

The cranial anatomy of the Early Jurassic turtle *Kayentachelys aprix*

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The fossil turtle *Kayentachelys aprix* is known from Early Jurassic sediments of the Kayenta Formation, Arizona, USA. The detailed description of this taxon's cranium offered in this paper demonstrates that this turtle presents a mixture of primitive and derived character states. Among others, the presence of an interpterygoid vacuity, a basiptyergoid process, a prootic that is exposed in ventral view, and a foramen posterius canalis carotici interni that is formed entirely by the basisphenoid are generally considered primitive for turtles. On the other hand, the presence of an undivided apertura narium, a well developed cavum tympani, an incipient cavum postoticum, and an unpaired vomer are considered to be derived. *Kayentachelys aprix* has previously been hypothesized to be the oldest stem cryptodiran turtle because of the presence of a flat, vertical plate on the processus pterygoideus externus, and the presence of a processus trochlearis oticum. However, the presence of these characters cannot be confirmed in the available specimens. Other putative stem-cryptodiran characters, such as the prefrontal-vomer contact and the presence of an epipterygoid, are herein corroborated as being symplesiomorphies, because they generally appear to be present in basal turtles.

Key words: Testudines, Cryptodira, cranial morphology, turtle evolution, stem turtles, Jurassic, Kayenta Formation.

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Introduction

The fossil record of turtles (i.e., amniotes with a turtle shell) firmly extends to the Upper Triassic as is demonstrated by the rare and primitive fossil taxa *Proganochelys quenstedti* Baur, 1887 and *Proterochersis robusta* Fraas, 1913 from Germany, and *Palaeochersis talampayensis* Rougier, de la Fuente, and Arcucci, 1995 from Argentina. The record remains scarce in the Early Jurassic, consisting of only three described species: *Australochelys africanus* Gaffney and Kitching, 1994 from South Africa, *Indochelys spatulatus* Datta, Manna, Ghosh, and Das, 2000 from India, and *Kayentachelys aprix* Gaffney, Hutchison, Jenkins, and Meeker, 1987 from Arizona, USA. During the Middle Jurassic fossil turtles continue to be scarce, skull material only being known for *Heckerochelys romani* Sukhanov, 2006 from Russia and *Xinjiangchelys tiangshanensis* Nessov, 1995 from Asia. Turtles later become far more common in the fossil record in Asia, Europe, South America, and North America and also decisively more evolutionary diverse and advanced (xinjiangchelyids, sinemyids, glyptopsids, plesiochelyids, platychelyids, among others). For this reason, the few available Early Jurassic turtles provide important insight into the early evolution of this group.

The present study is focused on the cranial anatomy of *Kayentachelys aprix* from the Kayenta Formation of Ari-

zona, USA. It was originally described by Gaffney et al. (1987) as the oldest known cryptodiran turtle, based in the putative presence of characters associated with the jaw closure system of that group. Other authors, however, concluded that *K. aprix* is not a cryptodiran turtle, but rather outside the turtle crown group, thus arguing that some characters thought by Gaffney et al. (1987) to be synapomorphies of Cryptodira are instead plesiomorphies for the turtle crown (Dryden 1988; Joyce 2007). To shed new light on this question, we herein describe all available cranial material of *K. aprix* and discuss previously used and new phylogenetic informative characters. The specimens recently collected by TMM were not available to Gaffney et al. (1987). This material is particularly relevant, because it includes the first skull with an uncrushed otic region (TMM43670-2).

All known *Kayentachelys aprix* material was found in the Gold Springs and Willow Springs localities of the Kayenta Formation in Coconino County, Arizona, USA (Fig. 1). The Kayenta Formation, the Moenave Formation, the Wingate Formation, and the Navajo Formation form the Glen Canyon Group, which is thought to span from the Late Triassic to the Early Jurassic. This sedimentary package of the Colorado Plateau outcrops in Arizona, Colorado, and Utah (Clark and Fastovsky 1986). The Kayenta Formation is formed by fluvial sediments and can be divided into two facies informally

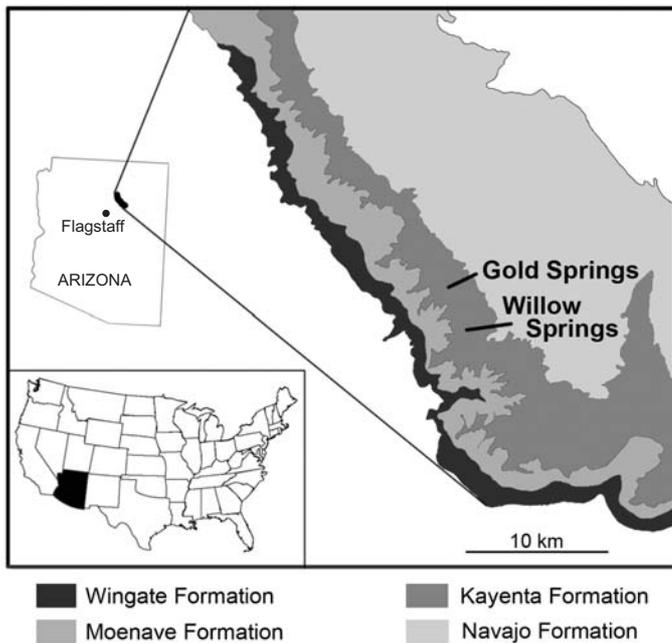


Fig. 1. The localities of the Early Jurassic Kayenta Formation (Glen Canyon Group) where specimens of *Kayentachelys aprix* have been recovered: Gold Springs and Willow Springs, both Adeii Eechii Cliffs, Coconino County, Arizona, USA.

referred to as the “typical facies” and the “silty facies” by Harshbarger et al. (1957). Both localities where *Kayentachelys aprix* remains were found, Gold Spring and Willow Springs, are located in the silty facies of Kayenta Formation.

The anatomical nomenclature of the turtle skull used in this paper follows Gaffney (1979) whereas all taxon names refer to phylogenetically defined clade names as defined by Joyce et al. (2004).

Institutional abbreviations.—MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; MNA, Museum of Northern Arizona, Flagstaff, Arizona, USA; TMM, Texas Memorial Museum, University of Texas, Austin, Texas, USA; UCMP, University of California Museum of Paleontology, Berkeley, California, USA.

Material

MCZ 8914: skull roof and right lower jaw ramus; MCZ 8915: both lower jaw rami without articular areas; MCZ 8916: complete basicranium and isolated skull fragments, including right maxilla, right quadrate, left frontal, and fragments of the left dentary and left articular area of the lower jaw; MCZ 8917: complete but heavily crushed skull; MCZ 8983: anterior skull roof, basisphenoid-basioccipital, anterior portion of both dentaries, and both articular areas of the lower jaw; MCZ 8999: isolated fragments of the skull roof, basisphenoid-basioccipital, left quadrate, and left maxilla, palatine, and jugal; MNA V1558 (also catalogued as MCZ

8913): complete skull only lacking the right temporal arch and mandible, holotype of *Kayentachelys aprix*; MNAV2664: anterior skull roof, snout, and basisphenoid-basioccipital; TMM 43647-1: almost complete skull roof, only lacking left parietal, both premaxillae, both maxilla, both prootics, fragments of both quadrates, basisphenoid, basioccipital, and anterior portion of the left dentary; TMM 43651-1: isolated skull fragments, basisphenoid-basioccipital, and fragments of the right pterygoid, left prefrontal, frontal, postorbital, and parietal; TMM 43653-1: isolated fragments of ventral region of basicranium, maxillae, left quadrate, left frontal, both lower jaw articular areas, and fragments of both dentaries; TMM 43669-2: anterior fragments of both dentaries and left articular area of the lower jaw; TMM 43670-2: complete skull except the posterior parts of the skull roof; TMM 43687-27, lower jaw fragments; UCMP 130408: parts of the basisphenoid-basioccipital, left quadrate, and almost complete skull roof lacking only the posterior region of both parietals. Only three skulls are nearly complete and only one of them is preserved in three dimensions (TMM 43670-2).

Systematic paleontology

Testudinata Klein, 1760

Genus *Kayentachelys* Gaffney, Hutchison, Jenkins, and Meeker, 1987

Kayentachelys aprix Gaffney, Hutchison, Jenkins, and Meeker, 1987

Type specimen: MNA V1558 (also catalogued as MCZ 8913).

Referred material: MCZ 8914, MCZ 8915, MCZ 8916, MCZ 8917, MCZ 8983, MCZ 8999, MNA V2664, TMM 43647-1, TMM 43651-1, TMM 43653-1, TMM 43669-2, TMM 43670-2, TMM 43687-27, and UCMP 130408.

Emended diagnosis (cranial characters).—Apertura narium externa not divided; prefrontals not in contact along the midline; lacrimals absent; frontals forms part of the orbit; processus inferior parietalis does not reach further anteriorly than the otic chamber; foramen nervi trigemini open anterodorsally; antrum postoticum incipient; vomer unpaired; cavum tympani well developed; pterygoid teeth present; vomerine and palatine teeth absent; interpterygoid vacuity present; epipterygoid rod-like and protruding into temporal cavity; canalis cavernosus partially floored by the pterygoid; hiatus acusticus well ossified; presence of a foramen (foramen jugulare intermedium) that is located in the posterior part of the skull between the exoccipital and opisthotic, that communicates with the foramen jugulare anterius and the fenestra perilymphatica; floor of the cavum cranii thick; pair of basioccipital tubera present; prootic exposed in ventral view; basiptyergoid process present; foramen posterius canalis carotici interni formed entirely by the basisphenoid; basisphenoid pits present; processus trochlearis oticum or pterygoidei absent; splenial forms part of the symphysis; presence of a retroarticular process.

Stratigraphic and geographic range.—Silty facies of Kayenta Formation, Early Jurassic (Clark and Fastovsky 1986). Gold Springs and Willow Springs, Adeii Eechii Cliffs, Coconino County, Arizona.

Description

The skull is as large as wide, the preorbital region being much shorter than the postorbital region. Upper or lower temporal emarginations are absent. The skull increases its height posteriorly. The crista supraoccipitalis is well developed but does not protrude posterior to the foramen magnum. The shortening of the preorbital region is not seen in the Triassic turtles *Proganochelys quenstedti* (Gaffney 1990) and *Palaeochersis talampayensis* (Rougier et al. 1995; Sterli et al. 2007) but the lack of emarginations is seen in these taxa as well.

Among the preserved skulls different sizes are apparent. The smallest skull (MCZ 8917) is approximately 40% smaller than the biggest specimen (TMM 43670-2). Considering that no significant amount of variation could be found in the cranium, we conclude that the available material represents different ontogenetic stages.

Ornamentation and scalation (Figs. 2, 3)

Several dermal bones exhibit ornamentation and/or evidence of scalation (MCZ 8914, MCZ 8917, MCZ 8983, MNA V1558, MNA V2664, TMM 43670-2, UCMP 130408). Some differences are nevertheless apparent. In MCZ 8917, which is the smallest specimen, the ornamentation consists of small but deep, randomly arranged grooves and ridges, while in the remaining specimens the ornamentation consists of small pits. Small pits are also seen in the lower jaw bones (e.g., MCZ 8914, MCZ 8915, MCZ 8916). We speculate that these differences are related to ontogenetic changes, because the smallest specimen is the only one that differs from the remaining specimens, but diagenetic effects may play a role as well.

The scales are represented by sulci as in most turtles, with exception *Meiolania platyceps* Owen, 1886 which exhibits ridges instead of sulci (Gaffney 1983). A number of specimens exhibit well-preserved scales, but in the two specimens in whom they are preserved the best, different patterns are apparent. Given that the scale pattern of turtles is highly variable (as seen in *Proganochelys quenstedti* and modern turtles), these two patterns are interpreted as intraspecific variation and no attempts are made to homologize them with the scales of other turtles. In TMM 43651-1 (Fig. 2), which consists of the left prefrontal, frontal, and fragments of the postorbital, and parietal, at least 16 scales are recognizable. In contrast, in TMM 43647-1, which is represented by a left nasal, right and left prefrontal and frontal, and right postorbital, only 4 scales are visible.

The following description relies mainly on TMM 43651-1. Scales are informally referred to by numbers. Scale 1 is triangular and completely located on the prefrontal. Medially

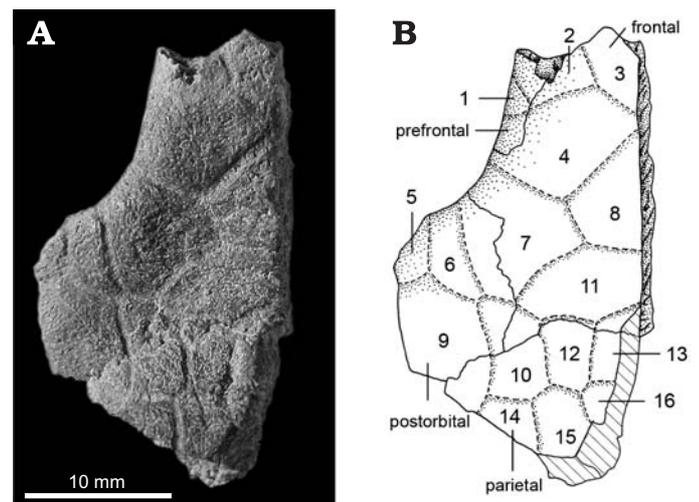


Fig. 2. The turtle *Kayentachelys aprix* Gaffney, Hutchison, Jenkins, and Meeker, 1987, specimen TMM 43651-1, from the Early Jurassic Kayenta Formation, Gold Springs, Arizona, USA. The scale areas (numbered) of the anterior part of the skull roof; photograph (A) and explanatory drawing (B).

scale 1 contacts scale 2 and posteriorly scale 4. Scale 2 is bigger than scale 1 and is located on the prefrontal and the frontal, and it maybe reached the nasal as well. It contacts scale 3 medially and scale 4 posteriorly. Scale 3 is located in the anterior region of the frontal and contacts scale 4 posteriorly and scale 2 laterally. The biggest preserved scale is number 4, which is wider than long and is located on the prefrontal and the frontal. It is surrounded by scales 1, 2, and 3 anteriorly and 7 and 8 posteriorly. Scale 5 is not complete, but it is located at the orbital margin of the postorbital together with scale 6. Both scales contact scale 9 posteriorly. Scale 6 is longer than wide and medially contacts scale 7, which is a big element. Scale 7 is located on the postorbital and frontal and contact medially scale 8, which is completely located on the frontal. Both scales 7 and 8 contact scale 11 posteriorly. The postorbital possesses two more scales, 9 and 10. The incompletely preserved scale 9 also reaches the parietal and scale 10 reaches the parietal and the frontal as well. Scale 10 is complete and is longer than wide and contacts scales 6 in the anterolateral corner, scales 7 and 11 anteriorly, scale 12 medially and scales 14 and 15 posteriorly. Scales 12–16 form two rows of scales; 12 and 13 form the anterior row (located on the frontal and on the parietal), while 14–16 form the posterior row (completely located on the parietal). Scale 12 is longer than wide, but the shape of the remaining scales cannot be established because they are incomplete.

TMM 43647-1, which constitutes the anterior region of the skull roof, also has scale marks, but they are quite different from TMM 43651-1. In the former, three sulci are clearly seen, which delimit four scales. The biggest scale is V-shaped and its tip points anteriorly. It is an unpaired element that is located along the midline of both frontals in the position of the scales 3, 4, and 8 of TMM 43651-1. Lateral to it, another scale is located on the frontal, prefrontal, and postorbital. Anteriorly

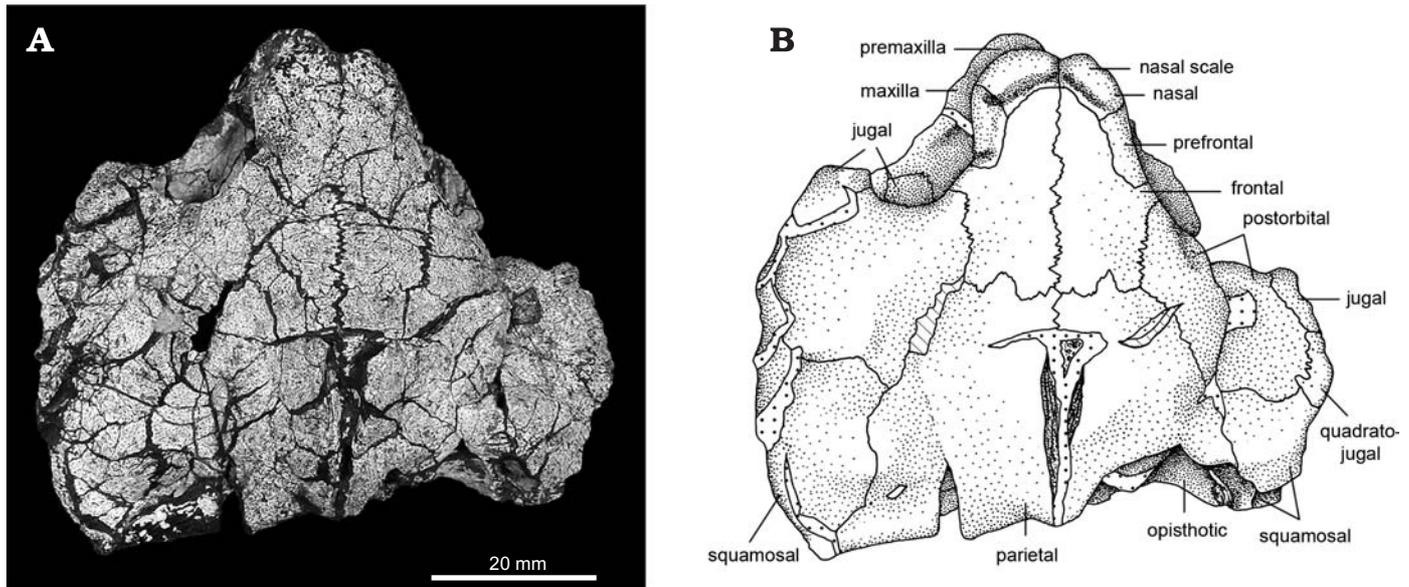


Fig. 3. The turtle *Kayentachelys aprix* Gaffney, Hutchison, Jenkins, and Meeker, 1987, specimen MNA V1558 (also catalogued as MCZ 8913), from the Early Jurassic Kayenta Formation, Gold Springs, Arizona, USA. Skull in dorsal view; photograph (A) and explanatory drawing (B).

there is a small, triangular scale that is located mainly on the nasal and prefrontal. The most anterior scale is located on the nasal alone, but it is not clear in this specimen.

Although a nasal scale is not clear in TMM 43651-1, it is well defined in others (MNA V1558, MNA V2664, TMM 43647-1). It has a triangular shape, with the apex pointing posteriorly. In MNA V1558 (Fig. 3), the two posterior sulci are deep and they run parallel to the suture between the nasal and frontal and between the nasal and prefrontal.

Dermal roofing elements (Figs. 2–4)

Nasal and sulcus olfactorius.—The nasal is a paired bone located in the anterior area of the skull roof. It is a pentagonal element that has an apex that points posteriorly and a main axis that is positioned transverse to the sagittal plane (TMM 43647-1). The nasal contacts the maxilla ventrally, the prefrontal posterolaterally, the frontal posteromedially, and the other nasal medially. The nasal has a triangular posterior expansion that partially separates the prefrontal and the frontal.

As in other turtles with nasals, this element frames the apertura narium externa dorsally and laterodorsally. Along the midline, both nasals form a minute descending process that separates the narial opening slightly. Internally, the ventrolateral process of the nasal forms the anterior part of the sulcus olfactorius, which is formed further posteriorly by the prefrontal and the frontal. The nasal portion of the sulcus olfactorius (TMM 43647-1, UCMP 130408) is broad. It becomes narrower posteriorly in the prefrontal and frontal portions, but is not as narrow as in some modern aquatic turtles.

Remains of the fossa nasalis can be observed in MNA V2664. The fossa nasalis is formed by the nasal, premaxilla, maxilla, and there may be a small contribution from the prefrontal as well. The posterior limit of this cavity cannot be

established accurately because of the preservation of this specimen.

Prefrontal.—The prefrontal contacts the nasal anteriorly, the frontal medially and posteriorly, and the maxilla ventrally (MNA V1558, MNA V2664, TMM 43647-1). The contact between the prefrontal and vomer is hard to establish because this region is not well preserved in any specimen. However, we conclude that the prefrontal indeed contacted the vomer and palatine, given that a well-developed descending process is visible in the orbits of TMM 43670-2 and that remains of bone and a suture are visible anterior to the palatine and lateral to the vomer in palatal view of MNA V1558. The prefrontals do not contact each other along the midline.

The horizontal portion of the prefrontal forms part of the skull roof and the anterodorsal margin of the fossa orbitalis. The exposure of the prefrontal in the skull roof is small, being rectangular, and anteroposteriorly elongated. Contrary to the condition seen in *Proganochelys quenstedti* but as in most turtles, the prefrontal does not bear any bosses in the dorsal orbital margin. The descending process reaches the maxilla and forms the anterior wall of the fossa orbitalis. In ventral view it is apparent that the prefrontal makes a small contribution to the sulcus olfactorius (MNA V2664).

Lacrimal.—No specimens show evidence of the presence of a lacrimal bone or foramen.

Frontal.—The frontal is one of the main elements of the skull roof. It is longer than wide and contacts the nasal anteriorly, the prefrontal anterolaterally, the postorbital laterally, and the parietal posteriorly (MNA V2664, TMM 43647-1). The frontals contact each other along the midline.

As in many turtles, the frontal contributes to the dorsal margin of the orbit. The remaining dorsal portions are

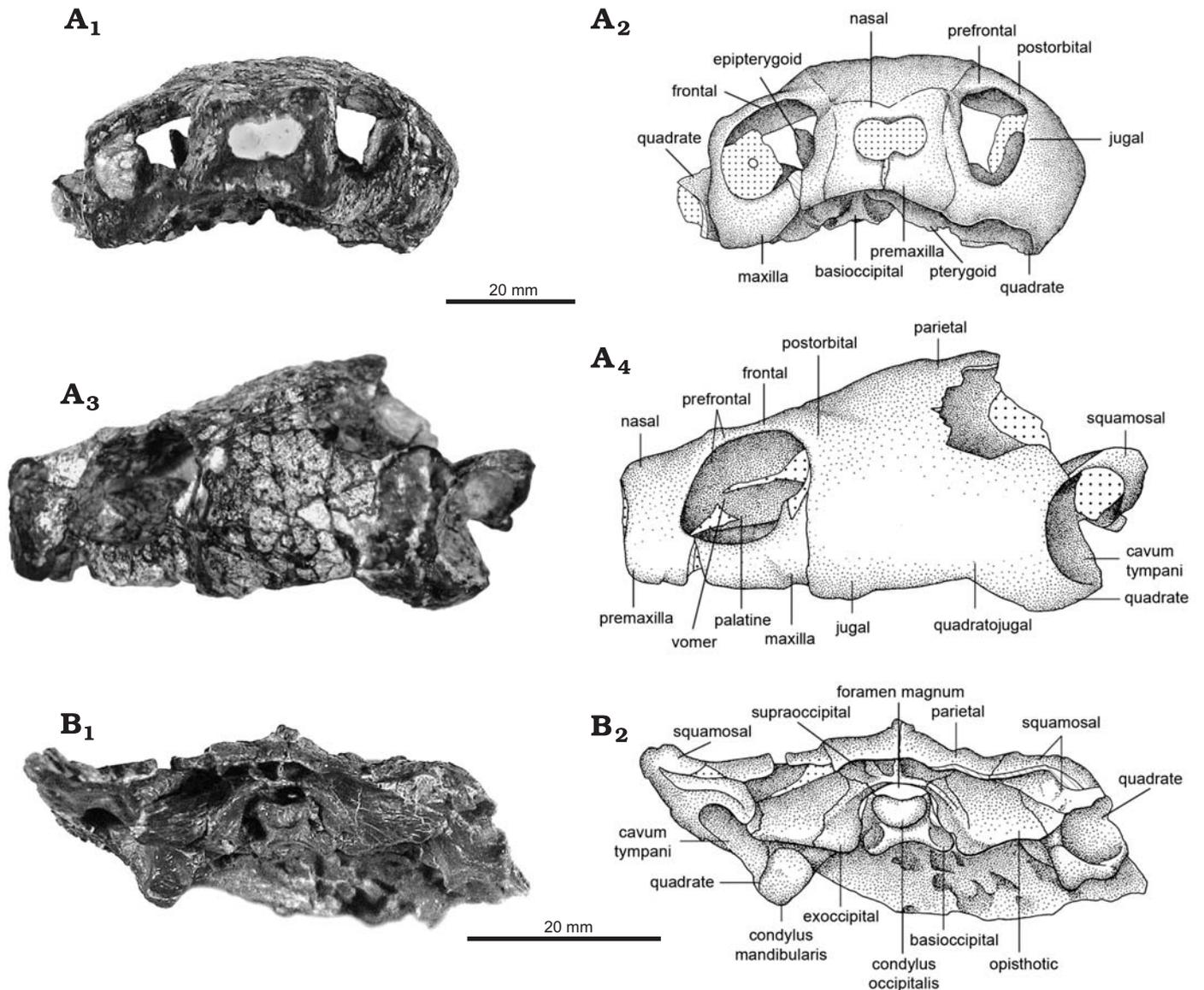


Fig. 4. The turtle *Kayentachelys aprix* Gaffney, Hutchison, Jenkins, and Meeker, 1987, from the Early Jurassic Kayenta Formation, Gold Springs, Arizona, USA. **A.** Specimen TMM 43670-2, photograph (A_1) and explanatory drawing (A_2) of the skull in rostral (A_1 , A_2) and lateral (A_3 , A_4) views. **B.** Specimen MCZ 8917, skull in occipital view. Photographs (A_1 , A_3 , B_1) and explanatory drawings (A_2 , A_4 , B_2).

formed by the prefrontal anteriorly and the postorbital posteriorly. Ventrally the frontals possess well developed parasagittal ridges that form an hourglass-shaped sulcus olfactorius (MNA V2664).

Parietal and foramen nervi trigemini.—The parietal is the main component of the skull roof (MCZ 8917, MNA V1558). Contrary to the condition seen in *Proganochelys quenstedti*, but as in most turtles, the parietal is longer than wide and is larger than the frontal. In dorsal view, the parietal contacts the frontal anteriorly, the postorbital anterolaterally, and the squamosal posterolaterally. The parietals meet each other along the midline. The posteroventral contact with the supraoccipital is barely visible just above the foramen magnum in MCZ 8917. The small processus inferior parietalis reaches the prootic, as

is seen in the sutural area preserved in MCZ 8916. Given that no upper temporal emargination is present, the parietal extends posteriorly almost to the same level as the condylus occipitalis (MCZ 8917, MNA V1558).

As in all turtles, the processus inferior parietalis is present, but it is only visible in TMM 43670-2. In contrast to other fossil turtles and modern turtles, this process is developed to the same degree as in *Proganochelys quenstedti* and *Palaeochersis talampayensis*, where the extension of the descending process does not go further anteriorly than the otic chamber. The processus inferior parietalis of *Proganochelys quenstedti* and *Palaeochersis talampayensis* does not close the foramen nervi trigemini dorsally, thus resulting in a cavum epiptericum that is not completely ossified (Gaffney 1990; Sterli et al. 2007). The foramen nervi trigemini area of

Kayentachelys aprix is not visible in known specimens. However, given that the remaining features are similar to *Pr. quenstedti* and to *Palaeochersis talampayensis*, it is likely that *K. aprix* had an open foramen nervi trigemini and a not completely ossified cavum epiptericum as well. In pleurodires the foramen nervi trigemini is closed anteriorly by the parietal, while in cryptodires it is closed by the parietal and the epipterygoid. *Kayentachelys aprix* possesses an epipterygoid, but its precise location remains somewhat unclear because its morphology is different from any other turtle (see Epipterygoid). We nevertheless conclude that the epipterygoid formed part of the anteroventral rim of an open foramen nervi trigemini.

Jugal.—The jugal forms part of the cheek margin and it has a quadrangular shape as in most turtles but in contrast to the triangular elements seen in *Proganochelys quenstedti* and *Palaeochersis talampayensis*. It contacts the maxilla anteriorly and ventrally, the quadratojugal posteriorly, the postorbital dorsally, and the pterygoid medially via a small contact. Although the jugal and quadratojugal are present in several specimens, the suture between both bones is not clearly seen in any.

In palatal view, the jugal has a medial process that articulates with the palatal bones. This process is laminar and overlaps the maxilla dorsally and scarcely contacts the pterygoid medially (MCZ 8999, MCZ 8917, MNA V1558, TMM 43653-1). The development of the pterygoid prevents the jugal palatine contact. Gaffney et al. (1987) noted that the jugal forms part of the foramen palatinum posterius, but we cannot confirm this observation. The jugal forms the posteroventral rim of the fossa orbitalis of *Kayentachelys aprix*, which is also surrounded by the postorbital, frontal, prefrontal, and maxilla.

Quadratojugal.—The quadratojugal is an almost quadrangular bone located in the cheek region (MCZ 8917). Posteriorly the quadratojugal has a C-shaped contact with the quadrate, but this quadratojugal does not outline the cavum tympani entirely. Anteriorly the quadratojugal contacts the jugal and dorsally the postorbital. The last two contacts are somewhat conjectural because they are badly defined in all the available specimens.

The quadratojugal does not contribute to the formation of the cavum tympani as seen in *Palaeochersis talampayensis*. As in *Proganochelys quenstedti*, *Palaeochersis talampayensis*, *Australochelys africanus* (Gaffney and Kitching 1994, 1995), and other turtles, *Kayentachelys aprix* does not have a cheek emargination.

Squamosal.—Although the squamosal is not preserved three dimensionally in any of the available material, it is nevertheless apparent that it contributes to the skull roof, the rim of the

cavum tympani, and the incipient antrum postoticum (MCZ 8917, MNA V1558). The squamosal contacts the opisthotic ventromedially within the temporal fossa, the quadrate ventrally, the postorbital anteriorly, and the parietal dorso-medially. Due to the development of an incipient antrum postoticum, the squamosal blocks the opisthotic in lateral view, unlike the condition seen in *Proganochelys quenstedti*.

Postorbital.—The postorbital is a well-developed bone that is longer than wide (MCZ 8917, MNA V1558). It contacts the frontal anterior and anteromedially, the parietal posteromedially, the squamosal and quadrate posteriorly, the jugal anteroventrally, and the quadratojugal posteroventrally. As in other turtles, this element contributes to the posterodorsal rim of the fossa orbitalis.

Supratemporal.—The posterior temporal region is not well-preserved in any of the available material. For this reason we neither confirm nor reject the presence of the supratemporal bone.

Palatal elements (Figs. 4, 5)

Premaxilla.—The premaxilla forms the anterior region of the snout and the triturating surface. It contacts the maxilla posterolaterally, the vomer posteromedially, and the other premaxilla along the midline (MNA V1558; MNA V2664).

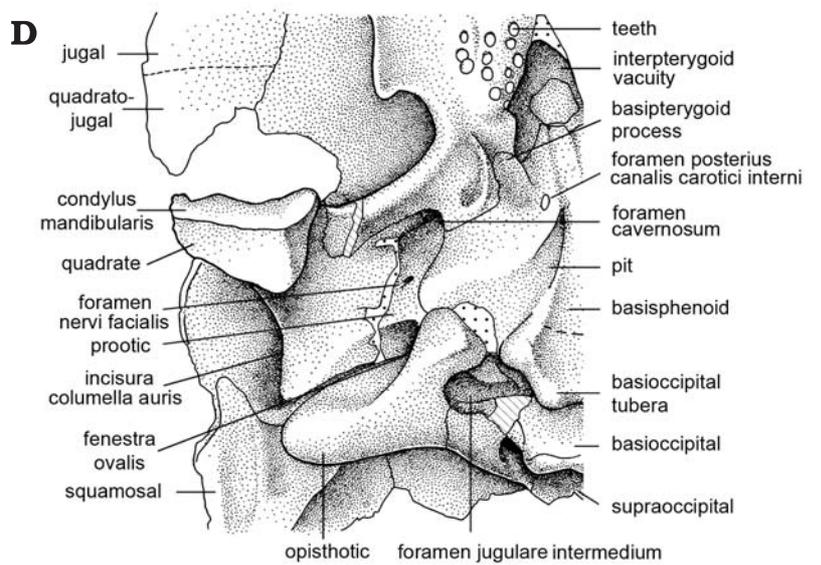
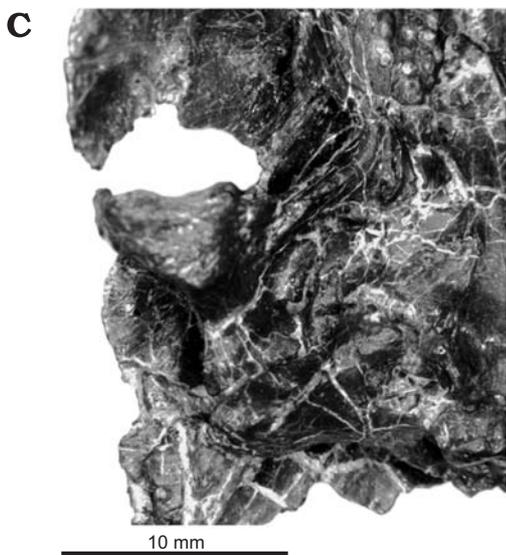
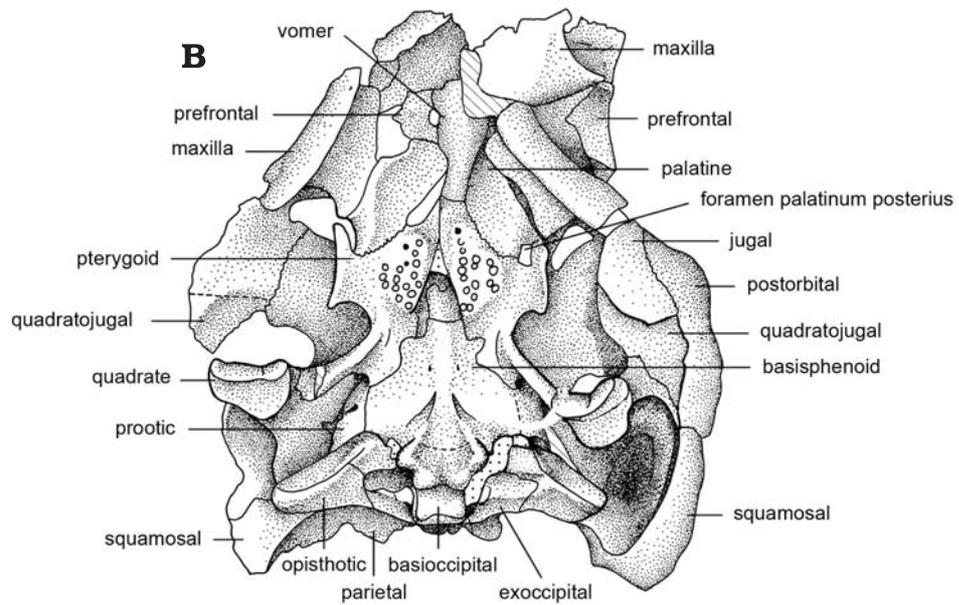
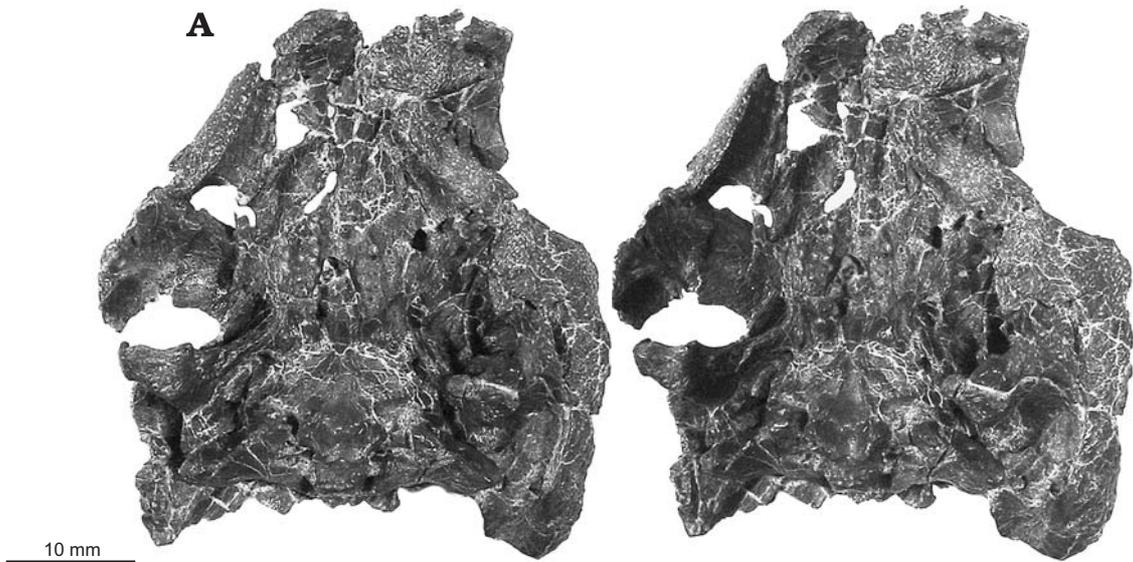
As in all turtles, the premaxilla forms the ventral margin of the apertura narium externa that is also bordered by the ascending process of the maxilla laterally and by the nasal dorsally. Contrary to the condition found in *Proganochelys quenstedti*, but similar to most turtles, the premaxilla does not have a dorsal process. The apertura narium externa is thus not divided (MNA V2664, TMM 43670-2).

Ventrally the premaxilla forms the triturating surface with the maxilla. However, it contributes only to the anteromedial portion of the triturating surface and the most anterior portions of the labial ridge. Those portions that normally hold the foramen praepalatinum are not well preserved in any of the available specimens. It is thus unclear if a foramen is present.

Maxilla and triturating surface.—The maxilla is a paired bone that forms the lateral margin of the apertura narium externa, the ventral margin of the orbit, and the majority of the triturating surface. It contacts the premaxilla anteriorly, the nasal, and the prefrontal dorsally, the jugal posteriorly and posterodorsally, the palatine medially, and the pterygoid posteromedially. Anteriorly, the maxilla has an ascending process which forms the lateral margin of the apertura narium externa and the anterior margin of the orbit.

The triturating surface is primarily formed by the maxilla with a small contribution from the premaxilla. The drawings provided by Gaffney et al. (1987) reveal a contribution of the

Fig. 5. The turtle *Kayentachelys aprix* Gaffney, Hutchison, Jenkins, and Meeker, 1987, specimen MCZ 8917, from the Early Jurassic Kayenta Formation, Gold Springs, Arizona, USA. **A, B.** Skull in ventral view; stereophotographs (**A**) and explanatory drawing (**B**). **C, D.** Detail of the right middle ear region; photograph (**C**) and explanatory drawing (**D**). →



jugal to the triturating surface, but in all the specimens where the posterior part of the maxilla is preserved (e.g., MCZ 8999, TMM 43647-1) we cannot confirm this observation. The triturating surface is framed by the labial and lingual ridges. The lingual ridge is shorter and lower than the labial and more poorly developed in smaller individuals. The ridges diverge posteriorly, resulting in a broad posterior triturating surface. The triturating surfaces do not meet another along the midline and frame an elongated, anteriorly rounded tongue groove.

Vomer.—As in all turtles, except *Proganochelys quenstedti* and *Palaeochersis talampayensis*, the vomer is an unpaired bone. It is a narrow and elongated bone with expanded anterior and posterior ends located in the anterior region of the palate. The only clearly visible contacts are with the palatine posterolaterally and the pterygoid posteriorly (MNA V1558, TMM 43670-2). Although no specimen preserves this area sufficiently, we presume that the vomer contacts the premaxilla and maxilla. The contact with the prefrontal is difficult to establish as well. However, we are confident that it can be seen in MNA V1558 (see Prefrontal).

The shape and distribution of the vomer prohibits a midline contact of the palatines, but allows a midline contact of both pterygoids. It does not curve dorsally as is the case in *Proganochelys quenstedti* and *Australochelys africanus*. As in all turtles, except *Proganochelys quenstedti*, there is no evidence of vomerine teeth. Unfortunately, no specimen preserves the ventral view of the anterior region of the palate in good condition. For this reason the presence and shape of the foramen praepalatinum, apertura narium interna, and foramen orbito-nasale cannot be determined.

Palatine and foramen palatinum posterius.—The palatine contacts the vomer medially, the maxilla laterally, and the pterygoid posteriorly (MCZ 8917, MNA V1558, TMM 43670-2). There is no contact between the palatine and the jugal, because the pterygoid is located in between (MCZ 8917, MCZ 8999, MNA V1558, TMM 43653-1).

Posterolaterally the palatine forms part of the foramen palatinum posterius. This foramen is also framed by the pterygoid and perhaps also by a small contribution of the maxilla (MNA V1558). The foramen palatinum posterius is relatively small compared to *Proganochelys quenstedti* and *Palaeochersis talampayensis*. As in all turtles, except *Proganochelys quenstedti*, palatine teeth are absent. Unfortunately, the foramen orbito-nasale is not seen in any specimen.

Palatoquadrate elements (Figs. 5, 6)

Quadrate.—As in all turtles, the quadrate forms many structures of the skull, including the cavum tympani, the anterolateral wall of the middle ear, and the condylus mandibularis. In ventral view, the quadrate (MCZ 8917) contacts the pterygoid anteroventrally, the prootic anteromedially, and the opisthotic posteriorly. In lateral view the quadrate (MCZ 8917) contacts the squamosal posterodorsally, the parietal

dorsally, the quadratojugal anteriorly, and the postorbital anteriorly and anterodorsally.

Laterally the quadrate forms the cavum tympani. As in all turtles, except *Proganochelys quenstedti*, *Palaeochersis talampayensis*, and *Australochelys africanus*, the cavum tympani is well developed, deep, and kidney-shaped (TMM 43670-2, MCZ 8917). The rim along which the tympanic membrane was attached is formed mainly by the quadrate and to a lesser extent by the squamosal, but the posteroventral portions were held by soft connective tissue. Gaffney et al. (1987) and Gaffney (1990) noted the presence of an antrum postoticum but provided no detailed description of the area. The cavum tympani expands posterodorsally and medially around the incisura columella auris and the posterior region includes a small contribution from the squamosal. This expansion can be homologized with the antrum postoticum of other fossil and modern turtles. However, the development of this structure is clearly intermediate between turtles that lack a well developed cavum tympani (e.g., *Proganochelys quenstedti* and *Palaeochersis talampayensis*) and modern turtles, which have a well developed cavum tympani and antrum postoticum. The quadrate also has a posterior notch, the incisura columella auris, which contains the stapes. As in *Proganochelys quenstedti*, *Palaeochersis talampayensis*, *Australochelys africanus*, and some fossil and modern turtles, the incisura columella auris is open.

Ventrally and anteriorly to the incisura columella auris, the ventral process of the quadrate forms the condylus mandibularis. The articular facet (TMM 43647-1, TMM 43670-2, MCZ 8917) is rectangular and divided in two areas, one area located medially and the other laterally. The medial area is almost flat, but the lateral one is slightly convex and slightly bigger than the medial part. The orientation of the area articularis could not be established with certainty because all available quadrate material is either crushed or isolated. However, when comparing the condylus mandibularis with the articular area of the lower jaw, we conclude that the medial part is located below the lateral one.

In an isolate quadrate (TMM 43647-1) the paths of the stapedia artery and lateral head vein are visible. The more dorsally positioned groove represents the lateral half of the canalis stapedio-temporalis, which opens dorsally into the temporal region via the foramen stapedio-temporalis. The lateral half of the canal and foramen is formed by the prootic (see Prootic). The more ventrally positioned groove represents the lateral half of the canalis cavernosus, which continues anteriorly in the ventral part of the prootic and is then floored by the pterygoid. The lateral head vein runs through this groove (Gaffney 1979).

As in all turtles, the quadrate has a vertical medial process (the pterygoid process) that overlaps the quadrate process of the pterygoid posteromedially and forms the anterior wall of the middle ear. The floor of the middle ear region is discussed below with the pterygoid.

TMM 43670-2 is the only specimen in which the otic chamber is preserved in its entirety. In this specimen, there is

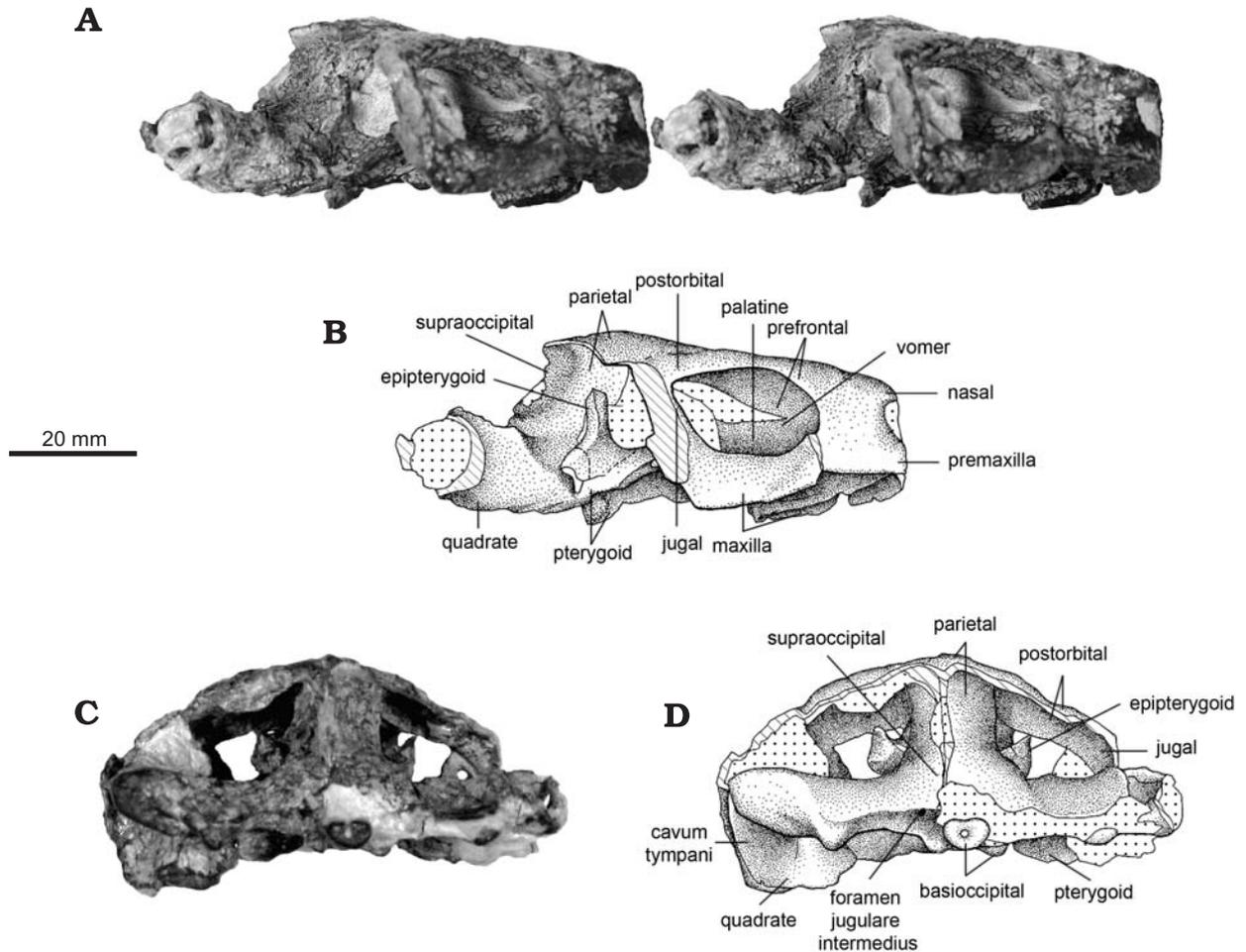


Fig. 6. The turtle *Kayentachelys aprix* Gaffney, Hutchison, Jenkins, and Meeker, 1987, specimen TMM 43670-2, from the Early Jurassic Kayenta Formation, Gold Springs, Arizona, USA. Skull in lateroanterior (A, B) and posterior (C, D) views; stereophotographs (A), photograph (C) and explanatory drawings (B, D).

no positive evidence for the development of a processus trochlearis oticum as was suggested by Gaffney et al. (1987). The anterodorsal wall formed by the quadrate and prootic is more robust than in *Proganochelys quenstedti* and *Palaeochersis talampayensis*, but neither a thickened knob nor a roughened area, as is seen in many cryptodiran turtles for the articular facet with the cartilago transiliens, is developed (Gaffney 1975, 1979). In addition, as in *Proganochelys quenstedti* and *Palaeochersis talampayensis*, the otic capsule is not in the way of the adductor muscle, producing no modification in the direction of this muscle when passing over the otic capsule.

Epipterygoid.—Both epipterygoids are clearly visible in TMM 43670-2. Although they are slightly damaged and somewhat displaced from their natural position, their general morphology is clear. The epipterygoid is located above the posterior portions of the pterygoid. What remains of this bone is rod-like dorsally and becomes wider and more laminar in the ventral part along the contact with the pterygoid. Due to minor crushing, however, it is unclear what the original shape was precisely, especially dorsally. The epiptery-

goid seems to contact the anteromedial part of the prootic posteroventrally and perhaps even the quadrate. This cannot be established with confidence, because the suture between these bones is not seen in TMM 43670-2. Somewhat uniquely, the dorsal portion of the bone is well-developed and free and protrudes diagonally outwards into the fossa temporalis (Fig. 6), instead of facing upwards as in modern cryptodires.

The morphology of this region is different from any other known turtle with an epipterygoid. Most cryptodiran turtles possess an epipterygoid, but in this clade the epipterygoid is situated between the pterygoid and parietal, is plate like, and forms parts of the foramen nervi trigemini (Gaffney 1979). *Meiolania platyceps* also exhibits an epipterygoid that is rather different to that found in cryptodiran turtles. In this taxon the epipterygoid is a large ascending element that contact the small processus parietalis inferior dorsally and encloses the foramen nervi trigemini anteriorly (Gaffney 1983). Gaffney (1990) also noted that an epipterygoid is present in *Proganochelys quenstedti*. In this taxon, this bone is not laminar, but also rather more rod-like, and it does not contact the parietal either. Given the fragmentary nature of

the *Proganochelys quenstedti* epipterygoid, this interpretation may be considered dubious (Gaffney 1990). However, the similar morphology seen in the *Kayentachelys aprix* epipterygoid appears to support this interpretation. In summary, the epipterygoid of *Kayentachelys aprix* resembles that of *Proganochelys quenstedti* and *Meiolania platyceps* more so than other turtles because they are rod-like, however, they differ in their orientation.

“Pleurospenoid”.—MNA V1558 is an almost complete skull that has suffered significant dorsoventral compression. Through the left fenestra temporalis inferior, a laminar bone with rounded edges is visible. Unfortunately, the real shape and location of this bone cannot be established. Given that the epipterygoid of *Kayentachelys aprix* is a rod-like element and that this element resembles the “pleurospenoid” of *Proganochelys quenstedti* (Gaffney 1990) we tentatively interpret this bone as a “pleurospenoid” as well. Following the convention of Gaffney (1990), the term pleurospenoid is chosen for lack of a better term, but it is placed in quotes to indicate that no homology is anticipated with the pleurospenoid of other tetrapods.

Pterygoid.—The pterygoid is a paired bone that forms the posterior part of the palate. It contacts the palatine and vomer anteriorly, the maxilla anterolaterally, the jugal anterodorsally, the quadrate posterolaterally, and the basisphenoid posteromedially. Medially the pterygoids frame the interpterygoid vacuity and contact one another anteromedially.

The pterygoid resembles that of basal turtles, such as *Proganochelys quenstedti*, *Palaeochersis talampayensis*, *Australochelys africanus*, and *Heckerochelys romani* because it is a triradiate structure consisting of the palatine process, the main body, and the quadrate ramus. The palatine process is a flat, long horizontal process that extends anteriorly between the palatines, and meet each other along the midline before the contact with the vomer. In *Proganochelys quenstedti* and in *Palaeochersis talampayensis*, this midline contact is relatively less extensive. Posteriorly to the anteromedial contact of both pterygoids, there is a V-shaped interpterygoid vacuity. The interpterygoid vacuity of *Kayentachelys aprix* is similar to that of *Heckerochelys romani* because they are reduced, compared to *Proganochelys quenstedti* and *Australochelys africanus*. All remaining turtles have a closed interpterygoid vacuity.

The transverse process and the main body of the pterygoid form the posterolateral border of the foramen palatinum posterius. This foramen is bordered anteromedially by the palatine and perhaps there is a small contribution from the maxilla as well. The jugal does not contribute to the foramen (see Jugal for more extensive discussion).

The main body of the pterygoid and the palatine process bear small pterygoid teeth (MCZ 8917, MNA V1558, TMM 43670-2). *Kayentachelys aprix* and *Proganochelys quenstedti* are the only known turtles that unambiguously possess teeth, but the arrangement of teeth is very different in both species. In *Kayentachelys aprix* the teeth are rod-like with a blunt apex

and are situated mainly in three rows (the mid row being the longest and the lateral row the shortest), while in *Proganochelys quenstedti* teeth are arranged in five to eight rows. The teeth in *Kayentachelys aprix* are restricted to the middle area of the pterygoid, while in *Proganochelys quenstedti* they are spread over the vomer, palatine, and pterygoid.

In lateral view, the lateral border of the main body of the pterygoid is curved concave posteriorly and convex anteriorly. In its convex and widest area, there is a small posteriorly directed lappet and the pterygoid continues anteriorly almost parallel to the sagittal plane from there. In some specimens (MNA V1558, TMM 43670-2) the lappets are a little thicker than in other specimens, but they never develop a clear vertical flange as was claimed by Gaffney et al. (1987). Although there are differences in the development of the anterolateral region of the pterygoid among turtles, all involved structures (e.g., processus trochlearis pterygoidei, vertical flange in the processus pterygoideus externus) have the same function, which is to guide the lower jaw during the closure of the mandible (Gaffney 1990; Joyce 2007) and they have the same topological position.

The posteromedial area of the main body of pterygoid of *Kayentachelys aprix* has a pocket into which the basiptyergoid process of the basisphenoid fits (MCZ 8917), as is the case of *Heckerochelys romani* (Sukhanov 2006) and *Pleurosternon bullockii* (Evans and Kemp 1975). The basiptyergoid articulation is sutured in *Kayentachelys aprix* as in all turtles, except *Proganochelys quenstedti*. Laterally to the basiptyergoid suture, the pterygoid forms a big triangular ridge that is directed ventrally and that has a drop-like depression (TMM 43651-1). Similar depressions are seen in *Judithemys sukhanovi* Parham and Hutchison, 2003 and *Ordosemys* Brinkman and Peng, 1993, and they could have served as a muscle attachment area for the pterygoideus musculature (Brinkman and Wu 1999). The lateral side of the triangular ridge is continuous with the quadrate ramus of pterygoid.

The remaining area of the pterygoid is the quadrate ramus. This is a posterolateral vertical process that laterally overlaps the quadrate. The quadrate ramus is long and almost reaches the condylus mandibularis. This condition is also found in modern turtles and in *Palaeochersis talampayensis*, but in *Proganochelys quenstedti* this process is shorter. The quadrate ramus of the pterygoid and the pterygoid process of the quadrate form the anterior wall of the middle ear region.

The quadrate ramus of the pterygoid possesses a small posterior horizontal process in the intersection with the basiptyergoid process that covers the anterior area of the floor of the cranioquadrate space, resulting in a partially enclosed cranioquadrate space. The posterior process of the pterygoid is more extensive than in *Proganochelys quenstedti*, *Palaeochersis talampayensis*, and *Australochelys africanus*, but not as large as in other fossil (e.g., *Kallokibotion bajazidi* Nopcsa, 1923, *Ordosemys*, *Pleurosternon bullockii*) and modern turtles. The enclosed cranioquadrate space is called the canalis cavernosus and contains, among others, the vena capitis late-

ralis. The posterior aperture of the canalis cavernosus, the foramen cavernosum is formed by the pterygoid ventrally, the prootic dorsally, and the quadrate laterally. The anterior opening of the canalis cavernosus is not seen in any specimen. Unfortunately, no dorsal view of the pterygoid is available.

Braincase elements (Figs. 4–8)

Supraoccipital.—The supraoccipital is a single bone that is located dorsal to the foramen magnum and that forms part of the brain case roofing. The supraoccipital contacts the exoccipital ventrally, the prootic anteriorly, and the opisthotic posterolaterally. It is not possible to see the contact between the supraoccipital and parietal in *Kayentachelys aprix* because this region is not well preserved in any specimen.

As in all turtles, the supraoccipital has paired ventrolaterally projecting processes that roof the cavum labyrinthicum and the dorsal rim of the hiatus acusticus (MCZ 8916). The hiatus acusticus is more ossified than in modern turtles (MNA V2664), but not as much as in baenids (Gaffney 1979, 1982). The hiatus acusticus is formed dorsally by the supraoccipital and ventrally by the basisphenoid. Through the hiatus acusticus, the nervi glossopharyngei (IX) exits the cavum cranii to enter the cavum labyrinthicum. Anteriorly to the hiatus acustici and surrounded by the basisphenoid and prootic (and may be by the supraoccipital dorsally) there is a big foramen, interpreted here as the foramen nervi acustici (VIII).

The supraoccipital forms the dorsal margin of the foramen magnum (MCZ 8917) and as in *Proganochelys quenstedti* the supraoccipital in this area is almost flat, giving an oval shape to the foramen. The supraoccipital also forms the crista supraoccipitalis. It is a tall element (TMM 43670-2) that does not protrude posteriorly to the foramen magnum.

On the dorsal surface of the supraoccipital there are two grooves. The longer of the two grooves runs the length of the supraoccipital from the midline to the quadrate with an anteromedial-posterolateral direction near the suture with the prootic. The smaller groove starts at a point near the suture with the opisthotic at the midline and runs with a posteromedial-anterolateral direction. It is unclear to us if these grooves have a function.

Exoccipital.—The exoccipital is a paired bone located in the posterior part of the skull. It contacts the opisthotic laterally, the supraoccipital dorsally (MCZ 8917), and the basioccipital ventrally (MCZ 8999). The contact between the basioccipital and the exoccipital is only seen in MCZ 8999. In all remaining specimens, both bones appear to be fused. The exoccipitals contact each other along the midline at the base of the foramen magnum.

The exoccipital forms half of the condylus occipitalis, the remaining condylus is formed by the basioccipital. The general shape of the condylus occipitalis is roughly triangular. In MCZ 8999 the exoccipital is pierced by the hypoglossal nerve (XII) that leaves the brain through two foramina in

each exoccipital. The exoccipital also forms the lateral and ventral margin of the foramen magnum. Although the foramen magnum is not preserved intact in any specimen, the shape of this foramen can be estimated from what is preserved in MCZ 8917. In this specimen, the relationships between the exoccipitals and the supraoccipital are intact but the exoccipitals are broken at their base and the lateral rims of the foramen magnum have collapsed over the condylus occipitalis. In spite of the collapsing of these elements, however, we estimate that the outline of the foramen magnum was slightly oval, the main axis being horizontal.

The exoccipital forms together with the opisthotic and basioccipital the rim of a large foramen, herein termed the foramen jugulare intermedium, that faces posteriorly (see Opisthotic). This foramen leads to the fenestra perilymphatica and to the foramen jugulare anterius.

Basioccipital.—The basioccipital is a triangular bone that contacts the basisphenoid anteriorly, the exoccipital dorsolaterally, and the opisthotic posterolaterally (MCZ 8999). The basioccipital and the basisphenoid are notably thick elements and they consequently preserve readily (e.g., MCZ 8916, MCZ 8983, MCZ 8999, MNA V2664, TMM 43653-1). The thickness of both bones is intermediate between the even thicker braincase floor of *Palaeochersis talampayensis* and *Proganochelys quenstedti* and the thinner floor of modern turtles.

The basioccipital forms together with the exoccipitals the condylus occipitalis. As in most of crown turtles, the shape of the condylus is that of a rounded triangle and the contribution of the basioccipital to the condylus occipitalis is approximately half. This is only apparent from MCZ 8999, because the contributing elements are fused in all remaining specimens. As in most turtles, the condylus occipitalis is separated from the main body of the basioccipital by a slight neck.

Along the ventral side of the basioccipital, just anterior to and slightly below the condylus occipitalis, a pair of distinct tubera basioccipitalia are present that likely served for neck muscle attachment (Gaffney 1979). The tubera are ridge shaped and do not meet another along the midline, yet they form together with the condylus occipitalis a distinct Y along the posterior edge of the skull. Well spaced paired tubera are developed in numerous basal and derived turtles, yet are notably lacking from *Proganochelys quenstedti*, which exhibits a single central tubercle only (Gaffney 1990).

The basioccipital forms the floor of the posterior part of the cavum cranii. A distinct crista dorsalis basioccipitalis is developed along the midline of the dorsal side that appears to extend just beyond the suture onto the basisphenoid (MNA V2664). The available specimens exhibit some variation in regards to this structure, much of which may be the result of taphonomic processes. In some specimens the crista appears to be elongate in shape and evenly low (MNA V2664), whereas in others a distinct V-shaped, anteriorly open knob is developed just posterior to the suture with the basisphenoid (e.g., MCZ 8916, MCZ 8999). In TMM 43647-1, two foramina are visible along each side of the posterior part of the crista dorsalis basi-

occipitalis. Their function is not known, but they may correspond to vascular foramina.

In the suture between the exoccipital and the basioccipital (MNA V2664) there is a groove through which the foramen jugulare anterius communicates with the cavum cranii. The vena cerebialis posterior and cranial nerves X and XI exit the skull through this groove (Gaffney 1979). Lateral to the groove, the ventral rim of the fenestra perilymphatica is formed by the basioccipital medially and the opisthotic laterally. The processus interfenestralis of the opisthotic is a robust structure and a posterior cranial wall formed by the opisthotic and the exoccipitals is lacking. The inner ear thus communicates with the unossified recessus scalae tympani through an opening that could be homologized to the fenestra perilymphatica of modern turtles. In modern turtles where the processus interfenestralis of the opisthotic is a delicate process and the posterior wall is well developed, the fenestra perilymphatica connects the inner ear with an ossified recessus scalae tympani (Gaffney 1979). The anterolateral part of the basioccipital of *Kayentachelys aprix*, as in other turtles, forms the posterior part of the rim of the hiatus acusticus, which connects the cavum cranii with the cavum labyrinthicum. The anterior part of the rim is formed by the basisphenoid.

Prootic.—The prootic is a paired bone and is exposed ventrally as in *Proganochelys quenstedti*, *Palaeochersis talampayensis*, *Heckerochelys romani*, and pleurodires. It contacts the supraoccipital dorsoposteromedially, the parietal dorsoanteromedially (inferred from suture area in MCZ 8916), the opisthotic posteriorly, the basisphenoid ventromedially, and the quadrate laterally (MCZ 8917). Close study of several specimens (MCZ 8916, MCZ 8917, MNA V2664, TMM 43653-1) allows us to conclude that no contact is present between prootic and pterygoid, as is the case in *Proganochelys quenstedti*.

Numerous structures are formed by the prootic. It forms the anterior rim of the fenestra ovalis (see Opisthotic and Ear), which is relatively small (compared with that of *Proganochelys quenstedti*) and completely ossified ventrally (MCZ 8916, TMM43653-1). In contrast to the condition seen in *Proganochelys quenstedti* where there are two openings for the foramen nervi facialis (VII), only a single opening is located anterior to the fenestra ovalis in *Kayentachelys aprix* (MCZ 8917). The location of this foramen is unknown in *Palaeochersis talampayensis* and *Australochelys africanus*. As a consequence, we cannot establish whether the condition found in *Proganochelys quenstedti* is autapomorphic for that taxon or plesiomorphic for turtles.

The ventral opening of the canalis stapedio-temporalis is formed by the quadrate and the prootic and is located at the same level or slightly anterior to the fenestra ovalis (MCZ 8917, TMM 43653-1). As in modern turtles, a true canalis stapedio-temporalis connects the ventral and dorsal openings. The canalis stapedio-temporalis runs up along the quadrate-prootic suture and opens dorsally into the fossa temporalis su-

perior through a dorsally facing foramen stapedio-temporalis (TMM 43653-1, TMM 43670-2).

Proganochelys quenstedti has an open cranioquadrate space and lacks sutural contact between the pterygoid, prootic, and quadrate. However, in *Kayentachelys aprix*, as in *Palaeochersis talampayensis* and *Australochelys africanus*, the cranioquadrate space is partially enclosed by bone compared with other fossil (*Kallokibotion bajazidi* and *Pleurosternon bullockii* among others) and modern turtles. The cranioquadrate space is floored in *K. aprix* ventrally by a posterior extension of the pterygoid, forming an enclosed canalis cavernosus. The foramen cavernosum, the posterior opening of the canalis cavernosus, is formed by the pterygoid ventrally, the prootic dorsally, and the quadrate laterally (MCZ 8917, TMM 43653-1). The anterior aperture of the canalis cavernosus cannot be identified in any specimen because of their state of preservation.

In dorsal view, the prootics of MCZ 8916, TMM 43653-1, and MNA V 2664-1 form the anterior wall of the foramen nervi acustici (VIII), through which the cavum cranii communicates with the cavum labyrinthicum. In addition, MNA V 2664 also preserves the foramen nervi facialis (VII), which pierces the prootic. The prootic forms at least the posterior wall of the prootic foramen through which rami V₂ and V₃ of the cranial nerve V exit the cavum cranii. The ventral rim of this foramen is formed by the basisphenoid. Unfortunately, the dorsal rim of the prootic foramen is missing preventing the identification of its size and the bones that surround it dorsally.

Opisthotic.—The opisthotic is a prominent bone that forms a portion of the posterior part of the skull. In dorsal view, the opisthotic contacts the exoccipital posteromedially, the supraoccipital anteromedially, the squamosal laterally, the quadrate anterolaterally, and the prootic anteromedially (MCZ 8916). In ventral view, the opisthotic contacts the quadrate anterolaterally, basioccipital posteromedially, and the basisphenoid anteromedially (MCZ 8916, MCZ 8917, MNA V2664).

The opisthotic has a well developed processus paroccipitalis, which reaches the squamosal laterally and is well fused with the quadrate (MCZ 8917). In posterior view, there is a big foramen in the suture with the exoccipital and the basioccipital. This foramen does not correspond to the foramen jugulare posterius, because there is no ossified recessus scalae tympani in *Kayentachelys aprix*, as in basal turtles (e.g., *Proganochelys quenstedti*, *Palaeochersis talampayensis*, *Australochelys africanus*, and *Heckerochelys romani*) due to the robust processus interfenestralis of the opisthotic and the lack of a posterior bony wall to the skull that is formed by the exoccipital and opisthotic. In addition, in MNA 2664-1 it is clear that this foramen splits into two channels, the foramen jugulare anterius medially and the fenestra perilymphatica laterally. For these reasons, we consider this big foramen to be a separate anatomical feature and call it “foramen jugulare intermedium” (for more detail see

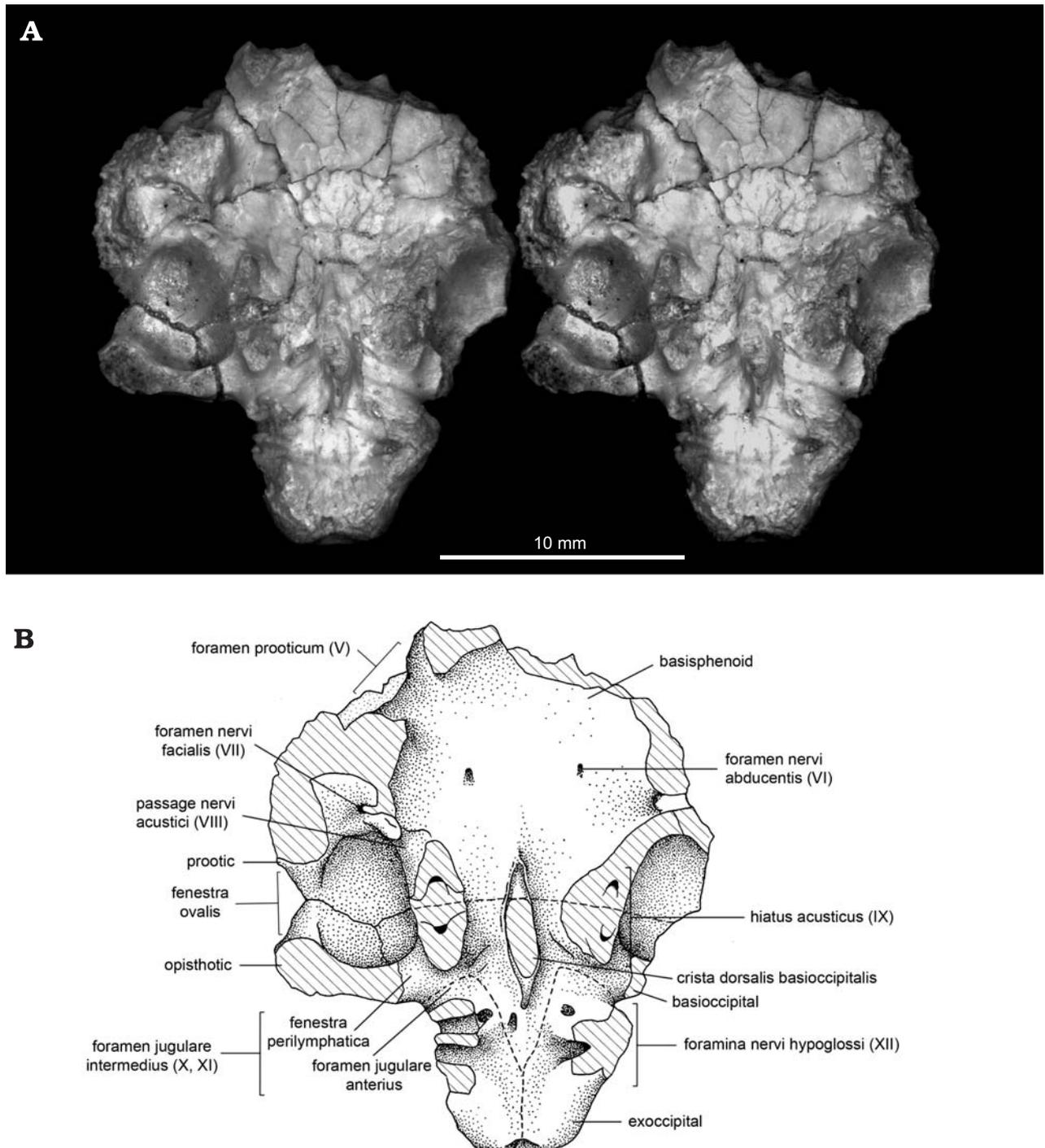


Fig. 7. The turtle *Kayentachelys aprix* Gaffney, Hutchison, Jenkins, and Meeker, 1987, specimen MNA V2664, from the Early Jurassic Kayenta Formation, Gold Springs, Arizona, USA. Basicranium in dorsal view; stereophotographs (A) and explanatory drawing (B).

Discussion and comparisons). Inside the skull it is apparent that the ventral rim of the foramen jugulare anterius is formed by the basioccipital and the exoccipital and holds the vena cerebialis posterior and the cranial nerves X and XI. These cranial nerves and the vena cerebialis posterior likely exited the skull through the foramen jugulare intermedium. The fenestra perilymphatica, which communicates the cavum labyrinthicum with the unossified recessus scalae tympani, is

located in the suture between opisthotic and basioccipital. This foramen is not documented for *Proganochelys quenstedti*.

The processus interfenestralis of the opisthotic is recognized by the presence of the foramen externum nervi glosso-pharyngei (IX), which is located posterior to the fenestra ovalis (MCZ 8916). As in *Proganochelys quenstedti*, *Palaeochersis talampayensis*, in *Australochelys africanus*, the pro-

cessus interfenestralis of *Kayentachelys aprix* is a robust structure that does not reach the floor of the basicranium. Conversely, in *Heckerochelys romani* (Sukhanov 2006), in other fossil turtles, and in modern turtles the processus interfenestralis of the opisthotic is a small structure that almost reaches the floor of the cavum acustico-jugulare (Gaffney 1979).

The opisthotic forms the posterolateral part of the inner ear cavity (MCZ 8916, MNA V2664). In MCZ 8916 and MCZ 8914 the left opisthotic is broken, allowing the description of the dorsal vestibular portion of the inner ear. In these specimens part of the recessus labyrinthicus opisthoticus is present which is covered above by the opisthotic. The roof of this recessus has two foramina, one located more medially and the other more laterally. The medial foramen is the canalis semicircularis posterior, through which the recessus labyrinthicus supraoccipitalis communicates with the recessus labyrinthicus opisthoticus. In contrast, the lateral foramen corresponds to the canalis semicircularis horizontalis, through which the recessus labyrinthicus opisthoticus communicates with the recessus labyrinthicus prooticus. The inner ear of *Kayentachelys aprix* is the oldest preserved inner ear of a turtle for which the internal structures and cavities can be described.

Basisphenoid.—The basisphenoid is located at the midline of the skull and in the anteroventral part of the cavum cranii. It has a triangular shape, with its apex pointing anteriorly. The total length of the basisphenoid cannot be established with certainty because the anterior end is missing in all. Like the basioccipital, the basisphenoid is a thick element in cross section. The basisphenoid contacts the basioccipital posteriorly, the prootic laterodorsally, the pterygoid lateroanteroventrally, and the opisthotic posterolaterally (TMM 43653-1, MNA V2664).

In the posterior region of the basisphenoid, near the midline a pair of scars termed basisphenoid pits are visible in ventral view (e.g., MCZ 8916, MCZ 8917, MNA V1558, MNA V2664, TMM 43653-7, TMM 43670-2). These pits have a semicircular shape, their straight margin pointing anteriorly, and are confluent anteriorly. They probably represent muscle attachment sites, such as those documented in pancryptodiran turtles such as *Judithemys sukhanovi* and *Ordosemys liaoxiensis* Tong, Ji, and Ji, 2004. Anterior to these scars at the base of the basiptyergoid process a pair of foramina posterioris canalis carotici interni are present, in the same location as in *Proganochelys quenstedti*, but more posteriorly located than in *Heckerochelys romani* (Sukhanov 2006). Posterolaterally to these foramina there is a groove that indicates the path of the internal carotid artery, which runs with a posterolateral-antero-medial direction near the suture with the pterygoid (MCZ 8916). The canalis carotici interni is short and ends in the foramen anterius canalis carotici interni at the base of the dorsum sellae, a few millimeters anterior to the foramen posterioris canalis carotici interni (see dorsum sellae, below).

In the anteroventral portion of the main body of the basisphenoid a paired basiptyergoid process is present (MCZ 8917, MNA V2664), as in *Proganochelys quenstedti*, *Palaeochersis talampayensis*, *Australochelys africanus*, *Heckerochelys romani*, *Pleurosternon bullocki*, and *Ordosemys*. As in all turtles except *Proganochelys quenstedti*, the basiptyergoid processes are tightly sutured to the pterygoid.

Although the anterior end of the basisphenoid is broken in all specimens, remains of the rostrum basisphenoidale are visible in the interptyergoid vacuity of MCZ 8917 and TMM 43670-2 that indicate that the rostrum basisphenoidale was at least as long as half the length of the interptyergoid vacuity.

The basisphenoid forms the anterior floor of the cavum cranii and, as in all turtles, the dorsal surface of this bone is concave. In the mid dorsal part of the basisphenoid both foramina of the canalis nervi abducentis (VI) are visible (MCZ 8916, MCZ 75-81, MMA 2664-1). The canalis nervi abducentis starts at the dorsal part of the basisphenoid and exits this bone lateral to the anterior opening of the canalis carotici interni (TMM 43651-1). In MCZ 8999 the dorsum sellae is preserved. It is slightly taller than in modern turtles, but not as tall as in *Proganochelys quenstedti* or *Palaeochersis talampayensis*. The posterior wall of the dorsum sellae is almost straight and at its base there is a pair of foramina that are the anterior aperture of the internal carotid artery (foramen anterius canalis carotici interni). Both foramina are close to each other, only separated by a small ridge that runs vertically.

The crista dorsalis basioccipitale is primarily developed on the basioccipital, but in some specimens (MCZ 8916, MNA V2664) it seems to continue onto the basisphenoid as well.

Posterolaterally the basisphenoid forms the anteromedial portion of the inner ear floor (see Opisthotic and Ear). The basisphenoid also forms the anteroventral rim of the hiatus acusticus, through which the cavum cranii communicates with the cavum labyrinthicum and through which the nervi glossopharyngei (IX) exits the cavum cranii. The basisphenoid part of the inner ear has another connection with the cavum cranii anterior to the hiatus acusticus. This connection is the foramen nervi acustici (VIII) which is closed dorsally by the supraoccipital.

Ear (Figs. 7, 8)

Cavum labyrinthicum and cavum acustico-jugulare.—In turtles, the elements that form the floor of the medial portions of the inner ear are variable. In many pleurodires, the floor of the cavum labyrinthicum is rather cartilaginous with osseous contributions from the quadrate and basisphenoid, while in pancryptodires the floor of the inner ear is usually formed by the prootic and opisthotic, with occasional contributions from the basisphenoid, pterygoid, or basioccipital (Gaffney 1979). In *Kayentachelys aprix* the floor of the cavum labyrinthicum is formed by bone. The basioccipital forms the posteromedial quarter of the flooring of the inner ear. The rest of this round depression is formed by the basisphenoid anteriorly and the opisthotic posterolaterally (MNA V2664).

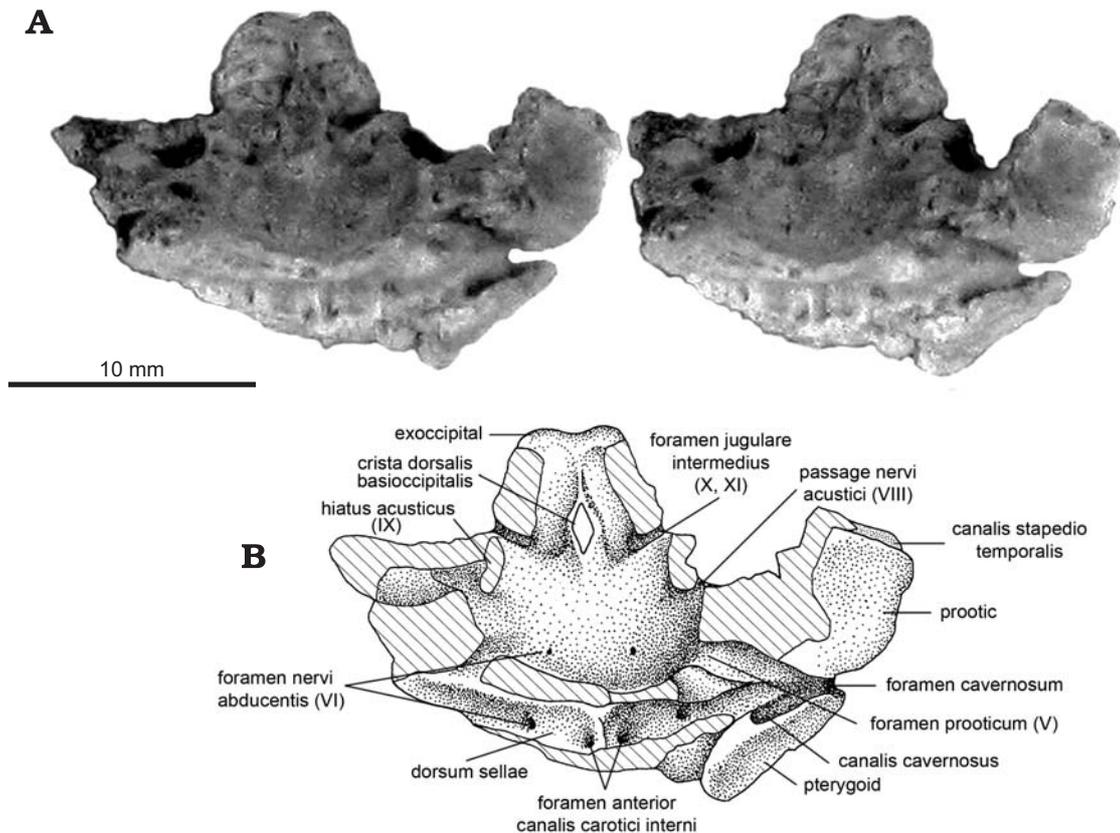


Fig. 8. The turtle *Kayentachelys aprix* Gaffney, Hutchison, Jenkins, and Meeker, 1987, specimen TMM 43653-1, from the Early Jurassic Kayenta Formation, Gold Springs, Arizona, USA. Basicranium in anterodorsal view; stereophotographs (A) and explanatory drawing (B).

In *Kayentachelys aprix* the ventral rim of the hiatus acusticus is formed by the basisphenoid anteriorly and the basioccipital posteriorly (MNA V2664). Dorsally the hiatus acusticus is bordered by the supraoccipital. The hiatus acusticus is more ossified than in modern turtles, but not as much as in baenids (Gaffney 1982). Anteriorly to the hiatus acusticus, the foramen nervi acustici (VIII) is located between the basisphenoid (posteriorly) and the prootic (anteriorly). The prootic is pierced by the nervi facialis (VII), which runs from the cavum cranii to the cranioquadrate space (see Prootic).

The limit between the cavum labyrinthicum (inner ear) and the cavum acustico-jugulare (middle ear) is marked by the fenestra ovalis. It is roughly oval and located parallel to the sagittal plane, as in modern turtles. As in *Proganochelys quenstedti*, *Palaeochersis talampayensis*, and *Australochelys africanus* (Gaffney 1990; Gaffney and Kitching 1995; Sterli et al. 2007) and contrary to most turtles, the fenestra ovalis is completely surrounded by bone, anteriorly by the prootic and posteriorly by the opisthotic (MCZ 8917).

As in *Proganochelys quenstedti*, *Palaeochersis talampayensis*, and *Australochelys africanus*, the floor of the cavum acustico-jugulare is mostly open. However, the quadrate ramus of the pterygoid develops a posterior, horizontal process that floors the anterior region of the cranioquadrate space of the cavum acustico-jugulare, forming a more closed canalis cavernosus than in the taxa listed above. Although this canalis

is more closed than in basal turtles, it is less extensive than in other fossil turtles (e.g., *Kallokibotion bajazidi*, *Pleurosternon bullockii*) and cryptodires. The foramen cavernosum is formed by the pterygoid ventrally, the quadrate laterally, and the prootic medially.

The processus interfenestralis of the opisthotic does not reach the floor of the cavum acustico-jugulare and is still a robust structure, as in *Proganochelys quenstedti*, *Palaeochersis talampayensis*, and *Australochelys africanus*. In addition to the lack of the ventral process of the exoccipital, this means that the recessus scalae tympani is not surrounded by bone. The unossified recessus scalae tympani communicates with the inner ear through the fenestra perilymphatica and with the cavum cranii through the foramen jugulare anterius (MNA V2664). Both foramina converge in the large foramen jugulare intermedium that faces posteriorly and is seen in posterior view (TMM 43670-2).

Columella auris.—There are no remains of the columella auris in any specimen. However, the quadrate does not have a quadrate pocket for the articulation of the columella auris, as seen in *Proganochelys quenstedti* or *Palaeochersis talampayensis*, the fenestra ovalis is small, and the quadrate possesses a well-developed incisura columella auris. For these reasons, we presume that the columella auris of *Kayentachelys aprix* was a slender rod-like element that has an impedance-matching function, as in modern turtles.

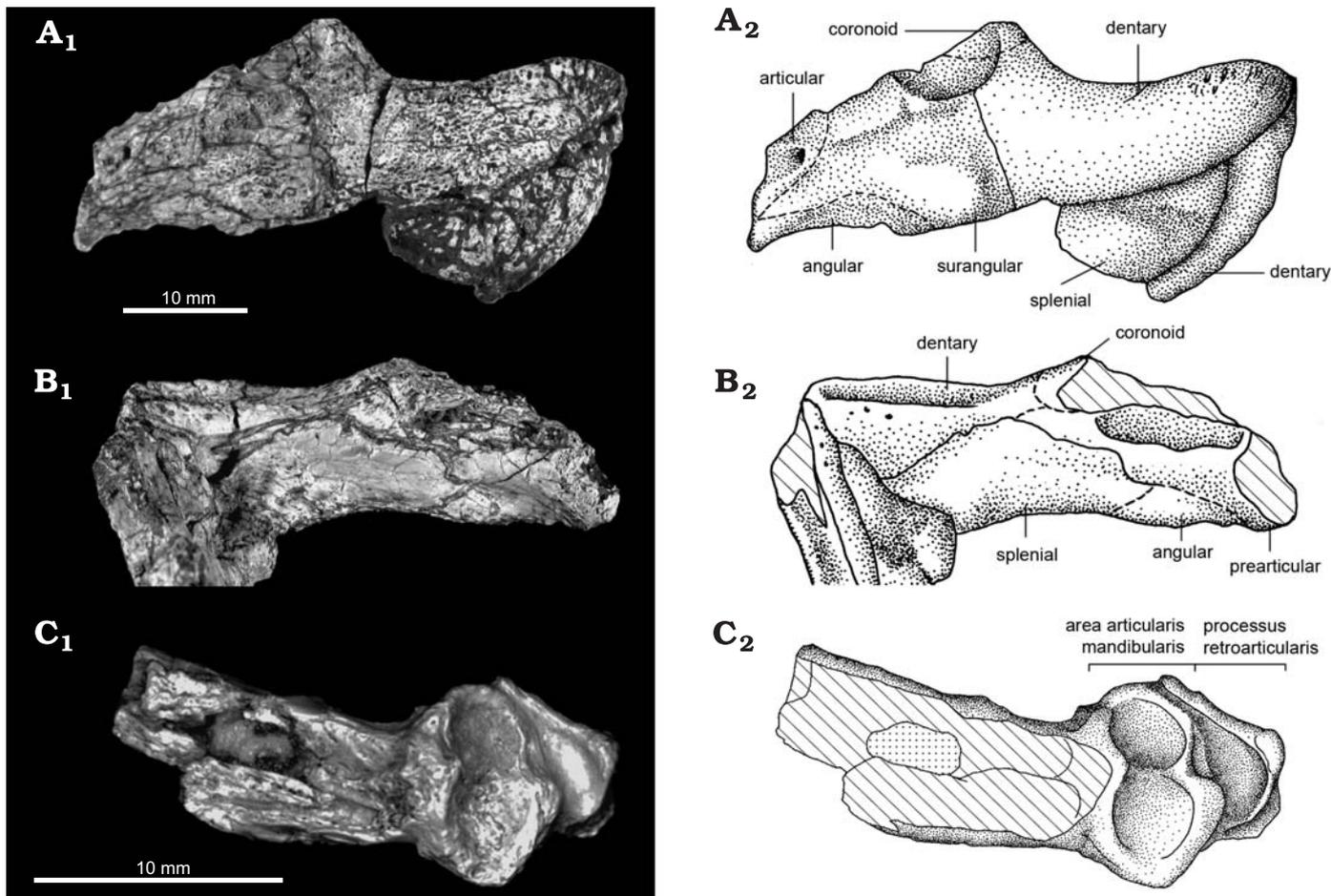


Fig. 9. The turtle *Kayentachelys aprix* Gaffney, Hutchison, Jenkins, and Meeker, 1987, from the Early Jurassic Kayenta Formation, Gold Springs, Arizona, USA. **A.** MCZ 8914, right lower jaw and part of the left dentary in lateral view; photograph (A₁) and explanatory drawing (A₂). **B.** MCZ 8915, right lower jaw medial view, with the left lower jaw conceptually removed; photograph (B₁) and explanatory drawing (B₂). **C.** MCZ 8916, mandibular articulation in dorsal view; photograph (C₁) and explanatory drawing (C₂).

Lower jaw elements (Fig. 9)

Dentary.—The dentary is the principal bone of the lower jaw and forms the symphysis and the triturating surface. In lateral view it presumably contacts the coronoid dorsally and the surangular posteriorly (MCZ 8914, MCZ 8915). In internal view (MCZ 8915, MCZ 8983) the dentary contacts the splenial, prearticular, and coronoid.

Anteriorly both dentaries meet along the midline, forming a symphysis. Notably, the dentaries (MCZ 8915) appear not to be fused, but rather just sutured and the splenials contribute to the symphysis as well. The symphysis is longer than in *Proganochelys quenstedti* or *Palaeochersis talampayensis*.

The triturating surface is formed completely by the dentary and it is characterized by two well developed lingual and labial ridges (MCZ 8914, MCZ 8983). Posteriorly, both ridges have the same height, but closer to the symphysis the labial ridge becomes higher than the lingual ridge. Both ridges are subparallel, but the triturating surface is slightly broader posteriorly than anteriorly. Posteriorly to the tri-

turating surface the dentary bears an ascending process that reaches the coronoid dorsally.

In MCZ 8983 the splenial is missing allowing study of the sulcus cartilaginis meckelii. It extends less than a half the length of the dentary (MCZ 8915, TMM 43669-2), as is the case in *Proganochelys quenstedti*.

Angular.—The internal contacts of the angular can be inferred from MCZ 8915. Dorsally the angular contacts the prearticular and anteriorly it contacts the splenial. The contact with the articular cannot be established; perhaps both bones are fused. Near the intersection of the splenial, prearticular, and angular, the foramen intermandibularis caudalis should be present, but this foramen is not clearly seen in any specimen.

Surangular.—The surangular is the second biggest bone of the lower jaw. The only contact that can be observed with certainty is the dentary-surangular suture, the remaining contacts are estimated. The surangular presumably contacts the angular ventrally, the articular posteriorly, and the coronoid dorsally.

In the lateral view of many specimens (MCZ 8914, MCZ 8916, MCZ 8983, TMM 43687-27) a foramen is visible, the foramen nervi auriculotemporalis. As the sutures in this area are not discernable and this foramen is usually formed by the surangular (Gaffney 1979), we speculate herein that this foramen is formed by the surangular in *Kayentachelys aprix* as well.

In lateral view the surangular, as in other turtles, has a well developed depression near the coronoid. This depression faces posterodorsally and represents the attachment area of the muscle adductor mandibulae externus (Schumacher 1973).

Coronoid.—Remains of the coronoid are present in MCZ 8915. The coronoid contacts the dentary lateral and anteriorly and the prearticular posteroventrally. The contact with the surangular is not clear.

The coronoid forms the anterior and anterodorsal border of the fossa Meckelii, but it does not participate in the formation of the triturating surface as in other turtles.

Prearticular.—The prearticular is seen in MCZ 8914 and MCZ 8915. This bone contacts the splenial anteriorly and the angular ventrally. The contact with the articular cannot be distinguished.

The prearticular forms a portion of the ventral margin of the fossa Meckelii. This fossa is elongated antero-posteriorly and faces medial and dorsally, as in *Proganochelys quenstedti* and *Palaeochersis talampayensis*. The fossa Meckelii is also surrounded anterior and anterodorsally by the coronoid and laterally by the surangular. Inside the fossa Meckelii (MCZ 8983) the foramen arterius chorda tympani is visible.

Splenial.—The splenial contacts the angular posteroventrally, the prearticular posteriorly, the coronoid dorsally, and the dentary laterally and anteriorly (MCZ 8915). The splenial is a well-developed bone that runs anteriorly along the inner part of the dentary, but bends ventrally before reaching the midline. Anteriorly both splenials meet along the midline below the suture between both dentaries, forming part of the symphysis mandibularis. Although this is a unique feature among turtles, it is seen in other amniotes such as captorhinids, the placodont *Placodus*, and pareiasaurs (Hill 2005). *Proganochelys quenstedti* has a long splenial, but both splenials never contact in the midline. In other turtles the splenial is reduced compared to *Proganochelys quenstedti* or is even absent (Gaffney 1979).

Articular area.—The articular area is preserved in many specimens, but in none the sutures between the articular and the angular, prearticular or surangular are visible. For this reason the articular area is described as a structure.

The area articularis mandibularis is well preserved in MCZ 8916. This concave area can be divided in two, equally sized concavities, one medial and the other lateral. Both concavities are separated by a small ridge; the medial concavity is located below the lateral one. In the posterior border of the medial concavity there is a small foramen interpreted herein as the foramen chorda tympani. Posteromedially to the area

articularis mandibularis a well-developed processus retroarticularis is present, which is the main attachment site for the muscle depressor mandibularis. A well-developed retroarticular process is also present in *Proganochelys quenstedti*, *Palaeochersis talampayensis*, some baenids, and trionychids (Gaffney 1979, 1990).

Discussion and comparisons

Prior to the discovery of *Kayentachelys aprix*, the fossil record of turtles was characterized by a significant gap that existed between the then known Late Triassic and Late Jurassic turtles (Gaffney et al. 1987). Other material has since been found from equivalent times in other parts of the world (Gaffney and Kitching 1995; Datta et al. 2000), but none of these compare to *Kayentachelys aprix* in the quality of preservation and the presence of both cranial and postcranial material. It is in this light that *Kayentachelys aprix* remains a central taxon when assessing early phases of turtle evolution (e.g., Dryden 1988; Gaffney 1996; Joyce 2007).

Kayentachelys aprix was originally described by Gaffney et al. (1987) as the oldest representative of the pancryptodiran clade (Cryptodira *sensu* Gaffney 1975) due to the putative presence of a processus trochlearis oticum, a processus pterygoideus externus with a posteriorly projecting flat, vertical plate, and a contact between the prefrontal and vomer. Although the use of these characters was later confirmed by some computer assisted analyses (e.g., Gaffney et al. 1991; Gaffney 1996), others have questioned the presence of these characters in *Kayentachelys aprix* or their utility in diagnosing the clade Pancryptodira Joyce, Parham, and Gauthier, 2004 versus a more inclusive clade that contains Panpleurodira Joyce, Parham, and Gauthier, 2004 as well (Dryden 1988; Sukhanov 2006; Joyce 2007; Fig. 10). These and other, perhaps phylogenetically informative characters are discussed below.

Processus pterygoideus externus.—The morphology of the processus pterygoideus externus has been utilized for systematic purposes since Gaffney (1975). He grouped all turtles with a small, laterally protruding processus pterygoideus externus with a vertical plate into the clade Pancryptodira (Cryptodira) and all turtles that possessed a trochlear system on the processus pterygoideus externus into the clade Panpleurodira (Pleurodira). The description of more fossils and the reinvestigation of extant turtles have since shown that the morphological variability of this region is far more complex (Joyce 2007). Although all known panpleurodires consistently exhibit a highly similar trochlear process on their pterygoids, the morphology of all remaining turtles is more heterogeneous. In the basal turtle *Proganochelys quenstedti*, the margin of the pterygoid has a descending process that becomes taller anteriorly (Gaffney 1990). *Palaeochersis talampayensis* is similar to *Proganochelys quenstedti* but also possesses a ridge that forms the lateral border of the fo-

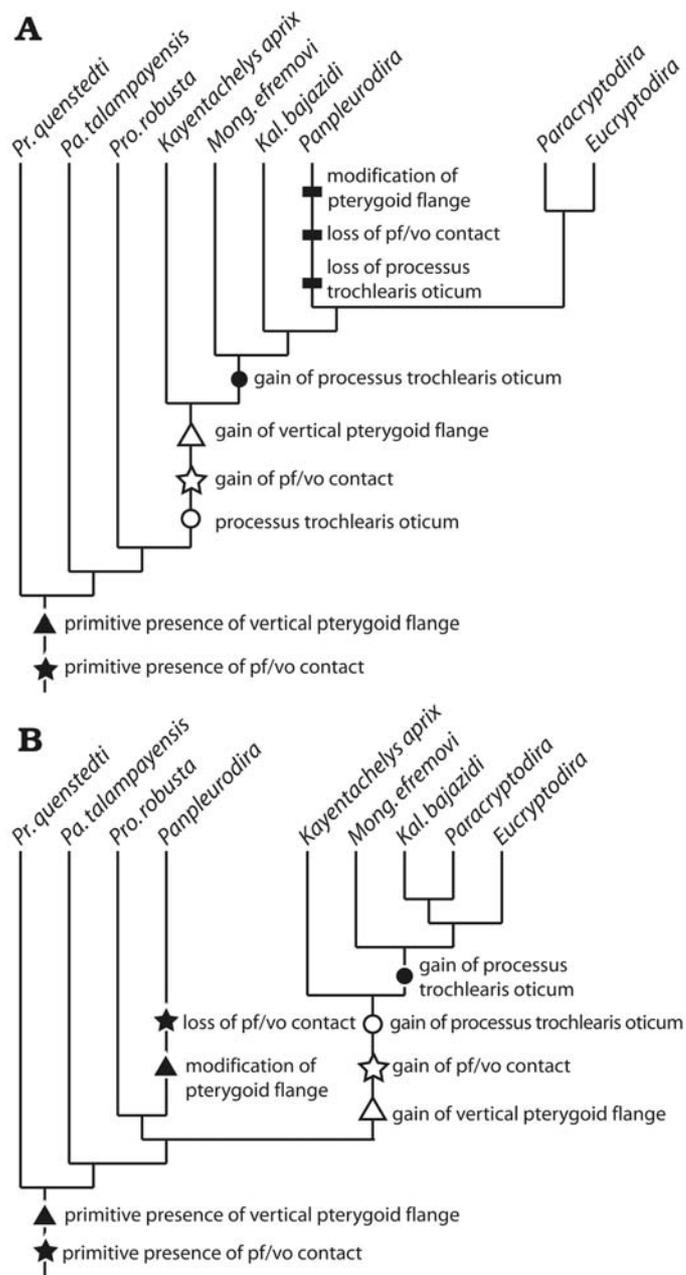


Fig. 10. Main hypotheses of turtle evolution. **A.** Joyce (2007). **B.** Gaffney et al. (2007). Outlined shapes document character evolution according to Gaffney (1996) and Gaffney et al. (2007). Solid shapes document the character evolution according to the interpretations argued in the present paper. Dashes indicate character changes that are the same in both interpretations. Abbreviations: *Kal.*, *Kallokibotia*; *Mong.*, *Mongolochelys*; *Pa.*, *Palaeocheilus*; *Pr.*, *Proganochelys*; *Pro.*, *Proterochersis*.

ramen palatinum posterius (Sterli et al. 2007). In *Kayentachelys aprix* we demonstrate the presence of a lateral protrusion, but not a distinct vertical plate. Among the Cryptodira, testudinoids and chelydrids possess highly distinct, laterally protruding vertical processes that resemble one another greatly. In trionychids, however, the vertical plate is still present, but the lateral protrusion is lacking. Conversely, kinosternids and cheloniids possess the lateral protrusion,

but lack the vertical plate. Given that phylogenetic information may indeed be extractable from the presence of different kinds of structures in the processus pterygoideus externus, we suggest that future researchers focus on defining the different states of this process to include all the variation found among turtles. Until then, the following points can safely be concluded: (1) the development of a processus trochlearis on the pterygoid of pleurodires is an unambiguous synapomorphy of that clade (Gaffney 1996; Joyce 2007; Gaffney et al. 2007); (2) considering the prevalent presence of some type of structure in the processus pterygoideus externus of basal turtles, the derived pleurodiran and cryptodiran conditions should be considered modifications from the ancestral condition and there is little reason to assume a priori that either derived condition cannot give rise to the other (Joyce 2007); (3) the processus pterygoideus externus of *K. aprix* is well developed laterally, however, it does not bear a vertical flange equivalent to that seen in some pancryptodires.

Processus trochlearis oticum.—The presence of a processus trochlearis oticum, the osteological manifestation of a trochlea on the ear capsule, was used by Gaffney (1975) as another character to unite pancryptodires (*Cryptodira sensu* Gaffney 1975) and applied as evidence to place *Kayentachelys aprix* within Pancryptodira. Based on the first complete skull with an uncrushed otic region, we conclude that *K. aprix* neither exhibits any type of protrusion that might be interpreted as a processus trochlearis oticum nor any roughening that may indicate the presence of a lubricated cartilage. However, the absence of these structures does not logically preclude that an otic trochlear system could have been present. Joyce (2007) noted this problem as well and concluded that the geometry of the skull can be used as another source of evidence, because some type of trochlear system must be present, if the otic region blocks the direct line between the origin of the temporal muscles on the mandible and its most distal insertion at the upper rim of the post-temporal opening. However, due to the lack of informative material, Joyce (2007) was not able to observe the skull geometry of *Kayentachelys aprix*. It is in this regard that the newly prepared skull TMM 43670-2 provides valuable insight, because the fully prepared temporal cavity of this three-dimensionally preserved specimen clearly indicates that the otic region did not block the temporal musculature. It is for this reason, that we confidently assert our claim that *Kayentachelys aprix* did not have an otic system.

Prefrontal vomer contact.—Another character that has repeatedly been used to place *Kayentachelys aprix* within Pancryptodira is a contact between the prefrontal and the vomer (Gaffney 1996; Gaffney et al. 1987, 1991). Although no single specimen is available that unambiguously reveals the presence of such a contact, we herein conclude that this contact must have been present, primarily because the descending process of the prefrontal is so well developed. In his phylogenetic review of basal turtles, Joyce (2007) concluded that the acquisition of a prefrontal vomer contact is a derived character that diagnoses a highly inclusive clade comprised of the crown

group and part of the stem and that the absence seen in pleurodires should be considered a secondary reversal. Interestingly, given the likely presence of a prefrontal vomer contact in *Proganochelys quenstedti* (Gaffney 1990) it appears more likely that the presence of this contact is a symplesiomorphy for all turtles. Unfortunately, in both *Palaeochersis talampayensis* and *Australochelys africanus* (Gaffney and Kitching 1995; Sterli et al. 2007) this contact is unknown because of the preservation of the available material, so this hypothesis cannot be tested further for the moment.

Epipterygoid.—Although an ossified epipterygoid is a characteristic of most cryptodiran turtles (Gaffney 1975), its presence is clearly a symplesiomorphy for turtles because of its presence in basal amniotes (e.g., Gaffney et al. 1991). An epipterygoid has been previously reported for *Proganochelys quenstedti* (Gaffney 1990) and we confirm its presence in *Kayentachelys aprix* as well. Interestingly, the morphology of the epipterygoid in *Kayentachelys aprix* more greatly resembles that of *Proganochelys quenstedti* and other amniotes (Hill 2005) than those of crown cryptodiran turtles by being rod shaped and not flat. *Meiolania platyceps*, a taxon considered by some to be a pancryptodire (Gaffney 1996; Hirayama et al. 2000; Gaffney et al. 2007) but a stem turtles by others (Joyce 2007) has a long rod-like epipterygoid as well that contacts an incipient processus inferior parietalis above. It thus appears, that *Kayentachelys aprix* and *Meiolania platyceps* bridge the morphological gap that exists between the purely rod shaped and dorsally free epipterygoid of *Proganochelys quenstedti* and the lamellar and dorsally connected epipterygoid of crown cryptodires.

Ear.—*Kayentachelys aprix* is the oldest turtle that shows the structure of the inner and middle ears and considering the placement of this taxon along the phylogenetic stem of turtles (Joyce 2007) or at the base of the turtle crown (Gaffney 1996; Gaffney et al. 2007) it may represent the primitive condition for turtles. The processus interfenestralis of the opisthotic is a robust process as in *Proganochelys quenstedti*, *Palaeochersis talampayensis*, and *Australochelys africanus* and the recessus scalae tympani is not surrounded by bone as in modern turtles. The foramen jugulare intermedium is located between the opisthotic, the basioccipital, and the exoccipital, which leads to the fenestra perilymphatica and foramen jugulare anterius. In a topologically similar location, there is a foramen recognized as the “foramen jugulare anterius” in *Proganochelys quenstedti* (Gaffney 1990) and *Palaeochersis talampayensis* (Sterli et al. 2007). Thanks to the preservation of the inner view of the cavum labyrinthicum and cavum tympani, we suggest that the foramen jugulare anterius of these Triassic turtles corresponds with the foramen jugulare intermedium and that the true foramen jugulare anterius is located more inside the skull. In modern turtles the exoccipital and the opisthotic develop the ossified posterior wall of the ear cavity, thus enclosing the recessus scalae tympani in bone. As a consequence, the recessus

scalae tympani communicates with the outside of the skull through the foramen jugulare posterius in modern turtles.

In conclusion, the skull of *Kayentachelys aprix* is characterized by a mosaic of primitive and derived character states. The presence of an interpterygoid vacuity, a basipterygoid process, a prootic that is exposed in ventral view, a foramen posterius canalis carotici interni that is formed entirely by the basisphenoid are, among others, characteristics that are considered primitive for turtles because they are also present in *Proganochelys quenstedti*, *Palaeochersis talampayensis*, and *Australochelys africanus*. However, *Kayentachelys aprix* also possesses an aperture narium externa that is not subdivided, a well developed cavum tympani, an incipient cavum postoticum, an unpaired vomer, which are considered, among others, to be derived characters. This combination of primitive and derived character states and the presence of unique characters highlight the importance of *Kayentachelys aprix* in understanding the early evolution of turtles.

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