

A new stem turtle from the Middle Jurassic of Scotland: new insights into the evolution and palaeoecology of basal turtles

Jérémy Anquetin^{1,2,*}, Paul M. Barrett¹, Marc E. H. Jones²,
Scott Moore-Fay¹ and Susan E. Evans²

¹Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

²Research Department of Cell and Developmental Biology, UCL University College London, Gower Street, London WC1E 6BT, UK

The discovery of a new stem turtle from the Middle Jurassic (Bathonian) deposits of the Isle of Skye, Scotland, sheds new light on the early evolutionary history of Testudinata. *Eileanchelys waldmani* gen. et sp. nov. is known from cranial and postcranial material of several individuals and represents the most complete Middle Jurassic turtle described to date, bridging the morphological gap between basal turtles from the Late Triassic–Early Jurassic and crown-group turtles that diversify during the Late Jurassic. A phylogenetic analysis places the new taxon within the stem group of Testudines (crown-group turtles) and suggests a sister-group relationship between *E. waldmani* and *Heckerochelys romani* from the Middle Jurassic of Russia. Moreover, *E. waldmani* also demonstrates that stem turtles were ecologically diverse, as it may represent the earliest known aquatic turtle.

Keywords: Testudinata; *Eileanchelys waldmani*; Middle Jurassic; Late Bathonian; phylogeny; palaeoecology

1. INTRODUCTION

The last two decades have witnessed a dramatic improvement in our understanding of basal turtle evolution. New discoveries have helped to narrow the major temporal and morphological gaps that existed between the earliest known turtles, the Late Triassic *Proganochelys quenstedti* and *Proterochersis robusta*, and the turtle crown group, which diversified during the Late Jurassic. These discoveries have included the recognition of additional taxa from the Late Triassic and Early Jurassic (Gaffney *et al.* 1987; Gaffney & Kitching 1994; Rougier *et al.* 1995; Joyce *et al.* 2009): *Palaeochersis talampayensis* (Late Triassic, Argentina); *Chinlechelys tenertesta* (Late Triassic, USA); *Australochelys africanus* (Early Jurassic, South Africa); and *Kayentachelys aprix* (Early Jurassic, USA). Perhaps more importantly, these discoveries have prompted major reappraisals of basal turtle relationships (Rougier *et al.* 1995; Joyce 2007) that have challenged what may be termed the ‘traditional’ interpretation of turtle phylogeny (e.g. Gaffney & Meylan 1988; Gaffney *et al.* 1991, 2007; Gaffney 1996). According to the traditional model, the turtle stem group contains only *P. quenstedti*, *P. talampayensis* and *A. africanus*: all remaining species were placed within the crown group and classified as either pleurodires or cryptodires. By contrast, Rougier *et al.* (1995) and Joyce (2007) suggested that the turtle

stem group was significantly more diverse and that several species previously thought to be basal members of the crown group should be considered as stem taxa. Following from this new interpretation of basal turtle relationships, the origin of the turtle crown group (Testudines *sensu* Joyce *et al.* 2004; see the electronic supplementary material for a definition of clade names used in this paper) moves from the Late Triassic to no later than Late Jurassic (Joyce 2007). Some evidences, including reappraisal of fragmentary material from the Bathonian of England (Scheyer & Anquetin 2008), suggest that the crown group may have arisen in the Middle Jurassic. In this context, the Middle Jurassic represents a critical interval for understanding turtle evolution and the origin of the crown group; however, the fossil record for this period is sparse and consists mainly of poorly known Pancryptodiran (*sensu* Joyce *et al.* 2004) taxa (e.g. Nessov 1995; Tong *et al.* 2002; Matzke *et al.* 2005; Peng *et al.* 2005; Scheyer & Anquetin 2008). However, two additional stem turtles from the Jurassic have been described recently: *Heckerochelys romani* (Sukhanov 2006; Middle Jurassic, Russia) and *Condorchelys antiqua* (Sterli 2008; Middle to Late Jurassic, Argentina). *Heckerochelys romani* and *C. antiqua* are both known on the basis of partial cranial and postcranial remains from a small number of individuals. Here, we describe a new stem turtle from the Bathonian (Middle Jurassic) of the Isle of Skye, Scotland. This new taxon is known from at least six individuals and represents the most complete Middle Jurassic turtle described to date. As a result, it provides valuable new insights into the evolution and palaeoecology of stem Testudines.

* Author and address for correspondence: Département de Géologie, Université de Rouen, IRESE A, Place Émile Blondel, 76821 Mont Saint Aignan, France (j.anquetin@gmail.com).

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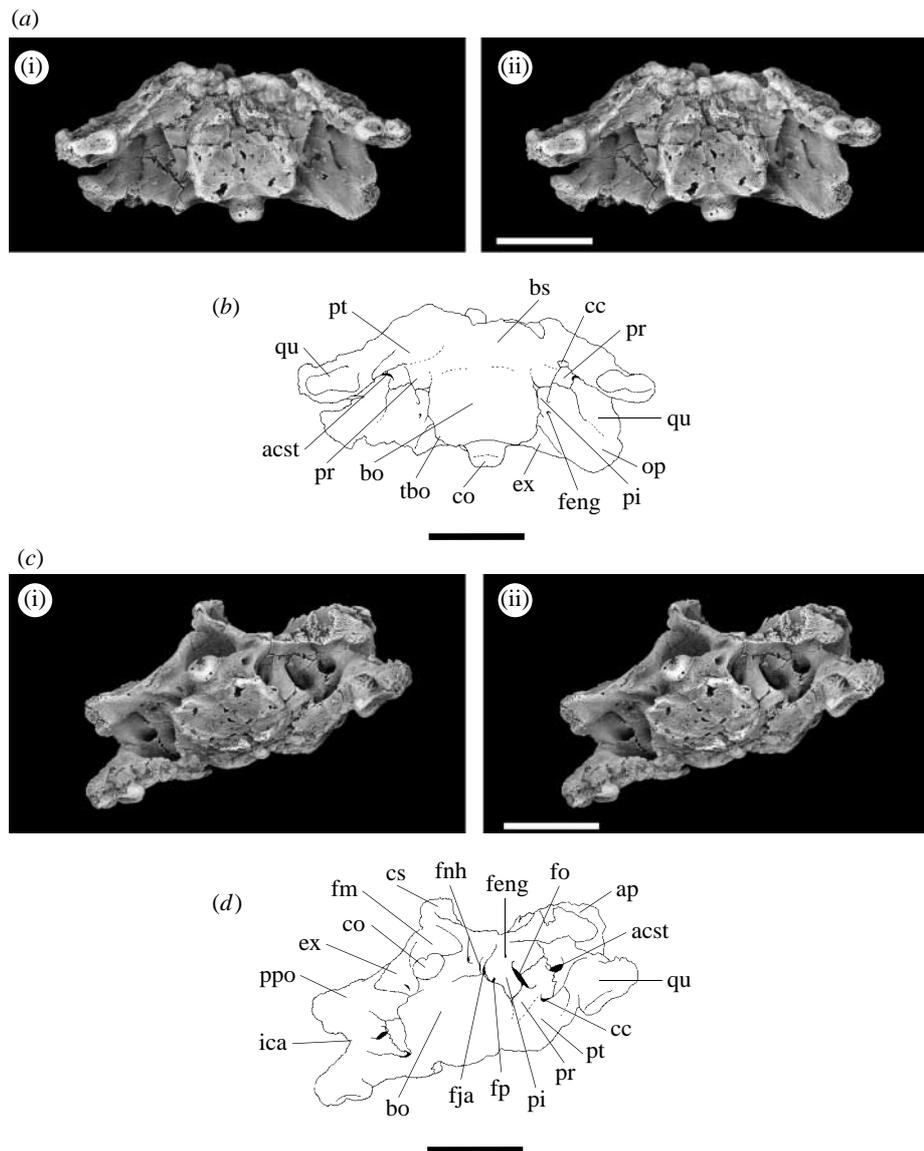


Figure 1. *Eileanchelys waldmani* gen. et sp. nov. Stereophotographs of the skull NMS G 2004.31.15 (holotype) in (a,b) ventral and (c,d) posteroventrolateral view. Scale bars 1 cm. Abbreviations: acst, aditus canalis stapedio-temporalis; ap, antrum postoticum; bo, basioccipital; bs, basisphenoid; cc, posterior opening of the canalis cavernosus; co, condylus occipitalis; cs, crista supraoccipitalis; ex, exoccipital; feng, foramen externum nervi glossopharyngei; fja, foramen jugulare anterius; fm, foramen magnum; fnh, foramen nervi hypoglossi; fo, fenestra ovalis; fp, fenestra perilymphatica; ica, incisura columellae auris; op, opisthotic; pi, processus interfenestralis of the opisthotic; ppo, processus paroccipitalis of the opisthotic; pr, prootic; pt, pterygoid; qu, quadrate; tbo, tuberculum basioccipitale.

2. SYSTEMATIC PALAEOONTOLOGY

Testudinata Klein 1760 (*sensu* Joyce *et al.* 2004)

Eileanchelys waldmani gen. et sp. nov.

(a) *Etymology*

Eilean from the Scottish Gaelic word for island; *chelys* from the Greek word for turtle; *waldmani* in honour of Dr Michael Waldman, co-discoverer of the Cladach a'Ghlinne locality (together with the late Prof. R. J. G. Savage) and the person responsible for introducing one of us (S.E.E.) to the site.

(b) *Holotype*

NMS G 2004.31.15 (National Museums of Scotland, Edinburgh), a partial skull (figure 1a–d).

(c) *Paratypes*

NMS G 2004.31.16a–f, an association comprising at least five and possibly six individuals in a single block (see figure

1a–d in the electronic supplementary material): (a) a partial shell (missing part of the left side of the plastron), with poorly preserved cervical vertebrae and a partial shoulder girdle; (b) a complete shell (carapace figured in figure 2c,d), with poorly preserved caudal vertebrae and a partial right hindlimb; (c), a nearly complete carapace (figure 2a,b); (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.

(d) *Locality and horizon*

All of the specimens were recovered in 2004 from the foreshore at the mouth of Cladach a'Ghlinne, Strathaird Peninsula, Isle of Skye, Scotland. Cladach a'Ghlinne represents the best exposure of the Kilmaluag Formation (Great Estuarine Group), which is of Late Bathonian age

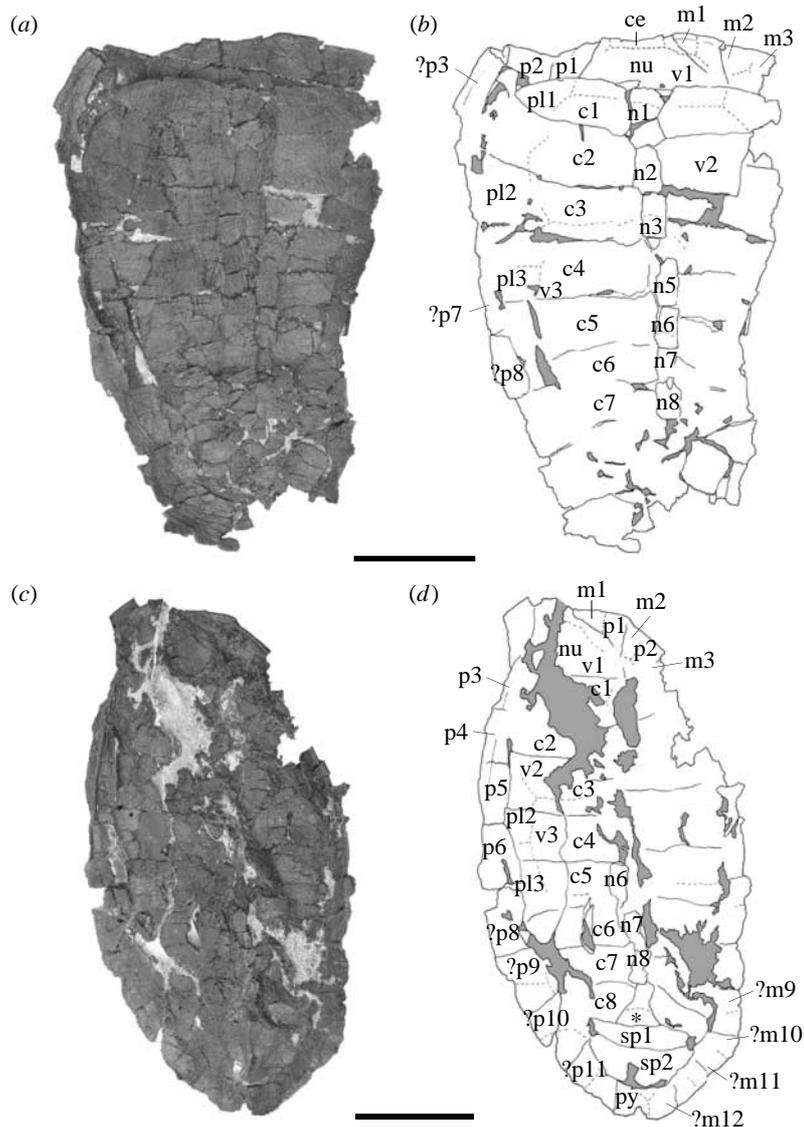


Figure 2. *Eileanchelys waldmani* gen. et sp. nov. (a,b) carapace NMS G 2004.31.16c in dorsal view and (c,d) shell NMS G 2004.31.16b in dorsal view. Scale bars 5 cm. Abbreviations: ce, cervical scute; c, costal; m, marginal scute; n, neural; nu, nuchal; p, peripheral; pl, pleural scute; py, pygal; sp, suprapygal; v, vertebral scute; *, supernumerary plate.

(Harris & Hudson 1980; Andrews 1985). This locality has yielded a diverse tetrapod fauna, including salamanders, the choristodere *Cteniogenys* sp., crocodylians, the lepidosauromorph *Marmoretta* sp., various squamates, pterosaurs, dinosaurs, the synapsid *Stereognathus hebridicus* and early mammals (Waldman & Savage 1972; Savage 1984; Evans & Milner 1994; Waldman & Evans 1994; Evans & Waldman 1996; Barrett 2006; Evans *et al.* 2006).

(e) *Diagnosis*

Relatively small turtle (carapace length of approx. 250–300 mm) characterized by the following list of features: presence of nasal; elongated postorbital skull; absence of flooring of the cavum acustico-jugulare; processus interfenestralis of the opisthotic more slender than that of more basal forms (e.g. *P. quenstedti*, *K. aprix*), but more robust than that of crown-group turtles; separate openings of the canalis cavernosum and canalis stapedio-temporalis present within the cavum acustico-jugulare; a reduced thickness of the basicranium 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; absence of carapacial or plastral fontanelle in adult individuals; one short but broad cervical scute present; vertebral scutes wider than pleurals; vertebral 3–4 sulcus on neural 6; reduced cleithrum present; arrow-shaped entoplastron that does not separate the epiplastra anteriorly; one pair of mesoplastra that meet medially; one small pair of extragulars present; and anal scute that does not reach the hypoplastron.

3. DESCRIPTION AND COMPARISONS

Bone surfaces are well preserved, although their black coloration and the intensive crushing of many specimens make interpretation difficult. No complete individuals are known, but the recovery of multiple specimens ensures that most parts of the skull and shell of *E. waldmani* can be described.

(a) Dermal roofing elements

Nasals are present and contact one another along the midline for all of their length. The prefrontal has a reduced dorsal exposure and does not meet the other prefrontal medially. The descending process of the prefrontal contacts the vomer ventrally, but it is unclear whether or not it contacts the palatine. No evidence supports the presence of a lacrimal or lacrimal foramen in any specimen. The frontal forms part of the dorsal margin of the orbit preventing contact between the prefrontal and postorbital. Internal parts of the parietal (representing the anterior extension of the braincase wall and processus inferior parietalis) are unknown in all specimens. NMS G 2004.31.16f shows 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 jugal is longer than high and forms a large part of the posteroventral margin of the orbit. There is no sign of a cheek (lower temporal) emargination. The quadratojugal has a long dorsal suture with the post-orbital, preventing the jugal from meeting the squamosal. Posteriorly, the quadratojugal does not participate in the formation of the cavum tympani.

(b) Palatal elements

The vomer of *E. waldmani* is a narrow and elongate unpaired bone. In contrast to most turtles, but similar to the condition in *P. quenstedti*, *A. africanus*, *P. talampayensis*, *K. aprix* and *H. romani*, the vomer is a flat element that lacks a medial septum dividing the apertura narium interna ventrally. However, it is planar, differing from the dorsally convex morphology seen in *P. quenstedti* and *A. africanus*. Vomerine teeth are absent. Anteriorly, the vomer contacts the premaxilla on the floor of the fossa nasalis. There is also a short but definite contact with the maxilla lateral to the premaxilla–vomer suture (NMS G 2004.31.16d). Posterior to these contacts, the margins of the vomer are exposed along almost its entire length, with the exception of a small suture with the prefrontal at a point level with the anterior wall of the orbit. It is likely that the vomer contacted the palatines and pterygoids posteriorly, but this area is not preserved in any specimen.

(c) Palatoquadrate elements

The quadrate forms a well-developed cavum tympani and antrum postoticum. The incisura columellae auris is widely open posteroventrally (figure 1c,d). There is no sign of a processus trochlearis oticum (see Joyce (2007), Sterli & Joyce (2007) and Sterli (2008) for a discussion of this feature). The basiptyergoid articulation is fused. Most of the pterygoid area of *E. waldmani* is unknown: only the posterior part of the pterygoid is preserved in NMS G 2004.31.15 (figure 1a,b). The posterior extent of the pterygoid is limited and there is no contact between this bone and the basioccipital. The cavum acustico-jugulare is unfloored. The flooring of the canalis cavernosus (created by the pterygoid) is more extensive posteriorly than in *K. aprix* (Sterli & Joyce 2007; figure 5) and covers the posterior opening of the canalis nervi facialis. This morphology is similar to that of *H. romani* (Sukhanov 2006; figure 1), whereas the posterior extent of the pterygoid is more strongly developed in *C. antiqua* (Sterli 2008; figure 1).

(d) Braincase elements

There is no foramen jugulare posterius, but a foramen jugulare intermedium (*sensu* Sterli & Joyce 2007) is present. The prootic is apparent in ventral view and forms part of the ventral surface of the skull (figure 1a,b). It forms the anterior half of a large fenestra ovalis and the anterior wall of the cavum labyrinthicum. Posteroven-trally, the prootic has a contact with the processus interfenestralis of the opisthotic that floors the cavum labyrinthicum. The development of the processus inter-fenestralis is intermediate between the robust, thick structure seen in the basal-most turtles (e.g. *P. quenstedti* and *K. aprix*) and the slender, flattened sheet of bone present in most crown-group turtles. In *E. waldmani*, the processus interfenestralis is a relatively large and thick structure compared with the size of the skull, but it is flattened and reaches the basicranium floor ventrally (figure 1c,d). It is difficult to assess the morphology of the processus interfenestralis in *H. romani* and *C. antiqua* based on their published descriptions, but it appears to be more robust in these taxa than in *E. waldmani*. The foramen posterius canalis carotici interni (fpcci) is not visible in any specimen. However, its position can be deduced from the anatomy of the basicranium and by comparison with *K. aprix*, *H. romani* and *C. antiqua*: the fpcci probably opens within the basisphenoid, which represents a plesiomorphic condition within Reptilia.

(e) Carapace

There is no sculpturing on the external surface of the carapace. Although all specimens have been crushed, the morphology of several bridge peripherals indicates that the shell of *E. waldmani* was domed significantly. Bridge peripherals form a distinct dorsal gutter, and the medial part of these peripherals forms an angle of at least 90° with their lateral part. This morphology is similar to that of *K. aprix*. The nuchal emargination is very shallow (figure 2a,b). The nuchal is a large and trapezoidal plate. Eight well-developed neurals are present. An additional elongate and trapezoidal plate with the posterior margin significantly wider than the anterior one (figure 2c,d) is present posterior to neural 8 and anterior to suprapygal 1. As no visceral view of the carapace is available, it is impossible to state whether this plate is a ninth neural or a supernumerary suprapygal. Suprapygal 1 is a short but wide plate that contacts, or nearly contacts, what is putatively peripheral 10 laterally. Suprapygal 2 is larger than suprapygal 1 and trapezoidal in shape (wider anteriorly). Suprapygal 2 contacts what is putatively peripheral 10 anterolaterally. This morphology of the suprapygals in *E. waldmani* is clearly different from that of *K. aprix*, *C. antiqua* and *H. romani*. No complete series of costals and peripherals are known, but combining information from all of the available specimens suggests that *E. waldmani* has eight costals and 11 peripherals. Small costal fontanelles are present in NMS G 2004.31.16a but are absent from other specimens, leading us to interpret NMS G 2004.31.16a as a slightly younger individual. As in *K. aprix* and *H. romani*, the cervical scute is short and proportionally wide. Five vertebral scutes are present and vertebrae 2–4 are very broad. The sulcus between vertebrae 3 and 4 passes through neural 6. The exact number of pleurals and marginals is unknown as no specimen shows a complete

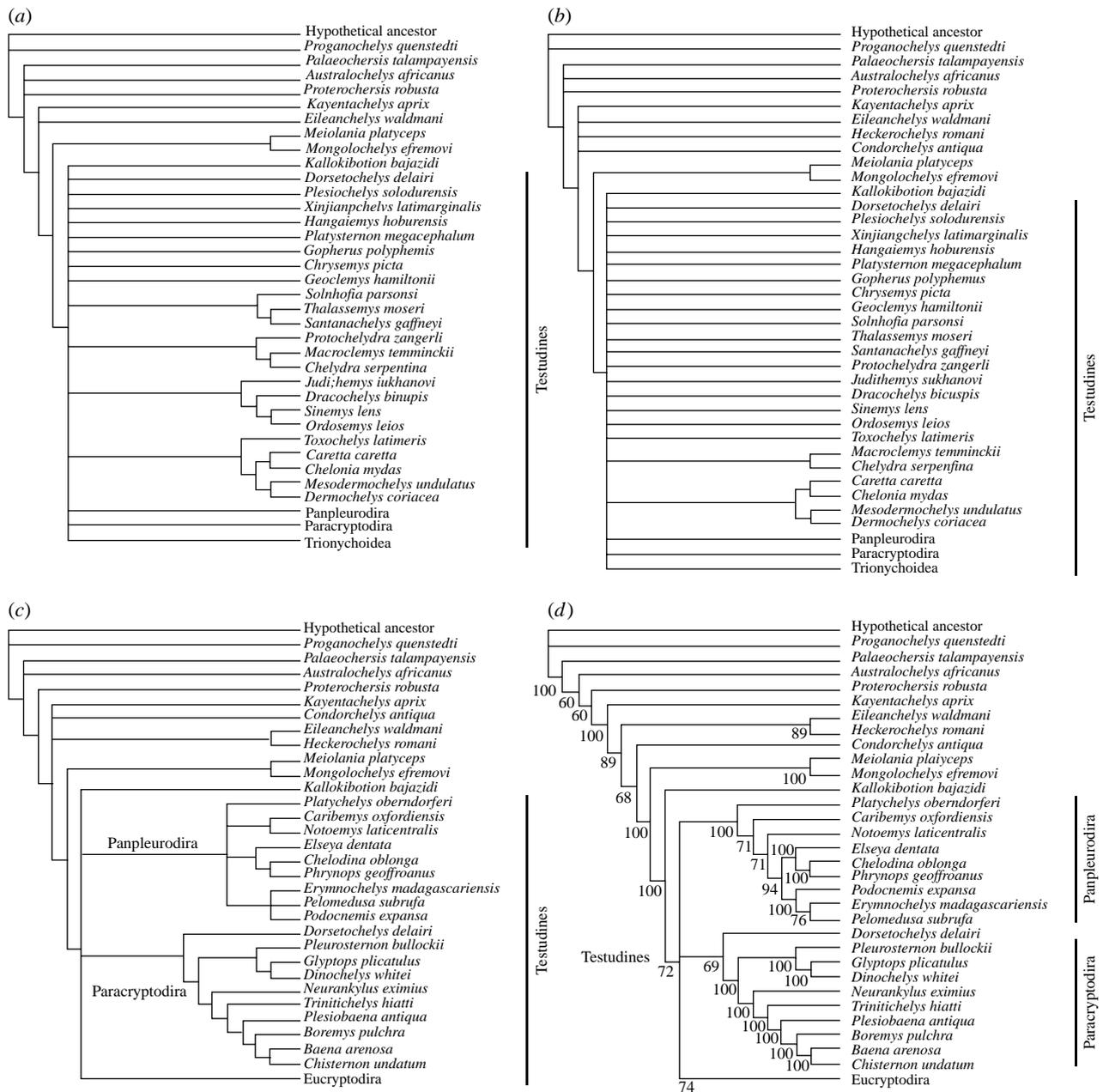


Figure 3. Phylogenetic relationships of *E. waldmani* gen. et sp. nov. (a) Strict consensus tree of 190 most parsimonious trees (MPTs) of 363 steps (analysis 1); 472 steps; consistency index (CI)=0.360; retention index (RI)=0.713; (b) strict consensus tree of 1800 MPTs of 366 steps (analysis 2); 511 steps; CI=0.333; RI=0.683; (c) Adams consensus tree of 1800 MPTs of 366 steps (analysis 2); 386 steps; CI=0.441; RI=0.800; (d) 50% majority rule consensus tree of 1800 MPTs of 366 steps (analysis 2); 370 steps; CI=0.460; RI=0.815. The clade Eucryptodira (*sensu* Joyce *et al.* 2004) is not detailed in trees (c, d).

series, but it is likely that there were four pleurals and 12 marginals in total. There is no indication that supramarginals were present.

(f) *Plastron*

In contrast to the condition in *H. romani* but similar to that of *K. aprix*, the connection between the carapace and plastron is osseous in *E. waldmani*. The entoplastron is a narrow and arrow-shaped element that does not separate the epiplastra anteriorly. Reduced cleithra are present (Joyce *et al.* 2006). One pair of mesoplastra meets along the midline. There is inconclusive evidence of a central plastral fontanelle in NMS G 2004.31.16a, but this specimen is probably a juvenile (see above). There is no distinct anal notch. Extragulars are reduced in size, whereas gulars are proportionally larger and extend on

the entoplastron posteromedially. The pectoral–abdominal sulcus is not preserved in any specimen, so that its position relative to the mesoplastron cannot be assessed. The anal scute lies entirely within the xiphiplastron. The number of inframarginals is unknown as no inframarginal sulcus is preserved.

4. PHYLOGENETIC ANALYSIS

In order to investigate the phylogenetic relationships of *E. waldmani*, we incorporated it into the most comprehensive recent analysis of turtle relationships (Joyce 2007). *Heckerochelys romani* and *C. antiqua* were also scored and added to this data matrix on the basis of published descriptions (Sukhanov 2006; Sterli 2008). Consequently, the data matrix consists of 139 characters

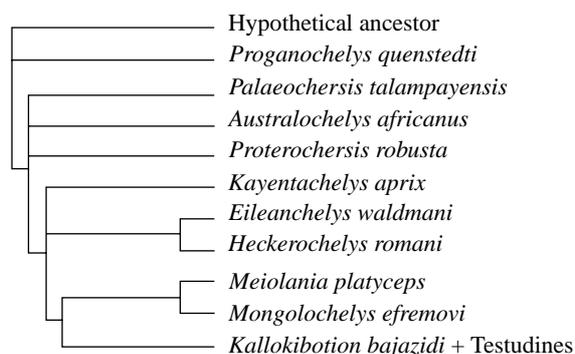


Figure 4. Strict reduced consensus (SRC) tree derived by *a posteriori* pruning of *C. antiqua* from the set of 1800 MPTs generated by the second analysis. This tree reveals a strictly supported sister-group relationship between *E. waldmani* gen. et sp. nov. and *H. romani*. The clade Testudines (*sensu* Joyce *et al.* 2004) is not detailed (other SRC trees are provided in the electronic supplementary material).

scored for 71 taxa (see the electronic supplementary material for matrix and methods of analysis).

The first analysis (excluding *H. romani* and *C. antiqua*) resulted in 190 most parsimonious trees (MPTs) of 363 steps. The consistency index (CI) of these trees was 0.469 after exclusion of parsimony uninformative characters, and their retention index (RI) was 0.817. The strict consensus of these 190 MPTs is presented in figure 3*a* and places *E. waldmani* within the stem of Testudines (*sensu* Joyce *et al.* 2004). It is more derived than *P. talampayensis*, *A. africanus* and *P. robusta*, but less derived than *Meiolania platyceps*, *Mongolochelys efremovi* and *Kallokibotion bajazidi*. Relationships between *E. waldmani* and *K. aprix* are unresolved in the strict consensus. Other consensus methods (50% majority rule and Adams) do not provide more resolution, nor does the application of the reduced consensus method (see the electronic supplementary material). In general, this analysis recovers overall topologies similar to those reported by Joyce (2007).

The second analysis (including *H. romani* and *C. antiqua*) resulted in 1800 MPTs (1965 before filtering) of 366 steps. The CI of these trees was 0.466 after exclusion of parsimony uninformative characters, and their RI was 0.819. The strict consensus tree of these 1800 MPTs is presented in figure 3*b*. *Kayentachelys aprix*, *E. waldmani*, *H. romani*, *C. antiqua* and a clade consisting of all more derived turtles form an unresolved polytomy. In the Adams consensus tree (figure 3*c*), *E. waldmani* and *H. romani* form a clade that branches off from the aforementioned polytomy. By contrast, the 50 per cent majority rule consensus tree (figure 3*d*) supports a more resolved topology where *K. aprix* is more basal than the clade (*E. waldmani*+*H. romani*), whereas *C. antiqua* is more derived than this clade. Among the 16 strict reduced consensus (SRC) trees (see the electronic supplementary material) only one resolves the relationships between the aforementioned taxa and *E. waldmani* (figure 4). As with the Adams and majority rule consensus trees, it supports a sister-group relationship between *E. waldmani* and *H. romani* and reveals that *C. antiqua* is unstable with respect to this relationship. The SRC method identifies all strictly supported relationships by overcoming the insensitivity of the strict consensus method due to unstable taxa (Wilkinson 1994, 1995, 2003). In other words, the

sister-group relationship between *E. waldmani* and *H. romani* is strictly supported by the analysis of the complete data matrix, even if the instability of *C. antiqua* with respect to these taxa prevents the representation of this relationship by the strict consensus method. More than simply confirming the results of the Adams and majority rule consensus methods, the SRC method ensures that this relationship is strictly supported by the data, which is not the case of the aforementioned techniques. It is interesting to note that the inclusion of *H. romani* and *C. antiqua* in the second analysis results in a loss of resolution within Pancryptodira (*sensu* Joyce *et al.* 2004) in the strict 50 per cent majority rule and Adams consensus trees (see the electronic supplementary material). This is probably in part due to the amount of missing data for these two taxa and may also illustrate some limitations of Joyce's (2007) matrix with respect to discriminating the relationships among basal turtles. The inclusion of *E. waldmani* alone (see analysis 1 above) does not have a similar effect on the relationships within the crown group: this is probably because the material of this taxon permits a more complete scoring of cranial characters.

5. DISCUSSION

(a) Anatomy

Eileanchelys waldmani bridges the morphological and temporal gap between the most basal turtles (e.g. *P. quenstedti* and *K. aprix*) and the post-Middle Jurassic diversification of the turtle crown group. *Eileanchelys waldmani* has an intermediate morphology that is characterized by a mosaic of derived and plesiomorphic features. Derived features 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. The latter feature is structurally intermediate in *E. waldmani*: although more slender than the robust structure seen in *P. quenstedti* or *K. aprix*, the processus interfenestralis of *E. waldmani* is proportionally thicker than that of most crown-group turtles. Its orientation also differs from that seen in crown-group turtles: in the latter, the processus is flattened anteroposteriorly and forms a vertical wall between the cavum labyrinthicum and the recessus scalae tympani. In *E. waldmani*, by contrast, the recessus scalae tympani *sensu stricto* is not developed, with the result that the processus merely forms the posterolateral margin of the cavum labyrinthicum and has a more oblique orientation (figure 1*c,d*). Plesiomorphic features of *E. waldmani* include a slender, arrow-shaped entoplastron; a reduced posterior extension of the pterygoid; an unfloored cavum acustico-jugulare; separate posterior openings of the canalis cavernosus and canalis stapediotemporalis 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 vomer is not preserved in either *H. romani* or *C. antiqua*, and this area is severely damaged in *K. aprix* (Sterli & Joyce 2007). Therefore, *E. waldmani* offers a unique opportunity to trace the evolution of the vomer within basal turtles. In the most basal forms (i.e. *P. quenstedti* and *A. africanus*), the vomer is a large sheet of bone that curves dorsally above the level of the palatine and pterygoid (figure 5*a,d*). It is free of contacts for most

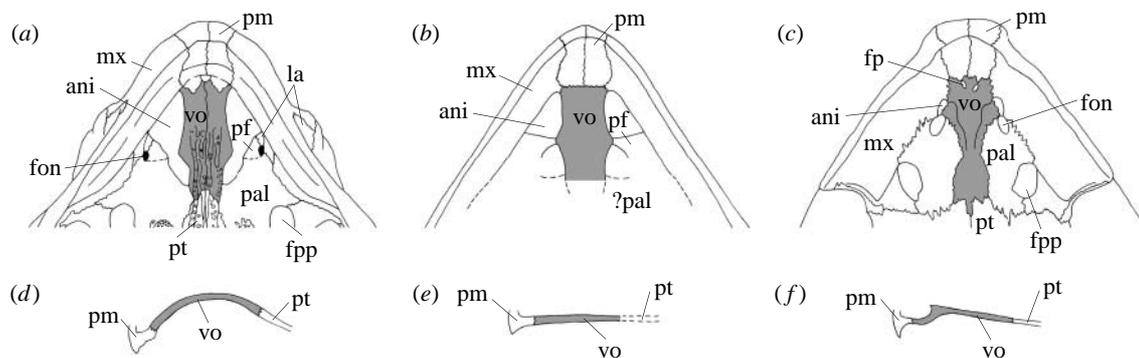


Figure 5. The evolution of the vomer among basal turtles. (a,d) *Proganochelys quenstedti*, (b,e) *E. waldmani*, and (c,f) *Chelydra serpentina*. (a–c) Ventral view and (d–f) sagittal section. (a) Redrawn from Gaffney (1990: fig. 27) and (c) redrawn from Gaffney (1979: fig. 217). Abbreviations: ani, 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.

of its length and it does not meet the descending process of the prefrontal. Then, as documented by *E. waldmani* and partly by *K. aprix* (Sterli & Joyce 2007), the vomer becomes a more horizontal sheet of bone in the same plan as the palatine and pterygoid (figure 5b,e). At this stage, the vomer is still free of contact for most of its length with the exception of anterior contacts with the premaxilla and maxilla, and posterior articulations with the palatine and pterygoid. In *E. waldmani*, the descending process of the prefrontal now has a sutural contact with the vomer. Sterli & Joyce (2007) tentatively proposed that a prefrontal–vomer contact was also present in *K. aprix*. In more derived turtles, beginning with the stem taxa *M. platyceps*, *M. efremovi* and *K. bajazidi*, the vomer progressively develops a ventral, medial septum that separates the internal narial canals (figure 5c,f). The vomer also progressively acquires the dumbbell-shaped cross section typical of the majority of turtles, with the ventral-most part of the vomer contributing to the formation of a variably developed secondary palate. The contacts with the maxilla and especially the palatine become extensive and the vomer is surrounded by bone.

(b) Palaeoecology

The palaeoecology of stem turtles has been debated intensively over the past two decades (Joyce & Gauthier 2004), as the purported ancestral ecology of the turtle lineage has been used as a circumstantial evidence in discussions on the origin of turtles. Although it is generally accepted that crown-group turtles were primitively aquatic, the habitat preference of stem turtles has remained controversial (see the electronic supplementary material). *Eileanchelys waldmani* can be plausibly interpreted as the earliest known aquatic turtle (see figure S2 in the electronic supplementary material). 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. By contrast, many of the turtle specimens consist of articulated skulls, shells, limbs and vertebrae, indicating the absence or near

absence of transport. Moreover, turtle remains represent some of the most abundant elements at the locality, along with those of aquatic forms (sharks and salamanders), whereas remains of terrestrial vertebrates (e.g. lizards, dinosaurs, synapsids) are exceptionally rare. This taphonomic evidence (the abundance of the remains, the numerical dominance of other aquatic taxa and the absence of transportation) suggests that *E. 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 fossilized in the aquatic facies. If this interpretation is accepted, *E. waldmani* plausibly represents the first aquatic turtles, and would also indicate that this transition occurred during, or prior to, the Middle Jurassic. However, it is important to note that the boundary between terrestrial and aquatic habitat preferences is often tenuous in turtles. Even if *E. waldmani* was aquatic, it is premature to speculate on whether the evolution of aquatic habitat preferences was a unique evolutionary event within turtles or if other lineages, including crown-group turtles, developed aquatic abilities independently. The fossil record of Early and Middle Jurassic turtles is poor, although evidence derived from palaeogeographic distributions and ghost lineages inferred from phylogenetic analyses suggests that the clade should have been diverse and widespread at this time. Nevertheless, the recent discoveries of *E. waldmani*, *C. antiqua* and *H. romani* partially close this gap and offer numerous insights into the evolution of stem turtles and the ecological and morphological features present at the base of the turtle crown group.

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