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A primitive protostegid from Australia and early sea turtle evolution

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Sea turtles (Chelonioidea) are a prominent group of modern marine reptiles whose early history is poorly understood. Analysis of exceptionally well preserved fossils of *Bouliachelys suteri* gen. et sp. nov., a large-bodied basal protostegid (primitive chelonioid) from the Early Cretaceous (Albian) of Australia, indicates that early sea turtles were both larger and more diverse than previously thought. The analysis implies at least five distinct sea turtle lineages existed around 100 million years ago. Currently, the postcranially primitive *Ctenochelys* and *Toxochelys* are interpreted as crown-group sea turtles closely related to living cheloniids (e.g. *Chelonia*); in contrast, the new phylogeny suggests that they are transitional (intermediate stem-taxa) between continental testudines and derived, pelagic chelonioids.

Keywords: sea turtles; protostegidae;
Early Cretaceous; Australia; stem chelonioids

1. INTRODUCTION

Sea turtles (Chelonioidea) have a long fossil record stretching back to the late Early Cretaceous (late Aptian/early Albian, *ca* 105 Myr ago; see Hirayama 1998). However, their early evolutionary history remains largely unknown, as recent phylogenies do not recognize any definitive stem-group taxa. At present, all fossil sea turtles are assigned to one of two extant lineages within crown chelonioids (Hirayama 1994, 1997, 1998; Joyce *et al.* 2004; Lehman & Tomlinson 2004): one leads to living cheloniids (Pancheloniidae: Joyce *et al.* 2004), and the other to living *Dermochelys* (Pandermochelys: Joyce *et al.* 2004). The latter group includes the extinct Protostegidae, a diverse Cretaceous clade containing some spectacular Late Cretaceous giants (e.g. *Archelon*, possibly up to 4 m maximum length; Wieland 1896). The cranial morphology of protostegids is poorly known (Hooks 1998). However, here we report on several exceptionally well preserved skulls belonging to one of the stratigraphically oldest and most primitive protostegids yet found. A re-evaluation of sea turtle phylogeny incorporating these new fossils (re)establishes the primitive, shallow-water *Toxochelys* and *Ctenochelys* (Gaffney & Meylan 1988) as stem chelonioids; these taxa are currently placed within crown-chelonioids, along the lineage leading to living cheloniids (see Hirayama 1994, 1997, 1998).

2. MATERIAL AND METHODS

Bouliachelys suteri gen. et sp. nov. (figure 1*a*–*g* and electronic supplementary material) was added to the most comprehensive published phylogenetic data set of sea turtles (Hirayama 1998), which was revised as follows. The chimera taxon *Osteopygis* was separated into two taxa (the cranial *Euclastes* and postcranial *Osteopygis*; Parham 2005), and additional postcranial characters for *Euclastes* scored from *E.* (*Erquelinnesia*) *gosseleti* (Lynch & Parham 2003; Hirayama 1994). Modifications were also made to the codings and/or character state definitions of 12 characters. A full matrix and character list with annotations discussing these points is provided in electronic supplementary material. Maximum parsimony trees, bootstrap frequencies (1000 replicates), and Bremer support were calculated using heuristic searches in phylogenetic analysis using parsimony (PAUP; Swofford 2000) employing 1000 random-addition replicates. Analyses performed with multi-state characters ordered or unordered (see electronic supplementary material) yielded similar results; the optimal tree ($L=211$) from the unordered analysis is shown in figure 2.

3. PHYLOGENETIC TAXONOMY

All higher taxon names *sensu* Joyce *et al.* 2004.

Testudines Batsch, 1788; Chelonioidea Baur, 1893; Pandermochelys Joyce *et al.* (2004); Protostegidae Cope, 1872

B. suteri gen. et sp. nov.

(a) *Etymology*

After Boulia township, the most productive locality for this taxon (see below); and Richard and John Suter who discovered many of the specimens.

(b) *Holotype, locality and horizon*

Holotype (figure 1*a*–*c*) QM F31669 (Queensland Museum, Brisbane, Australia) from Dunraven Station, near Hughenden, central-northern Queensland, Australia; referred specimen (figure 1*d*–*g*) SAM P41106 (South Australian Museum, Adelaide, Australia) from Boulia region, western Queensland, Australia. Both localities are Toolebuc Formation (Rolling Downs Group), Eromanga Basin, latest middle to late Albian, *P. ludbrookiae* Zone/upper *C. paradoxa*–*P. pannosus* Zone (McMinn & Burger 1986; Alexander & Sansome 1996).

(c) *Diagnosis*

Identical for genus and species due to monotypy. *Bouliachelys* possesses the unique derived features (within chelonioids) of highly sculpted skull roof bones, a rugose boss anterior to each orbit, and double longitudinal keels (formed by the basisphenoid and pterygoids) on the ventral surface of the basicranium and palate. *Bouliachelys* differs from *Notochelone* (the only other Australian fossil sea turtle known from cranial remains) in several additional traits: it is larger, lacks a jugal-quadrate contact$_{9}$, possesses hooked premaxillae$_{13}$, and an upper triturating surface incorporating the palatine$_{15}$ but not vomer$_{16}$, a pterygoid excluded from the mandibular condyle$_{24}$, and a basiphenoid-pterygoid with a V-shaped crest$_{31}$ (character subscript numbering follows the data matrix in the electronic supplementary material, where distributions are scored across all chelonioids). *Bouliachelys* is distinguished from all

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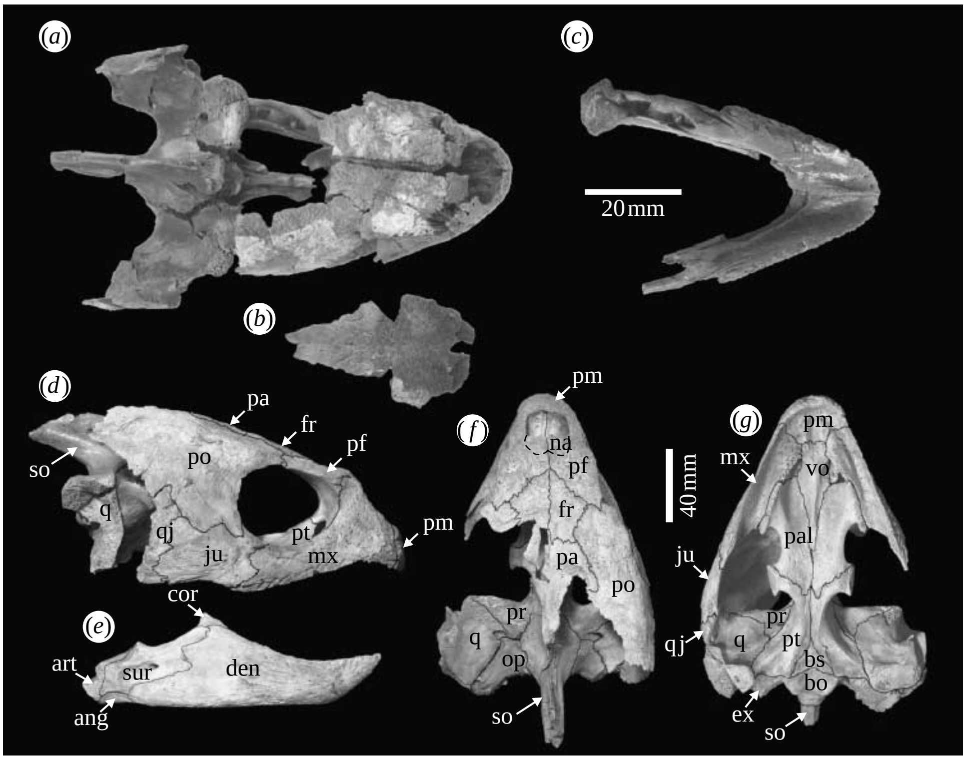

Figure 1. Skulls of *Bouliachelys suteri* gen. et sp. nov. (*a*) Holotype (QM F31669) skull, (*b*) parietal section, and (*c*) mandible in dorsal view. Referred (SAM P41106) (*d*) skull and (*e*) mandible in lateral, (*f*) dorsal and (*g*) ventral views (sutures highlighted). Additional photos can be found in the electronic supplementary material. Abbreviations: ang, angular; art, articular; bo, basioccipital; bs, basisphenoid; cor, coronoid; den, dentary; ex, exoccipital; fr, fontal; ju, jugal; mx, maxilla; na, nasal; op, opisthotic; pa, parietal; pal, palatine; pf, postfrontal; pm, premaxilla; po, postorbital; pr, prootic; pt, pterygoid; q, quadrate; qj, quadratojugal; so, supraoccipital; sur, surangular; vo, vomer.

other chelonioids in displaying a unique mosaic of primitive and derived features that suggest it is a basal protostegid (figure 2). All protostegids can be diagnosed by presence of nasal bones$_{2}$, palatines meeting medially$_{20}$, foramen palatinum posterius open posteriorly$_{21}$, biconvex second or third cervical vertebra$_{50}$, lateral process restricted to anterior surface of humerus shaft$_{71}$, and a curved radius$_{75}$ (c.f. Hirayama 1998). *Santanachelys* is the most basal known protostegid; *Bouliachelys* and later forms share the loss of the ventral cheek emargination$_{12}$, and a strong lingual ridge of the maxilla$_{19}$. Finally, protostegids above *Santanchelys* and *Bouliachelys* are united in having a triturating surface that excludes the palatine$_{15}$ but includes the vomer$_{16}$.

4. EVOLUTIONARY IMPLICATIONS

A phylogenetic analysis of major sea turtle lineages, including *Bouliachelys*, was conducted (see electronic supplementary material). The traits discussed above robustly place *Bouliachelys* within crown (living) Chelonioidea, Pandermochelys and Protostegidae; and (with less certainty) suggest it is the most basal protostegid after *Santanachelys* (figure 2). While this phylogeny is similar to other previous studies (Hirayama 1998; Lehman & Tomlinson 2004), it is more pectinate. *Toxochelys* and *Ctenochelys* are no longer allied with derived Cheloniidae (*sensu* Hirayama 1994, 1997, 1998; Joyce *et al.* 2004; Lehman & Tomlinson 2004), but rather are reinterpreted as stem sea turtles outside crown Chelonioidea (an arrangement proposed elsewhere on braincase traits; see Gaffney and Meylan 1988; Hooks 1998). This hypothesis is further supported here by limb and girdle morphology, with *Toxochelys* and *Ctenochelys* retaining primitive postcranial features lost in crown chelonioids (figure 2): ischium with a well developed lateral process$_{64}$, humerus with a capitellum that is upturned and shouldered$_{68}$, first and second digits incorporated into paddle$_{78}$, and femur with distinct trochanters$_{79}$. The derived states of these postcranial characters—functionally related to pelagic natatory habits—thus appear only once and were present in the ancestor of crown chelonioids; consequently they do not need to evolve convergently in the lineages leading to living cheloniids and dermochelyids. The dorsally oriented orbits$_{5}$ of *Toxochelys* and *Ctenochelys* also suggest that they retained the primitive condition of shallow-water and/or benthic habits (and potentially a less pelagic existence; c.f. Hirayama 1997); in contrast, the orbits of most crown chelonioids face laterally, implying a more ‘pelagic-adapted’ skull.

This new data clarifies other evolutionary trends within sea turtles. (i) The Australian fossil taxa are amongst the largest known before the Late Cretaceous; the skull of *Bouliachelys* suggests an animal some 50% larger than *Notochelone* (maximum adult body length reconstructed at less than 1 m; Molnar 1991); an even bigger sympatric taxon, *Cratochelone* (inferred maximum body length approaching 4 m; Longman 1915), is known from fragmentary postcranial remains only (Kear 2003). This shows that large body size in chelonioids was achieved very early in the

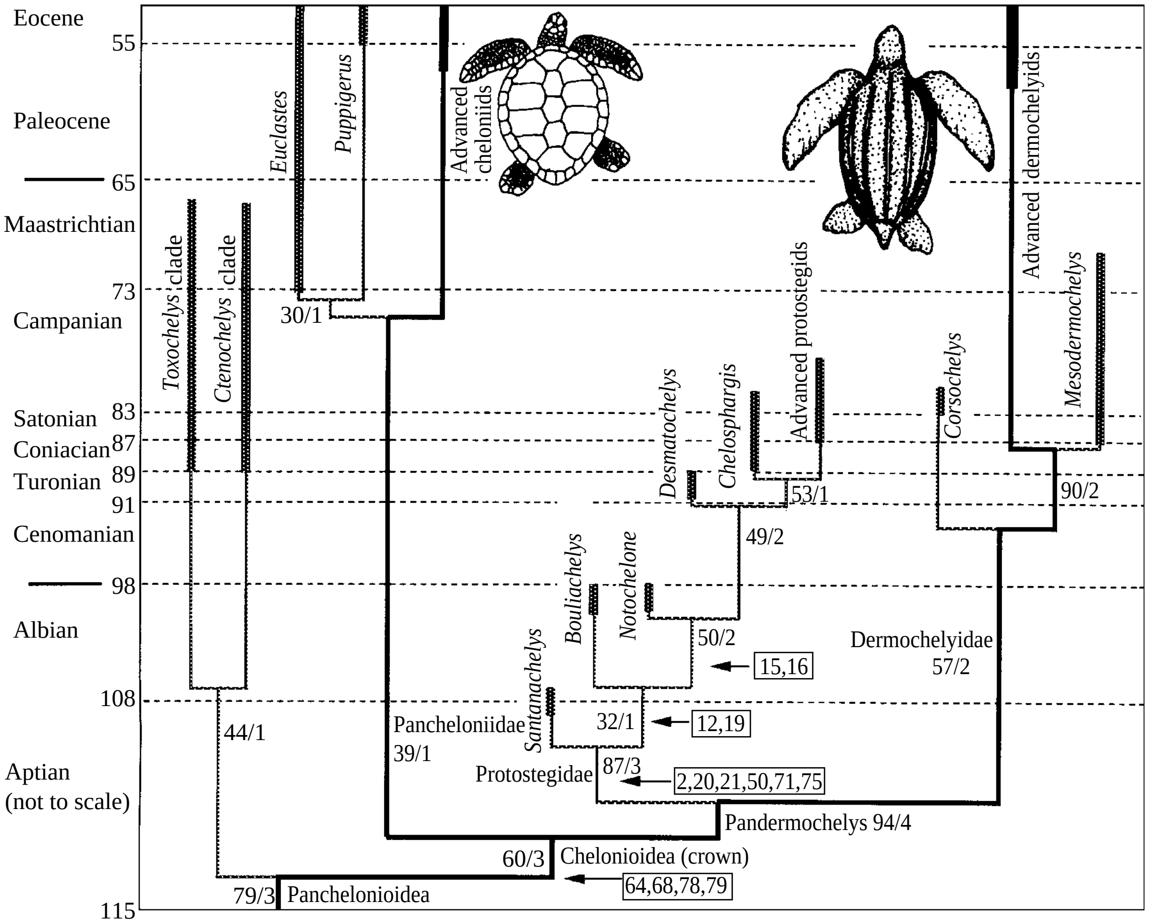

Figure 2. Phylogeny and stratigraphic record of sea turtles, including *Bouliachelys* (see electronic supplementary material). Living lineages in black lines, extinct lineages in grey. Boxed numbers at selected nodes refer to synapomorphies discussed in the main text. Other numbers refer to bootstrap/Bremer support. The deep nesting of the ancient *Santanachelys* suggests the existence of at least five lineages in the Aptian (depending on how polytomies are resolved).

group's history, some 25 Myr earlier (during the Albian *ca* 100 Myr ago, rather than Campanian *ca* 75 Myr ago) than commonly thought. (ii) Primitive protostegids (*Bouliachelys*, *Santanachelys*) have poorly developed secondary palates, demonstrating that this feature probably evolved convergently in advanced protostegids and cheloniids. (iii) The hooked beak (supposedly an adaptation for feeding on pelagic ammonites; Hirayama 1994, 1997) of *Bouliachelys* and more derived giant protostegids (e.g. *Protostega*) may also represent convergent adaptations. Finally, the phylogenetic position of the oldest-known sea turtle (the 105 Myr-old *Santanachelys* from the Aptian–Albian boundary; Hirayama 1998) indicates that a diversity of sea turtles existed during the Aptian, with at least five lineages present: these include *Santanachelys*, derived protostegids, dermochelyiids, cheloniids and the *Toxochelys–Ctenochelys* clade (Hirayama 1997).

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