0
Arundelemys dardeni	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dorsetochelys delairi	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Pleurosternon bullockii	0	1	?	?	?	1	0	0	?	?	0	0	0	0	0	0	1	0	0	0
Glyptops plicatulus	0	?	0	0	1	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0
Dinochelys whitei	?	?	?	?	?	1	0	0	?	?	?	0	0	0	0	0	1	0	0	0
Neurankylus eximius	0	1	?	0	?	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0
Trinitichelys hiatti	0	1	0	0	1	1	0	0	1	0	0	0	0	?	?	0	?	?	0	0
Plesiobaena antiqua	0	1	0	0	1	1	0	0	1	0	0	0	0	0	?	0	1	0	0	0
Boremys pulchra	0	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0
Baena arenosa	0	1	0	1	1	1	0	0	1	0	0	0	0	0	?	0	1	0	0	0
Chisternon undatum	0	1	0	1	1	1	0	0	1	0	0	0	0	0	?	0	1	0	0	0
Naomichelys speciosa	0	?	?	?	?	1	0	0	?	?	?	0	0	0	1	0	?	?	0	0
Sichuanchelys chowi	?	?	?	?	?	1	0	0	?	?	?	?	0	?	?	0	?	?	?	?
Siamochelys peninsularis	?	?	?	?	?	1	0	0	?	?	?	0	0	0	0	0	1	0	0	0
Chengyuchelys baenoides	?	?	?	?	?	1	0	0	?	?	?	0	0	?	?	0	?	?	0	0
Chengyuchelys zigongensis	?	?	?	?	?	1	0	0	?	?	?	0	0	?	?	0	?	?	?	?
'Chengyuchelys' dashanpuensis	?	?	?	?	?	1	0	0	?	?	?	0	0	?	?	0	?	?	0	?
Xinjiangchelys tianshanensis	?	?	?	?	?	1	0	0	?	?	?	0	0	1	0	0	1	0	?	0
Xinjiangchelys latimarginalis	?	?	?	?	?	1	0	0	1	0	0	0	0	0	1	0	1	0	0	0
Xinjiangchelys qiguensis	?	?	?	?	?	1	0	0	?	?	?	0	0	0	?	0	1	0	0	0
Annemys levensis	0	?	?	?	?	1	0	0	?	?	?	0	0	1	0	0	1	0	?	0
Portlandemys mcdowelli	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Plesiochelys solodurensis	1	0	0	0	1	1	0	0	1	0	0	0	0	0	1	0	1	0	0	0
Solnhofia parsonsi	1	0	0	0	1	1	0	0	?	?	?	0	0	0	?	0	1	0	?	0

	81	**82**	**83**	**84**	**85**	**86**	**87**	**88**	**89**	**90**	**91**	**92**	**93**	**94**	**95**	**96**	**97**	**98**	**99**	**100**
'Thalassemys moseri'	1	0	?	?	?	1	0	0	1	0	0	0	0	?	?	0	?	?	0	0
Sandownia harrisi	1	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Santanachelys gaffneyi	?	?	0	?	1	1	0	0	?	?	?	0	0	0	?	0	1	0	0	0
Hangaiemys hoburensis	1	?	?	?	?	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0
Judithemys sukhanovi	1	?	0	?	?	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0
Dracochelys bicuspis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Sinemys lens	1	0	0	?	?	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0
Ordosemys leios	1	?	?	?	?	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0
Toxochelys latiremis	1	?	0	1	1	1	0	0	1	1	0	0	0	0	0	0	1	0	0	0
Mesodermochelys undulatus	?	?	0	1	1	1	1	0	1	1	0	0	0	1	?	0	1	0	0	0
Caretta caretta	1	0	0	1	1	1	0	0	1	1	0	0	0	0	?	0	0	0	0	0
Chelonia mydas	1	0	0	1	1	1	0	0	1	1	0	0	0	0	?	0	1	0	0	0
Dermochelys coriacea	1	0	0	1	1	1	1	0	1	1	0	0	-	-	-	1	-	-	-	-
Protochelydra zangerli	1	0	?	?	?	1	?	?	?	?	?	?	?	?	?	0	?	?	?	?
Macrochelys temminckii	1	0	0	1	1	1	0	0	1	0	1	0	0	0	0	0	1	0	0	0
Chelydra serpentina	1	0	0	1	1	1	0	0	1	0	1	0	0	0	0	0	1	0	0	0
Platysternon megacephalum	1	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0
Mongolemys elegans	1	0	0	1	?	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0
Gopherus polyphemus	1	0	0	1	1	1	0	0	1	0	0	0	0	0	?	0	1	0	0	0
Chrysemys picta	1	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0
Geoclemys hamiltonii	1	0	0	1	1	1	0	1	1	0	0	0	0	0	?	0	1	0	0	0
Emarginachelys cretacea	1	?	?	?	?	1	0	1	1	0	1	0	0	0	0	0	1	0	0	0
Baptemys wyomingensis	1	0	0	1	1	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0
Dermatemys mawii	1	0	0	1	1	1	0	0	1	0	?	0	0	1	0	0	1	0	0	0
Hoplochelys crassa	?	?	?	?	?	1	0	1	1	0	1	0	0	0	0	0	1	0	0	0
Staurotypus triporcatus	1	0	0	1	1	1	0	1	1	0	1	0	0	?	?	0	1	1	1	0
Sternotherus odoratus	1	0	0	1	1	1	0	1	1	0	1	0	0	1	0	0	1	1	1	1
Kinosternon flavescens	1	0	0	1	1	1	0	1	1	0	1	0	0	1	?	0	1	1	1	1
Zangerlia neimongolensis	1	?	0	1	1	1	0	0	?	?	?	1	0	0	0	0	1	0	?	?
Basilemys variolosa	?	?	0	1	1	1	0	0	1	0	0	1	0	0	0	0	1	0	0	0
Adocus beatus	1	0	0	1	1	1	0	0	1	0	0	1	0	1	0	0	1	0	0	0
Peltochelys duchastelli	?	?	?	?	?	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0
Apalone ferox	1	0	0	1	1	1	1	0	1	0	0	0	0	1	?	1	-	-	-	0
Lissemys punctata	1	0	0	1	1	1	1	0	1	0	0	0	0	1	?	1	-	-	-	0
Pseudanosteira pulchra	1	0	?	?	?	1	0	0	1	0	0	0	0	1	?	0	1	1	0	0
Carettochelys insculpta	1	0	0	1	1	1	1	0	1	0	0	0	0	1	?	0	1	1	0	0

	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
Anthodon serrarius	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Owenetta kitchingorum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Simosaurus gaillardoti	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gephyrosaurus bridensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Protorosaurus speneri	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Araeoscelidia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Captorhinidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Odontochelys semitestacea	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	?	0	?	?	0
Proganochelys quenstedti	0	0	0	?	0	0	-	0	?	0	0	0	0	0	0	0	0	0	0	0
Palaeochersis talampayensis	0	?	?	?	0	?	?	?	?	0	0	0	0	0	0	0	0	?	0	0
Australochelys africanus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Proterochersis robusta	0	0	0	?	0	0	?	0	?	0	0	0	0	0	0	0	0	0	0	0
Kayentachelys aprix	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Indochelys spatulata	0	0	0	0	?	0	0	0	?	0	?	0	0	?	0	0	0	0	?	0
Eileanchelys waldmani	0	0	0	?	1	0	0	0	0	0	0	0	1	?	0	0	0	0	?	0
Heckerochelys romani	0	0	0	0	1	0	?	?	0	1	1	0	1	?	0	0	0	0	0	0
Condorchelys antiqua	0	?	?	?	?	0	0	0	?	?	1	0	1	0	0	?	0	?	?	?
Meiolania platyceps	0	0	0	?	1	0	?	0	?	1	1	0	1	0	0	0	0	1	0	?
Ninjemys oweni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Niolamia argentina	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Chubutemys copelloi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Otwayemys cunicularius	0	?	?	?	?	0	?	?	?	?	1	0	1	?	0	0	0	0	0	1
Mongolochelys efremovi	0	0	0	0	1	0	1	0	1	1	1	0	1	0	0	0	0	1	0	0
Kallokibotion bajazidi	0	?	?	?	1	0	0	0	0	0	0	0	1	?	0	0	0	0	1	0
Platychelys oberndorferi	0	0	0	0	?	0	0	0	0	0	1	0	1	1	0	0	0	0	1	0
Caribemys oxfordiensis	0	?	?	?	1	?	?	?	?	0	1	0	1	1	0	0	0	0	1	0
Notoemys laticentralis	0	0	0	0	1	0	0	0	0	0	1	0	1	1	0	0	0	0	1	0
Elseya dentata	0	1	-	0	1	1	-	0	?	0	0	0	1	1	0	0	0	0	1	1
Chelodina oblonga	0	0	0	0	1	1	-	0	?	0	0	0	1	1	0	0	0	0	1	1
Phrynops geoffranus	0	0	0	0	1	1	1	0	?	0	0	0	1	1	0	0	0	0	1	1
Erymnochelys madagascariensis	0	1	-	0	1	1	1	0	?	0	0	0	1	1	0	0	0	0	1	0
Pelomedusa subrufa	0	1	-	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	1	0
Podocnemis expansa	0	1	-	0	1	1	1	0	?	0	0	0	1	1	0	0	0	0	1	0
Arundelemys dardeni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dorsetochelys delairi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Pleurosternon bullockii	0	1	-	1	1	0	1	0	1	0	0	0	1	?	0	0	0	0	?	0
Glyptops plicatulus	0	0	0	1	1	1	1	0	1	0	0	0	1	1	0	0	0	0	1	0
Dinochelys whitei	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0
Neurankylus eximius	0	0	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	1	0
Trinitichelys hiatti	0	0	0	?	1	1	1	0	0	0	0	0	1	1	0	0	0	0	1	0
Plesiobaena antiqua	0	0	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	1	0
Boremys pulchra	0	0	1	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	1	0
Baena arenosa	0	0	1	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	1	0
Chisternon undatum	0	0	1	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	1	0
Naomichelys speciosa	0	0	0	0	1	0	1	0	1	0	1	0	1	?	0	0	0	1	0	0
Sichuanchelys chowi	0	0	0	?	1	0	0	0	?	0	0	0	1	?	0	?	0	?	?	0
Siamochelys peninsularis	0	0	0	0	1	1	1	0	1	1	0	0	1	?	0	0	0	0	?	?
Chengyuchelys baenoides	0	0	0	?	1	1	0	1	?	0	0	0	1	?	0	1	0	0	0	0
Chengyuchelys zigongensis	0	?	?	?	1	1	0	1	?	0	0	0	1	?	0	1	0	?	?	0
'Chengyuchelys' dashanpuensis	0	?	?	?	1	0	0	0	?	0	0	0	1	?	0	0	0	0	?	0
Xinjiangchelys tianshanensis	0	0	0	?	1	1	1	0	1	1	0	0	1	?	0	0	0	0	0	1
Xinjiangchelys latimarginalis	0	0	0	1	1	1	1	0	1	1	0	0	1	1	0	0	0	0	0	1
Xinjiangchelys qiguensis	0	0	0	1	1	1	1	0	0	?	0	0	1	1	0	0	0	0	1	1
Annemys levensis	0	0	0	?	1	1	0	1	0	?	0	0	1	?	0	0	0	0	?	1
Portlandemys mcdowelli	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Plesiochelys solodurensis	0	0	1	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0	1	1
Solnhofia parsonsi	0	0	0	0	1	0	1	0	?	1	1	0	?	?	0	0	0	0	0	1

	101	**102**	**103**	**104**	**105**	**106**	**107**	**108**	**109**	**110**	**111**	**112**	**113**	**114**	**115**	**116**	**117**	**118**	**119**	**120**
'Thalassemys moseri'	0	?	?	?	?	0	?	?	?	?	1	0	?	?	?	?	?	?	1	1
Sandownia harrisi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Santanachelys gaffneyi	1	0	0	?	1	0	1	0	?	1	1	0	1	1	0	0	0	0	-	1
Hangaiemys hoburensis	0	0	0	0	1	1	1	0	0	1	0	0	1	1	0	0	0	1	0	1
Judithemys sukhanovi	0	0	0	0	1	1	1	0	0	1	0	0	1	1	0	0	0	1	0	1
Dracochelys bicuspis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Sinemys lens	0	1	-	0	1	1	1	0	0	1	1	?	1	1	0	0	0	?	0	1
Ordosemys leios	0	0	0	0	1	1	1	0	0	1	1	?	?	?	?	?	?	?	0	1
Toxochelys latiremis	1	0	0	?	1	1	1	0	?	1	1	0	1	1	0	0	0	1	0	1
Mesodermochelys undulatus	1	?	?	?	1	?	1	0	?	1	1	0	1	1	0	0	0	1	0	1
Caretta caretta	1	0	0	?	1	1	1	0	?	1	1	0	1	1	0	0	0	1	0	1
Chelonia mydas	1	0	0	?	1	1	1	0	?	1	1	0	1	1	0	0	0	1	0	1
Dermochelys coriacea	1	-	-	-	1	-	-	-	-	1	1	-	1	1	0	0	0	1	0	1
Protochelydra zangerli	0	?	?	?	?	?	?	?	?	1	0	0	1	1	0	0	0	1	0	1
Macrochelys temminckii	0	0	0	?	0	1	1	0	?	1	1	0	1	1	0	0	0	1	0	1
Chelydra serpentina	0	0	0	0	1	1	1	0	0	1	1	0	1	1	0	0	0	1	0	1
Platysternon megacephalum	0	0	0	0	1	1	1	0	0	1	0	0	1	1	0	0	0	1	0	1
Mongolemys elegans	0	0	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	1	1
Gopherus polyphemus	0	0	0	?	1	1	1	?	?	0	0	0	1	1	0	0	0	0	1	1
Chrysemys picta	0	0	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	1	1
Geoclemys hamiltonii	0	0	0	?	1	1	1	?	?	0	0	0	1	1	0	0	0	0	1	1
Emarginachelys cretacea	0	?	?	?	1	1	1	0	0	1	0	0	1	1	0	0	0	0	0	1
Baptemys wyomingensis	0	0	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	1	1
Dermatemys mawii	0	0	0	?	1	1	1	0	0	0	0	0	1	1	0	0	0	0	1	1
Hoplochelys crassa	0	0	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	1
Staurotypus triporcatus	0	0	0	?	1	1	1	0	?	0	0	1	1	1	0	0	0	0	0	1
Sternotherus odoratus	0	0	0	0	1	1	1	0	0	0	0	1	-	-	-	-	1	0	0	1
Kinosternon flavescens	0	0	0	0	1	1	1	0	0	0	0	1	-	-	-	-	1	0	0	1
Zangerlia neimongolensis	0	?	?	0	1	1	?	?	1	0	0	0	1	1	0	0	0	0	0	1
Basilemys variolosa	0	0	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	1
Adocus beatus	0	0	0	1	1	1	1	0	1	0	0	0	1	1	0	0	0	0	0	1
Peltochelys duchastelli	0	?	?	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	1
Apalone ferox	-	-	-	-	-	-	-	-	-	1	1	-	1	1	1	0	0	-	0	1
Lissemys punctata	-	-	-	-	-	-	-	-	-	1	1	-	1	1	1	0	0	-	0	1
Pseudanosteira pulchra	0	0	0	0	1	1	?	0	?	1	0	-	1	1	0	0	0	0	0	1
Carettochelys insculpta	0	-	-	-	-	-	-	-	-	1	0	-	1	1	0	0	0	0	0	1

	121	**122**	**123**	**124**	**125**	**126**	**127**	**128**	**129**	**130**	**131**	**132**	**133**	**134**	**135**	**136**	**137**	**138**	**139**	**140**
Anthodon serrarius	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Owenetta kitchingorum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Simosaurus gaillardoti	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gephyrosaurus bridensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Protorosaurus speneri	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Araeoscelidia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Captorhinidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Odontochelys semitestacea	1	0	?	0	0	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?
Proganochelys quenstedti	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?
Palaeochersis talampayensis	?	0	0	0	0	0	?	?	?	?	?	0	?	?	?	?	?	0	?	?
Australochelys africanus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Proterochersis robusta	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kayentachelys aprix	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Indochelys spatulata	0	0	?	0	0	0	?	?	?	?	?	1	?	?	?	?	?	?	?	?
Eileanchelys waldmani	0	0	?	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	?	?
Heckerochelys romani	0	0	0	0	0	0	?	0	0	0	0	1	0	0	0	0	0	0	0	0
Condorchelys antiqua	?	?	?	?	?	0	?	?	?	?	?	?	?	0	0	?	?	?	?	?
Meiolania platyceps	?	?	0	0	0	0	0	0	0	0	0	1	0	0	?	?	?	?	?	?
Ninjemys oweni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Niolamia argentina	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Chubutemys copelloi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Otwayemys cunicularius	-	-	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	?	0	0
Mongolochelys efremovi	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
Kallokibotion bajazidi	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Platychelys oberndorferi	0	1	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	-
Caribemys oxfordiensis	0	1	1	?	0	0	0	1	0	0	0	1	0	0	0	0	0	?	1	-
Notoemys laticentralis	0	1	?	1	0	0	0	1	0	?	?	1	?	0	0	0	0	?	1	-
Elseya dentata	-	-	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	-
Chelodina oblonga	-	-	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	-
Phrynops geoffranus	-	-	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	-
Erymnochelys madagascariensis	0	1	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	-
Pelomedusa subrufa	0	1	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	-
Podocnemis expansa	0	1	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	-
Arundelemys dardeni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dorsetochelys delairi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Pleurosternon bullockii	0	0	?	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Glyptops plicatulus	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Dinochelys whitei	0	0	?	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	?
Neurankylus eximius	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Trinitichelys hiatti	0	0	1	?	0	0	0	0	0	0	0	1	0	0	0	0	0	?	0	0
Plesiobaena antiqua	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0
Boremys pulchra	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	?	0	0
Baena arenosa	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0
Chisternon undatum	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0
Naomichelys speciosa	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Sichuanchelys chowi	0	0	?	0	0	0	0	0	?	0	?	1	0	0	0	0	0	0	0	0
Siamochelys peninsularis	?	?	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0
Chengyuchelys baenoides	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
Chengyuchelys zigongensis	0	0	?	0	0	0	0	?	?	?	?	?	?	0	0	0	0	1	0	0
'Chengyuchelys' dashanpuensis	0	0	?	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0
Xinjiangchelys tianshanensis	-	-	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0
Xinjiangchelys latimarginalis	-	-	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0
Xinjiangchelys qiguensis	-	-	1	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0
Annemys levensis	-	-	?	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0
Portlandemys mcdowelli	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Plesiochelys solodurensis	-	-	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Solnhofia parsonsi	-	-	0	0	0	0	0	?	?	?	?	?	?	0	0	0	0	0	0	0

	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140
'Thalassemys moseri'	-	-	?	?	?	0	0	?	?	?	?	?	?	0	0	0	0	?	0	0
Sandownia harrisi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Santanachelys gaffneyi	-	-	-	0	0	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?
Hangaiemys hoburensis	-	-	0	0	0	0	0	0	0	1	-	1	0	0	0	0	0	0	0	0
Judithemys sukhanovi	-	-	0	0	0	0	0	0	?	1	-	1	0	0	0	0	0	0	0	0
Dracochelys bicuspis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Sinemys lens	-	-	0	0	0	0	0	?	?	?	?	1	?	0	0	0	0	?	0	0
Ordosemys leios	-	-	0	0	0	0	0	?	?	?	?	1	?	0	0	0	0	1	0	0
Toxochelys latiremis	-	-	0	0	1	0	0	?	?	?	?	1	?	0	?	0	0	1	0	0
Mesodermochelys undulatus	-	-	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Caretta caretta	-	-	0	0	1	0	0	0	?	1	-	1	1	0	0	0	0	0	0	0
Chelonia mydas	-	-	0	0	1	0	0	0	?	1	-	1	1	0	0	0	0	0	0	0
Dermochelys coriacea	-	-	0	0	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Protochelydra zangerli	-	-	0	0	0	0	0	?	0	1	-	1	0	0	0	0	1	1	0	0
Macrochelys temminckii	-	-	0	0	0	0	0	0	0	1	-	1	0	0	0	0	1	1	0	0
Chelydra serpentina	-	-	0	0	0	0	0	0	?	1	-	1	0	0	0	0	1	1	0	0
Platysternon megacephalum	-	-	0	1	0	0	0	0	0	1	-	1	0	0	0	0	0	0	0	0
Mongolemys elegans	-	-	1	0	0	0	0	0	0	1	-	1	0	0	0	0	0	0	0	0
Gopherus polyphemus	-	-	1	1	0	0	0	0	?	1	-	1	0	0	0	0	0	0	0	1
Chrysemys picta	-	-	1	0	0	0	0	0	0	1	-	1	0	0	0	0	0	0	0	1
Geoclemys hamiltonii	-	-	1	1	0	0	0	0	?	1	-	1	0	0	0	0	0	0	0	1
Emarginachelys cretacea	-	-	0	0	0	0	0	0	0	1	-	1	0	0	?	?	?	0	0	0
Baptemys wyomingensis	-	-	1	0	0	0	0	0	0	1	-	1	0	0	1	0	0	0	0	0
Dermatemys mawii	-	-	0	1	0	0	0	0	0	1	-	1	1	0	1	0	0	0	0	0
Hoplochelys crassa	-	-	0	0	0	0	0	0	?	1	-	1	0	0	1	0	1	0	0	0
Staurotypus triporcatus	-	-	0	0	0	0	0	0	?	1	-	1	0	0	1	1	-	0	0	0
Sternotherus odoratus	-	-	0	0	0	0	0	0	-	1	-	1	1	1	1	1	-	0	0	0
Kinosternon flavescens	-	-	0	0	0	0	0	0	-	1	-	1	1	1	1	1	-	0	0	0
Zangerlia neimongolensis	-	-	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0
Basilemys variolosa	-	-	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0
Adocus beatus	-	-	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
Peltochelys duchastelli	-	-	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0
Apalone ferox	-	-	0	0	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Lissemys punctata	-	-	0	0	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Pseudanosteira pulchra	-	-	0	0	0	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Carettochelys insculpta	-	-	0	0	0	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-

	141	142	143	144	145	146	147	148	149	150	151	152	153	154	155	156	157	158	159	160
Anthodon serrarius	0	?	?	?	0	-	-	-	-	-	-	0	-	-	-	0	0	0	0	0
Owenetta kitchingorum	?	?	?	?	0	-	-	-	-	-	-	0	-	-	-	0	0	?	0	0
Simosaurus gaillardoti	0	?	?	?	0	-	-	-	-	-	-	0	-	-	-	0	0	0	?	0
Gephyrosaurus bridensis	0	1	?	?	0	-	-	-	-	-	-	0	-	-	-	0	0	?	0	0
Protorosaurus speneri	0	1	?	?	0	-	-	-	-	-	-	0	-	-	-	0	0	0	0	0
Araeoscelidia	0	1	?	?	0	-	-	-	-	-	-	0	-	-	-	0	0	0	0	0
Captorhinidae	0	1	?	?	0	-	-	-	-	-	-	0	-	-	-	0	0	0	0	0
Odontochelys semitestacea	0	0	0	0	0	-	-	-	-	-	-	?	0	?	?	0	?	0	1	0
Proganochelys quenstedti	0	0	0	0	0	-	-	-	-	-	-	0	0	0	0	1	0	0	0	0
Palaeochersis talampayensis	?	0	0	0	0	-	-	-	-	-	-	0	0	0	?	1	0	0	1	0
Australochelys africanus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Proterochersis robusta	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Kayentachelys aprix	?	0	0	?	0	-	-	-	-	-	-	?	0	0	0	1	?	0	1	?
Indochelys spatulata	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Eileanchelys waldmani	?	0	?	?	0	-	-	-	-	-	-	?	?	?	?	?	?	?	?	?
Heckerochelys romani	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	0	?	?	?
Condorchelys antiqua	0	0	0	?	0	-	-	-	-	-	-	?	?	0	?	?	?	?	1	?
Meiolania platyceps	0	0	0	0	1	0	0	1	1	1	1	0	0	0	?	1	0	0	0	1
Ninjemys oweni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?
Niolamia argentina	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Chubutemys copelloi	?	?	?	?	1	?	?	?	?	?	0	0	?	?	?	?	0	?	?	?
Otwayemys cunicularius	?	0	?	?	1	?	?	?	?	?	0	0	0	?	?	1	0	?	?	1
Mongolochelys efremovi	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	1	0	0	1	1
Kallokibotion bajazidi	?	0	?	?	0	-	-	-	-	-	-	?	0	?	?	1	0	0	?	0
Platychelys oberndorferi	?	0	?	?	1	?	?	?	?	?	?	?	0	0	1	?	0	1	?	?
Caribemys oxfordiensis	?	0	?	?	1	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?
Notoemys laticentralis	?	0	?	?	1	0	0	?	?	?	?	?	1	0	1	1	?	?	?	?
Elseya dentata	1	0	0	0	1	0	0	0	1	1	0	0	1	0	1	1	0	1	1	1
Chelodina oblonga	1	0	0	0	1	0	0	0	1	1	0	0	1	0	1	1	0	1	1	1
Phrynops geoffranus	1	0	0	0	1	0	0	0	1	1	0	0	1	0	1	1	0	1	1	1
Erymnochelys madagascariensis	1	0	0	0	1	1	1	1	1	1	1	0	1	0	1	1	0	1	1	1
Pelomedusa subrufa	1	0	0	0	1	1	1	1	1	1	1	0	1	0	1	1	0	1	1	1
Podocnemis expansa	1	0	0	0	1	1	1	1	1	1	1	0	1	0	1	1	0	1	1	1
Arundelemys dardeni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dorsetochelys delairi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Pleurosternon bullockii	?	0	?	?	0	-	-	-	-	-	-	?	0	0	1	1	?	?	?	?
Glyptops plicatulus	?	0	0	0	0	-	-	-	-	-	-	?	0	0	1	?	0	?	?	?
Dinochelys whitei	1	0	?	?	0	-	-	-	-	-	-	?	0	?	1	?	?	?	1	?
Neurankylus eximius	?	?	?	?	?	?	?	?	?	?	?	?	0	0	1	?	?	?	?	?
Trinitichelys hiatti	?	0	0	0	0	-	-	-	-	-	-	?	?	?	1	?	0	?	?	?
Plesiobaena antiqua	1	0	0	0	1	?	?	?	1	1	1	0	0	0	1	?	0	0	1	0
Boremys pulchra	1	0	0	0	0	-	-	-	-	-	-	?	0	0	1	?	0	0	1	1
Baena arenosa	?	?	?	?	?	?	?	?	?	?	?	?	0	0	1	?	0	?	?	?
Chisternon undatum	?	0	0	0	1	0	0	1	1	1	1	0	0	0	1	?	0	0	1	1
Naomichelys speciosa	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	?	?	?
Sichuanchelys chowi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Siamochelys peninsularis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Chengyuchelys baenoides	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Chengyuchelys zigongensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
'Chengyuchelys' dashanpuensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Xinjiangchelys tianshanensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Xinjiangchelys latimarginalis	?	1	0	0	0	-	-	-	-	-	-	0	1	0	1	1	0	0	1	1
Xinjiangchelys qiguensis	?	1	?	?	0	-	-	-	-	-	-	?	?	0	1	1	?	?	?	?
Annemys levensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Portlandemys mcdowelli	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Plesiochelys solodurensis	?	?	?	?	?	?	?	?	?	?	?	?	0	0	1	?	0	?	?	?
Solnhofia parsonsi	1	1	0	?	0	-	-	-	-	-	-	?	?	?	1	?	?	?	1	0

	141	142	143	144	145	146	147	148	149	150	151	152	153	154	155	156	157	158	159	160
'Thalassemys moseri'	1	1	?	?	0	-	-	-	-	-	-	?	0	?	?	1	?	?	?	?
Sandownia harrisi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Santanachelys gaffneyi	1	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?
Hangaiemys hoburensis	1	1	1	?	1	0	0	1	1	1	1	0	1	?	1	?	0	?	?	?
Judithemys sukhanovi	1	1	1	?	1	0	0	1	1	1	1	0	1	?	1	1	0	1	1	1
Dracochelys bicuspis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Sinemys lens	?	?	?	0	?	?	?	?	?	?	?	?	0	?	?	?	?	?	1	?
Ordosemys leios	1	1	?	0	1	?	0	1	?	?	0	0	0	?	1	1	0	1	1	1
Toxochelys latiremis	1	1	?	1	1	0	0	1	1	1	1	0	?	0	1	?	0	0	1	1
Mesodermochelys undulatus	1	1	1	0	1	?	?	?	?	?	?	?	1	0	1	?	0	1	1	1
Caretta caretta	1	1	1	1	1	0	0	1	1	1	1	0	1	0	1	?	1	1	1	1
Chelonia mydas	1	1	1	1	1	0	0	1	1	1	1	0	1	0	1	?	1	1	1	1
Dermochelys coriacea	1	1	1	1	1	0	0	1	1	1	1	0	1	-	-	1	0	1	1	1
Protochelydra zangerli	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Macrochelys temminckii	1	1	1	1	1	0	0	1	1	1	1	0	1	0	1	1	1	0	1	1
Chelydra serpentina	1	1	1	1	1	0	0	1	1	1	1	0	1	0	1	1	1	0	1	1
Platysternon megacephalum	1	1	1	1	1	0	0	1	1	1	0	0	1	0	1	1	1	0	1	1
Mongolemys elegans	?	?	?	?	1	0	0	1	1	1	0	0	1	?	1	?	1	0	1	?
Gopherus polyphemus	1	1	1	1	1	0	0	1	1	1	0	0	1	0	1	?	1	1	1	1
Chrysemys picta	1	1	1	1	1	0	0	1	1	1	0	0	1	0	1	1	1	1	1	1
Geoclemys hamiltonii	1	1	1	1	1	0	0	1	1	1	0	0	1	0	1	?	1	1	1	1
Emarginachelys cretacea	1	1	?	?	1	0	0	1	1	1	1	0	?	?	?	?	?	?	?	?
Baptemys wyomingensis	1	1	1	1	1	0	1	1	1	1	1	0	1	?	?	?	1	1	1	1
Dermatemys mawii	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	?	1	1	1	1
Hoplochelys crassa	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	?	?	?	?	?
Staurotypus triporcatus	1	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1
Sternotherus odoratus	1	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1
Kinosternon flavescens	1	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1
Zangerlia neimongolensis	1	1	1	1	1	0	0	0	0	0	0	0	1	?	?	?	1	?	?	?
Basilemys variolosa	1	1	1	1	1	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?
Adocus beatus	1	1	1	1	1	0	0	0	0	0	0	0	1	?	1	?	1	?	?	?
Peltochelys duchastelli	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Apalone ferox	1	1	0	1	1	0	0	0	0	0	0	1	1	0	1	?	-	1	1	1
Lissemys punctata	1	1	0	1	1	0	0	0	0	0	0	1	1	0	1	?	-	1	1	1
Pseudanosteira pulchra	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Carettochelys insculpta	1	1	0	1	1	0	0	0	0	0	0	0	1	0	1	?	1	1	1	1

	161	162	163	164	165	166	167	168	169	170	171	172	173	174	175	176	177	178
Anthodon serrarius	0	1	-	-	-	0	0	-	0	-	0	-	?	0	1	0	0	0
Owenetta kitchingorum	0	0	-	-	-	0	0	-	0	-	0	-	?	0	0	0	0	0
Simosaurus gaillardoti	0	1	-	-	-	0	0	-	0	-	0	-	?	1	?	?	?	?
Gephyrosaurus bridensis	0	1	-	-	-	0	0	-	0	-	0	-	?	1	?	?	0	?
Protorosaurus speneri	0	?	-	-	-	0	?	-	0	-	0	-	?	?	0	0	0	0
Araeoscelidia	0	0	-	-	-	0	0	-	0	-	0	-	?	1	0	0	0	0
Captorhinidae	0	?	-	-	-	0	0	-	0	-	0	-	?	0	0	0	0	0
Odontochelys semitestacea	1	0	-	0	?	0	0	0	0	-	0	?	0	1	0	0	0	?
Proganochelys quenstedti	1	0	0	0	0	0	0	0	0	-	0	0	0	1	1	1	0	0
Palaeochersis talampayensis	1	0	0	0	0	0	0	1	0	?	?	?	0	1	1	1	0	?
Australochelys africanus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Proterochersis robusta	?	0	0	?	?	?	?	?	1	?	0	0	?	?	?	?	?	?
Kayentachelys aprix	1	0	1	0	0	0	1	0	1	-	0	1	1	?	?	?	?	?
Indochelys spatulata	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Eileanchelys waldmani	?	0	1	?	?	?	?	?	1	?	?	?	?	1	?	?	?	?
Heckerochelys romani	?	0	1	?	?	?	?	0	?	-	?	?	?	?	?	?	?	?
Condorchelys antiqua	1	?	?	?	?	?	1	0	?	-	?	1	1	?	?	?	?	?
Meiolania platyceps	1	0	1	1	0	0	1	0	1	-	0	1	?	1	1	1	0	?
Ninjemys oweni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Niolamia argentina	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Chubutemys copelloi	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Otwayemys cunicularius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Mongolochelys efremovi	1	0	1	1	0	0	1	0	1	-	0	?	?	1	1	0	0	1
Kallokibotion bajazidi	1	0	1	?	?	0	?	0	?	-	?	?	?	?	?	?	?	?
Platychelys oberndorferi	?	?	?	?	?	?	?	1	1	0	0	1	?	?	?	?	?	?
Caribemys oxfordiensis	?	?	?	?	?	?	?	1	?	0	?	?	?	?	?	?	?	?
Notoemys laticentralis	?	?	?	?	?	?	?	1	?	1	?	?	?	?	?	?	0	?
Elseya dentata	1	1	-	1	1	1	1	1	1	1	0	1	1	?	1	0	0	1
Chelodina oblonga	1	1	-	1	1	1	1	1	1	1	0	1	1	?	1	0	0	1
Phrynops geoffranus	1	1	-	1	1	1	1	1	1	1	0	1	1	?	1	0	0	1
Erymnochelys madagascariensis	1	1	-	1	1	0	1	1	1	1	0	1	1	?	1	0	0	1
Pelomedusa subrufa	1	1	-	1	1	0	1	1	1	1	0	1	1	?	1	0	0	1
Podocnemis expansa	1	1	-	1	1	1	1	1	1	1	0	1	1	?	1	0	0	1
Arundelemys dardeni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dorsetochelys delairi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Pleurosternon bullockii	1	0	?	?	?	?	?	0	1	-	0	?	?	?	?	?	?	?
Glyptops plicatulus	1	0	1	1	1	1	1	0	1	-	0	1	1	?	?	?	?	?
Dinochelys whitei	?	0	1	?	?	?	?	?	?	?	?	?	?	?	1	0	0	1
Neurankylus eximius	?	?	?	?	?	?	?	0	?	-	?	?	?	?	?	?	?	?
Trinitichelys hiatti	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Plesiobaena antiqua	?	?	?	1	1	1	1	0	1	-	0	1	1	?	1	?	0	1
Boremys pulchra	?	1	-	?	?	?	?	0	?	-	?	?	?	?	?	?	?	?
Baena arenosa	?	1	-	?	?	?	?	0	?	-	0	1	1	?	?	?	?	?
Chisternon undatum	?	?	?	1	1	1	1	0	1	-	?	1	1	?	?	?	?	?
Naomichelys speciosa	1	?	?	1	1	0	1	0	1	-	0	1	?	1	1	0	0	?
Sichuanchelys chowi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Siamochelys peninsularis	?	?	?	?	?	?	?	0	1	-	?	?	?	?	?	?	?	?
Chengyuchelys baenoides	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Chengyuchelys zigongensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
'Chengyuchelys' dashanpuensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Xinjiangchelys tianshanensis	1	?	?	1	1	1	1	0	1	-	0	?	?	1	?	?	?	?
Xinjiangchelys latimarginalis	1	0	1	1	1	1	1	0	1	-	0	1	1	1	?	?	?	?
Xinjiangchelys qiguensis	1	0	1	1	1	1	1	0	1	-	?	1	?	?	?	?	?	?
Annemys levensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Portlandemys mcdowelli	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Plesiochelys solodurensis	?	?	?	1	1	1	1	0	1	-	0	1	1	?	1	0	0	1
Solnhofia parsonsi	1	?	?	1	1	1	1	0	?	-	?	1	1	1	1	0	0	1

	161	**162**	**163**	**164**	**165**	**166**	**167**	**168**	**169**	**170**	**171**	**172**	**173**	**174**	**175**	**176**	**177**	**178**
'Thalassemys moseri'	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Sandownia harrisi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Santanachelys gaffneyi	1	?	?	1	1	?	1	0	?	-	0	1	1	1	1	0	0	?
Hangaiemys hoburensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Judithemys sukhanovi	1	?	?	1	1	?	1	0	1	-	0	1	1	1	?	?	0	1
Dracochelys bicuspis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Sinemys lens	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1
Ordosemys leios	1	?	?	1	1	1	1	0	1	-	0	1	1	1	?	?	?	?
Toxochelys latiremis	1	?	?	1	1	1	1	0	?	-	0	1	1	?	1	0	1	1
Mesodermochelys undulatus	1	1	-	1	1	1	1	0	1	-	0	1	1	1	?	?	?	?
Caretta caretta	1	1	-	1	1	1	1	0	1	-	0	1	1	1	1	0	1	1
Chelonia mydas	1	1	-	1	1	1	1	0	?	-	0	1	1	1	1	0	1	1
Dermochelys coriacea	1	1	-	1	1	1	1	0	1	-	0	1	1	1	1	0	1	1
Protochelydra zangerli	1	1	-	1	1	0	1	0	1	-	0	?	?	?	?	?	?	?
Macrochelys temminckii	1	1	-	1	1	0	1	0	1	-	0	1	1	1	1	0	0	1
Chelydra serpentina	1	1	-	1	1	0	1	0	1	-	0	1	1	1	1	0	0	1
Platysternon megacephalum	1	1	-	1	1	0	1	0	1	-	0	1	1	1	1	0	0	1
Mongolemys elegans	1	1	-	1	1	0	1	0	1	-	0	1	1	?	1	0	0	?
Gopherus polyphemus	1	1	-	1	1	0	1	0	1	-	0	1	1	1	1	1	0	1
Chrysemys picta	1	1	-	1	1	0	1	0	1	-	0	1	1	1	1	0	0	1
Geoclemys hamiltonii	1	1	-	1	1	0	1	0	1	-	0	1	1	1	1	0	0	1
Emarginachelys cretacea	1	?	?	1	1	0	1	0	1	-	0	1	1	1	1	0	0	1
Baptemys wyomingensis	1	1	-	1	1	0	1	0	1	-	1	1	1	1	1	0	0	1
Dermatemys mawii	1	1	-	1	1	0	1	0	1	-	0	1	1	1	1	0	0	1
Hoplochelys crassa	1	1	-	?	?	0	1	0	?	-	?	?	?	?	?	?	?	?
Staurotypus triporcatus	1	1	-	1	1	0	1	0	?	-	1	1	1	1	1	0	0	1
Sternotherus odoratus	1	1	-	1	1	0	1	0	1	-	1	1	1	1	1	0	0	1
Kinosternon flavescens	1	1	-	1	1	0	1	0	?	-	1	1	1	1	1	0	0	1
Zangerlia neimongolensis	1	?	?	1	1	0	1	0	1	-	0	1	1	?	1	1	0	?
Basilemys variolosa	1	1	-	1	1	?	1	0	1	-	0	1	1	?	1	1	0	?
Adocus beatus	1	1	-	1	1	0	1	0	1	-	0	1	1	?	1	0	0	1
Peltochelys duchastelli	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Apalone ferox	1	1	-	1	1	0	1	0	1	-	0	1	1	1	1	0	0	1
Lissemys punctata	1	1	-	1	1	0	1	0	1	-	0	1	1	1	1	0	0	1
Pseudanosteira pulchra	1	?	?	1	1	?	?	0	?	-	?	1	1	?	1	0	0	1
Carettochelys insculpta	1	1	-	1	1	0	1	0	1	-	0	1	1	1	1	0	0	1

APPENDIX 6: REJECTED CHARACTERS

FROM JOYCE (2007)

Character 8 - Prefrontals heavily sculptured with prominences and bosses: 0 = present; 1 = absent
Rationale for rejection: Uninformative in the context of the present analysis, autapomorphic for *Proganochelys quenstedti*.

Character 18 - Squamosal-postorbital contact: 0 = present; 1 = absent, temporal roofing well developed, but postorbital short; 2 = absent, due to lower temporal emargination; 3 = absent, due to upper temporal emargination
Rationale for rejection: This coding refers to independent features: contact squamosal-postorbital absent/present; postorbital reduced in length; deep lower temporal emargination; deep upper temporal emargination. The repartition of these different features should be scrutinised but the presence of a deep lower or upper temporal emargination should not be hypothesised to be homologous with the absence of contact between the squamosal and postorbital in a well ossified skull roof. Moreover, this character is partly redundant with characters 16, 21 and 22 of the present analysis.

Character 52 - Path of hyomandibular branch of the facial nerve: 0 = hyomandibular nerve passes through cranioquadrate space parallel to vena capitis lateralis; 1 = hyomandibular nerve runs independent from vena capitis lateralis
Rationale for rejection: In contrast to the scoring of this character suggested by Joyce (2007), it is not possible to score this character for most fossil taxa, especially without first hand examination. The presence or absence of a separate path for the hyomandibular branch of the facial nerve is in most cases concealed from external examination (see Gaffney, 1979: 121-126).

Character 72 - Number of vertebrals: 0 = four present; 1 = five or more present
Rationale for rejection: Uninformative in the context of the present analysis, autapomorphic for *Proganochelys quenstedti*.

Character 80 - Distinct posterolateral entoplastral processes: 0 = present; 1 = absent
Rationale for rejection: Uninformative in the context of the present analysis, autapomorphic for *Proganochelys quenstedti*.

Character 127 - Iliac scar: 0 = extends from costals onto the peripherals and pygal; 1 = positioned on costals only
Rationale for rejection: Uninformative in the context of the present analysis, autapomorphic for *Platychelys oberndorferi*.

Character 134 - Flippers: 0 = absent; 1 = short flippers present; 2 = elongate flippers present
Rationale for rejection: The recognition of flippers in fossil taxa is rather difficult and no indication is given as to the distinction between short and elongate flippers, which only appears to support carettochelyids (see Chapter 5). The scoring of this character is not reproducible and it appears more prudent to omit it pending further investigation.

Character 136 - Metatarsal V and "functional metatarsal V": 0 = metatarsal V functions as true metatarsal; 1 = metatarsal V functions as a tarsal, with first phalanx of digit V functioning as a metatarsal
Rationale for rejection: According to Fabrezi *et al.* (2009), the hooked element in the turtle tarsus is actually the fifth tarsal rather than the fifth metatarsal as previously thought. Consequently, this character would need to be redefined. Moreover, according to Joyce (2007), state 0 is only known in *Proganochelys quenstedti* and *Meiolania platyceps*, but the character is impossible to score for the latter species because no phalanges of the fifth toe are preserved in any specimens (Gaffney, 1996). If coded, this character would consequently be uninformative because only present in *Proganochelys quenstedti*.

FROM STERLI (2008)

Character 13 - Posterodorsal margin of the temporal fossa roofed by an overhanging process of the skull roof: 0 = absent; 1 = present
Rationale for exclusion: This character corresponds to the development of the upper temporal emargination and is already coded by characters 10 of Sterli (2008) and 11 of Joyce (2007), which corresponds to character 16 of the present analysis (see Chapter 5).

Character 38 - Dorsal surface of quadrate (or quadrate and prootic) with a roughened area or with a process showing the presence of a processus trochlearis oticum: 0 = absent; 1 = present
Rationale for exclusion: As pointed out by Joyce (2007: 78), this character cannot be scored objectively for fossil taxa. For example, many fossil pancryptodires actually lack a proper processus trochlearis oticum but have been scored as having one in previous analyses because the presence of such a processus is mistakenly associated with the presence of a 'cryptodiran' type trochlear system for the lower jaw musculature.

Character 48 - Vertical flange on processus pterygoideus externus: 0 = absent; 1 = present
Rationale for exclusion: The development of a vertical flange on the processus pterygoideus externus appears to be truly continuous (Joyce, 2007: 42).

Character 52 - Morphology of the anteriormost part of the basioccipital: 0 = with a ventral tubercle; 1 = with a groove, limited by two lateral ridges, which finish in horns; 2 = tubercle absent
Rationale for exclusion: The different states are clearly not homologous to one another and states 1 and 2 are not mutually exclusive. Moreover, the definition of state 1 is obscure so that the scoring of Sterli (2008) is not reproducible.

Character 54 - Wide transverse occipital plane with depressions for the nuchal musculature: 0 = absent; 1 = present
Rationale for exclusion: According to the scorings of Rougier *et al.* (1995) and Sterli (2008), state 1 is only present in *Palaeochersis talampayensis* and *Australochelys africanus*. However, these depressions are also present in *Proganochelys quenstedti* and *Kayentachelys aprix*. In these species, the depressions are less developed and this feature appears to be relatively continuous. In the current state of knowledge, it is preferable to avoid using this non-discrete character.

Character 55 - Ventral ridge on opisthotic: 0 = absent; 1 = present, with an incipient enclosed middle ear region; 2 = present, but modified with an enclosed middle ear region
Rationale for exclusion: The character appears to be non-discrete and the scoring is not reproducible.

Character 56 - Processus interfenestralis: 0 = present, but not reaching the floor of the cavum acustico-jugulare; 1 = present, reaching the floor of the cavum acustico-jugulare but robust; 2 = present, reaching the floor of the cavum acustico-jugulare but small
Rationale for exclusion: This character codes two independent features that are the thickness of the basicranium floor and the development of the processus interfenestralis. Both features appear to be rather continuous (i.e., non-discrete). It would be impossible to score *Eileanchelys waldmani* for example (see Chapter 3).

Character 64 - Foramen caroticum laterale: 0 = arteria palatina enters the skull through the interpterygoid vacuity; 1 = foramen caroticum laterale located between the basisphenoid and the pterygoid with the foramen posterius canalis carotici interni formed by the basisphenoid; 2 = the canalis caroticus internus is not completely floored making the foramen caroticum laterale and the foramen basisphenoidale visible in ventral view, foramen posterius canalis carotici interni is formed by the pterygoid or the pterygoid and the basisphenoid; 3 = the arteria palatina branches from the arteria carotici interna inside the skull, so the foramen caroticum laterale is formed by the pterygoid as the foramen posterior canalis carotici interni; 4 = the arteria palatina branches from the arteria carotici interna inside the skull, foramen posterius canalis carotici interni is formed by the pterygoid and the prootic; 5 = foramen caroticum laterale absent; 6 = foramen caroticum laterale formed within the pterygoid, foramen posterior canalis carotici interni formed along midway between pterygoid and basisphenoid
Rationale for exclusion: This character is clearly not constructed for use in a cladistic analysis and

Sterli (2008) simply included every observed configurations of this region of the skull into a single character without considering neither the absence of homology between the character states nor the dependence of these characters on others included in her analysis. Moreover, the scoring of fossil taxa is difficult to reproduce.

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APPENDIX 7: LIST OF APOMORPHIES (ADAMS CONSENSUS TREE)

Clades	Unambiguous synapomorphies (complete matrix)
Testudinata	14(1); 86(1); 142(0); 161(1)
Clade A	39(1); 121(0); 156(1); 175(1)
Clade B	20(1); 45(1); 49(1); 52(1); 58(1); 71(1)
Clade C	3(1); 11(1); 30(1); 31(1); 40(1); 42(1); 48(1); 51(1); 105(1); 132(1); 163(1); 167(1); 169(1); 173(1)
Clade D	57(1); 113(1)
Heckerochelys romani + *Condorchelys antiqua*	111(1)
Chengyuchelyidae	106(1); 108(1); 116(1); 138(1)
Clade E	95(1)
Clade F	43(1); 60(1); 78(1)
Clade G	109(1); 111(1); 145(1); 160(1)
Meiolaniidae + *Mongolochelys efremovi*	25(1); 68(1); 110(1)
Meiolaniidae	26(1); 67(1)
Meiolania platyceps + *Ninjemys oweni*	32(1)
Clade H	17(1); 56(1); 61(1); 119(1); 123(1)
Clade I	89(1); 166(1)
Paracryptodira	10(1); 80(1)
Pleurosternidae	2(1); 104(1)
Arundemys dardeni + *Pleurosternon bullockii* + *Glyptops plicatulus*	28(1)
Pleurosternon bullockii + *Glyptops plicatulus*	65(1); 74(0)
Baenidae	55(1); 106(1)
Trinitichelys hiatti + remaining baenids	9(1)
Plesiobaena antiqua + remaining baenids	131(1)

Clades	Unambiguous synapomorphies (complete matrix)
Boremys pulchra + *Baena arenosa* + *Chisternon undatum*	103(1); 160(1)
Baena arenosa + *Chisternon undatum*	16(0); 84(1)
Clade J	5(1); 120(1); 142(1)
Clade K	18(0); 81(1)
Solnhofia parsonsi + '*Thalassemys moseri*' + *Santanachelys gaffneyi*	44(1); 111(1)
'*Thalassemys moseri*' + *Santanachelys gaffneyi*	5(0); 64(1)
Clade L	16(1); 106(1); 153(1); 160(1)
Xinjiangchelyidae	127(1); 129(1)
Siamochelys peninsularis + remaining xinjiangchelyids	109(1); 123(0)
X. latimarginalis + *X. tianshanensis* + *Annemys levensis*	138(1)
X. tianshanensis + *Annemys levensis*	94(1)
Clade M	145(1); 158(1); 162(1)
Panpleurodira	60(0); 124(1); 128(1); 139(1); 142(0); 168(1)
Notoemys laticentralis + *Platychelys oberndorferi* + *Caribemys oxfordiensis*	106(0); 107(0); 111(1)
Platychelys oberndorferi + *Caribemys oxfordiensis*	170(0)
Pleurodira	47(1); 53(1)
Chelidae	5(0); 10(1); 22(1); 79(1); 148(0)
Chelodina oblonga + *Phrynops geoffroanus*	68(0); 70(1); 83(1)
Pelomedusoides	1(1); 41(1); 50(1); 94(1); 146(1); 147(1)
Erymnochelys madagascariensis + *Pelomedusa subrufa*	166(0)
Clade N	54(0); 81(1); 119(0); 123(0); 130(1); 143(1)

Clades	Unambiguous synapomorphies (complete matrix)
Hangaiemys hoburensis + *Judithemys sukhanovi*	73(1); 118(1)
Dracochelys bicuspis + *Sinemys lens* + *Ordosemys leios*	50(1)
Sinemys lens + *Ordosemys leios*	5(0); 10(1)
Panchelonioidea	90(1); 101(1); 111(1); 118(1); 125(1); 177(1)
Chelonioidea	1(1); 16(0); 63(1); 72(1); 144(1)
Chelonia mydas + *Caretta caretta*	34(1); 157(1)
Clade O	1(1); 66(1); 157(1); 166(0)
Testudinoidea	119(1); 123(1); 140(1)
Gopherus polyphemus + *Geoclemys hamiltonii*	124(1)
Panchelydridae + *Platysternon megacephalum*	13(0); 53(1); 118(1); 158(0)
Panchelydridae	137(1); 138(1)
Chelydridae	111(1)
Trionychoidea	46(1)
Kinosternoidea	135(1); 147(1)
Kinosternidae	13(0); 23(1); 98(1); 99(1); 112(1); 136(1); 154(1)
Sternotherus odoratus + *Kinosternon flavescens*	100(1); 117(1); 133(1); 134(1)
Pantrionychia	127(1); 130(0); 148(0); 149(0); 150(0)
Clade P	44(1); 53(1)
Clade Q	131(1); 176(1)
Sandownia harrisi + *Zangerlia neimongolensis* + *Chubutemys copelloi*	16(0)
Zangerlia neimongolensis + *Chubutemys copelloi*	13(0)
Peltochelys duchastelli + Trionychia	98(1)
Trionychia	94(1); 110(1); 126(1)

Clades	**Unambiguous synapomorphies (complete matrix)**
Carettochelys insculpta + *Apalone ferox* + *Lissemys punctata*	87(1)
Apalone ferox + *Lissemys punctata*	21(1); 36(1); 96(1); 111(1); 115(1); 152(1)