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ANATOMY OF *CONDORCHELYS ANTIQUA* STERLI, 2008, AND THE ORIGIN OF THE MODERN JAW CLOSURE MECHANISM IN TURTLES

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ABSTRACT—Here we present a detailed anatomical description of cranial and post-cranial remains of a Jurassic turtle, *Condorchelys antiqua* Sterli, 2008, from the Cañadón Asfalto Formation (Middle Jurassic) in central Patagonia. Although *C. antiqua* is similar in morphology to the Early Jurassic turtles *Kayentachelys aprix* and *Indochelys spatulata*, it differs in that it lacks both pterygoid teeth and a V-shaped suprapygal 2, respectively. In light of new discoveries and reinterpretations of other fossil taxa, we suggest that several changes in the evolution of the skull morphology of turtles (such as the closure of the basiptyergoid articulation, the closure of the interptyergoid vacuity, the development of the secondary lateral wall in the braincase, the development of temporal emargination and/or the posterior extension of the crista supraoccipitalis) could be related to the acquisition of a stronger skull to accommodate the modern pulley system. The optimization of these characters in a phylogenetic framework shows that they are coincident with the appearance of trochlear systems (oticum or pterygoidei) in turtles, suggesting a functionally correlated relationship among them.

INTRODUCTION

Until recently, the occurrence of Jurassic turtles in Patagonia was documented only by the presence of *Notoemys laticentralis* and *Neusticemys neuquina* from the marine sequences of the Upper Jurassic Vaca Muerta Formation (Neuquén Basin) in north-western Patagonia (de la Fuente, 2007, and references therein). This scarce turtle record was augmented recently with the description of the Middle Jurassic continental turtle *Condorchelys antiqua* (Sterli, 2008). Discovery of this turtle was the result of fieldwork conducted by Dr. Guillermo Rougier (University of Louisville) and a crew of the Museo Paleontológico Egidio Feruglio (Trelew, Argentina) during the austral summers of 2001 to 2007. During these field seasons, many tetrapods were recovered from outcrops of the Cañadón Asfalto Formation at the Queso Rallado locality in Chubut Province, and include anurans, small dinosaurs, mammals, sphenodontians, and pterosaurs. Rougier et al. (2007) suggest that this bone-bearing deposit, situated in the middle part of the lower section of the formation, represents a relatively small and shallow lacustrine body placed in a supralittoral environment adjacent to the main water body of the basin.

The turtle remains found at the Queso Rallado locality became the basis of *Condorchelys antiqua*. Sterli's (2008) cladistic analysis showed that *C. antiqua* is a stem turtle (Fig. 1A) that branches from the same node as the Jurassic turtles *Kayentachelys aprix* and *Indochelys spatulata* (Gaffney et al., 1987; Datta et al., 2000). The position of *C. antiqua* among stem turtles is also supported by Anquetin et al.'s (2009) cladistic analysis. Although the main objective of this paper is to present a detailed anatomical description of *C. antiqua*, we also discuss the possibility that several modifications of the cranial morphology seen in some stem turtles could be related to the acquisition of a rigid skull. It is

interesting to note that these changes coincide with the appearance of a more complex jaw closure system, particularly the evolution of a trochlear system in chelonians.

The suprageneric names used here refer to phylogenetically defined clade names as defined by Joyce et al. (2004).

Institutional Abbreviations—**MH**, Naturhistorisches Museum, Basel, Switzerland; **MPEF-PV**, Museo Paleontológico Egidio Feruglio-Paleontología Vertebrados, Trelew, Chubut, Argentina; **UMZC**, University Museum of Zoology, Cambridge, U.K.

Anatomical Abbreviations—**bo**, basioccipital; **bp**, basitrabecular (basiptyergoid) process; **bs**, basisphenoid; **c**, costal plate; **cac**, caudal centra; **caj**, cavum acustico-jugulare; **cc**, cervical centra; **cl**, cavum labyrinthicum; **cm**, condylus mandibularis; **col**, columella auris; **con**, condylus occipitalis; **ct**, cavum tympani; **ds**, dorsum sellae; **em**, encephalic mould; **exo**, exoccipital; **fc**, foramen caroticum basisphenoidale; **fcl**, foramen caroticum laterale; **feng**, foramen externum nervi glossopharyngei; **fing**, foramen internum nervi glossopharyngei; **fja**, foramen jugulare arterius; **fji**, foramen jugulare intermedium; **fjp**, foramen jugulare posterius; **fmng**, foramen medialis nervi glossopharyngei; **fnh**, foramen nervi hypoglossi; **fo**, fenestra ovalis; **fpcci**, foramen posterior canalis carotici interni; **fpl**, fenestra perilymphatica; **fr**, frontal; **ha**, hiatus acusticus; **HU**, humeral scale; **ica**, incisura columella auris; **il**, ilium; **is**, ischium; **iv**, interptyergoid vacuity; **ju**, jugal; **la**, lacrimal; **M**, marginal scale; **mi**, muscular insertion; **mx**, maxilla; **n**, neural plate; **na**, neural arch; **nc**, neural channel; **ns**, nasal; **op**, opisthotic; **p**, peripheral plate; **pa**, parietal; **pal**, palatine; **pb**, pubis; **PE**, pectoral scale; **pf**, prefrontal; **pi**, processus interfenestralis of opisthotic; **Pl**, pleural scale; **pm**, premaxilla; **po**, postorbital; **pr**, prootic; **prz**, prezygapophysis; **pt**, pterygoid; **py**, pygal plate; **pz**, postzygapophysis; **qu**, quadrate; **rb**, rostrum basisphenoidale; **rst**, recessus scalae tympani; **so**, supraoccipital; **sp**, suprapygal plate; **sq**, squamosal; **taw**, thickening of the anterior wall of the middle ear; **tbo**, tubera basioccipitale; **tp**, transverse process; **tv**, thoracic vertebrae; **V**, vertebral scale; **vo**, vomer.

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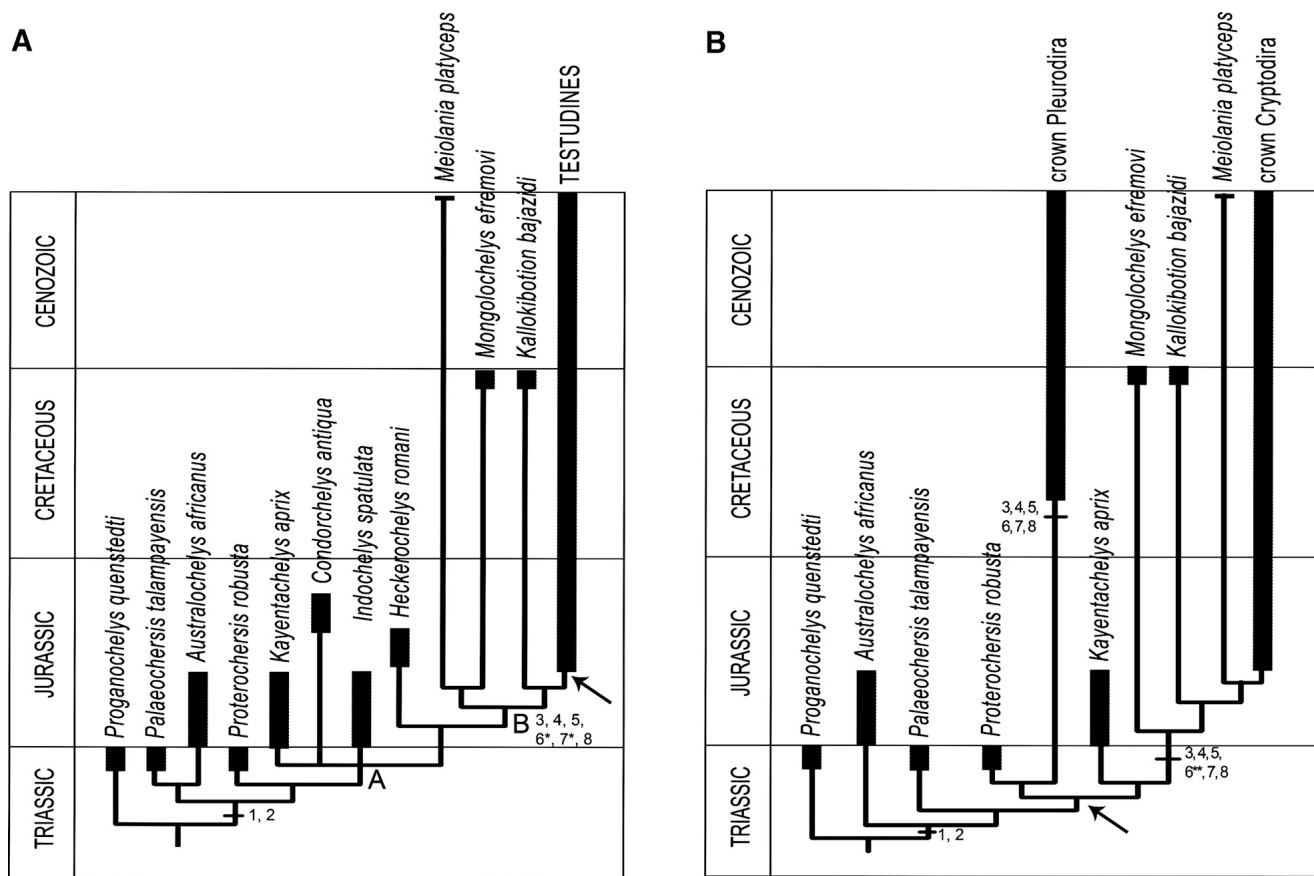


FIGURE 1. Character mapping in two phylogenetic hypotheses. **A**, Sterli (2008) tree; **B**, Gaffney et al. (2007) tree. **Abbreviations:** 1, opisthotic tightly sutured to the squamosal; 2, basitrabecular process sutured with the pterygoid; 3, basitrabecular process absent; 4, interpterygoid vacuity partially or completely closed; 5, canalis carotici interni partially or completely floored; 6, processus inferior parietalis closing foramen nervi trigemini; 7, temporal emargination present and/or crista supraoccipitalis posteriorly developed; 8, presence of a processus trochlearis (oticum or pterygoidei). Characters marked with an asterisk (*) have an ambiguous optimization on the previous node because the states of those characters are unknown for *Heckerochelys romani*. The character marked with two asterisks (**) has an ambiguous optimization because the state is unknown for *Mongolochelys efreмовi*. Triassic is not to scale. The arrow indicates the crown group.

SYSTEMATIC PALEONTOLOGY

TESTUDINATA Klein, 1760 (sensu Joyce et al., 2004)
CONDORCHELYS ANTIQUA Sterli, 2008
 (Figs. 2, 3, 5–9)

Holotype—MPEF-PV 1152, a basicranium.

Referred Material—Present in the collection of the MPEF-PV are: 1783A, B, and C, bone and a natural mould of a neural series, costal bones and thoracic vertebrae in visceral view, and fragments of plastron; 1784, 3149, 3150, and 3153, humeri; 1785A, left dentary; 1875A and B, basicranial remains in two pieces; 1998, basicranium; 3131, basicranium with skull roof; 3132, an almost complete carapace, only lacking the anterior part, with remains of caudal vertebrae; 3133, pectoral girdle; 3134, entoplastron; 3135, pelvic girdle; 3136, left hyoplastron; 3147, partial neural series and costals in visceral view; 3148, coracoid; 3151 and 3152, femora; 3154, tibia; 3155, 3156, 3157, and 3159, cervical vertebrae; 3158, caudal vertebra; 3160, carapace.

Locality and Horizon—Queso Rallado Locality, Cerro C6ndor Village, Chubut Province, Argentina (Rauhut et al., 2002), Cañad6n Asfalto Formation (Stipanovic et al., 1968), Middle Jurassic (Volkheimer et al., 2008).

Diagnosis—*Condorchelys antiqua* shares with *Proganochelys quenstedtii*, *Palaeochersis talampayensis*, *Australochelys africanus*, *Proterochersis robusta*, *Kayentachelys aprix*, and *Indochelys spatulata* (all turtles below node A in Fig. 1A) the presence of an open interpterygoid vacuity, a canalis cavernosus that is not completely floored, a thick basicranial floor, the presence of a pair of basioccipital tubera, prootics that are not covered by the pterygoid, the presence of a basipterygoid process and basisphenoid pits, the presence of a foramen caroticum basisphenoidale, the presence of the foramen jugulare intermedium, the absence of the processus trochlearis oticum or pterygoidei, broad vertebral scales that are broader than the pleural scales, the location of the vertebral 3 and 4 scale sulcus on neural 6, the presence of an anterior process of the entoplastron at least partially separating the medial contact of the epiplastra, a long posterior process of the entoplastron, and the presence of a long epipubic process. *Condorchelys antiqua* shares with more derived turtles (node A in Fig. 1A) the presence of a pterygoid that covers at least part of the canalis cavernosus, a well-developed cavum tympani with an incipient antrum postoticum, the absence of pterygoid teeth, and the presence of a triradiate pectoral girdle. *Condorchelys antiqua* differs from *Kayentachelys aprix* in the absence of pterygoid teeth and from *Indochelys spatulata* in the absence of a V-shaped suprapygial 2.

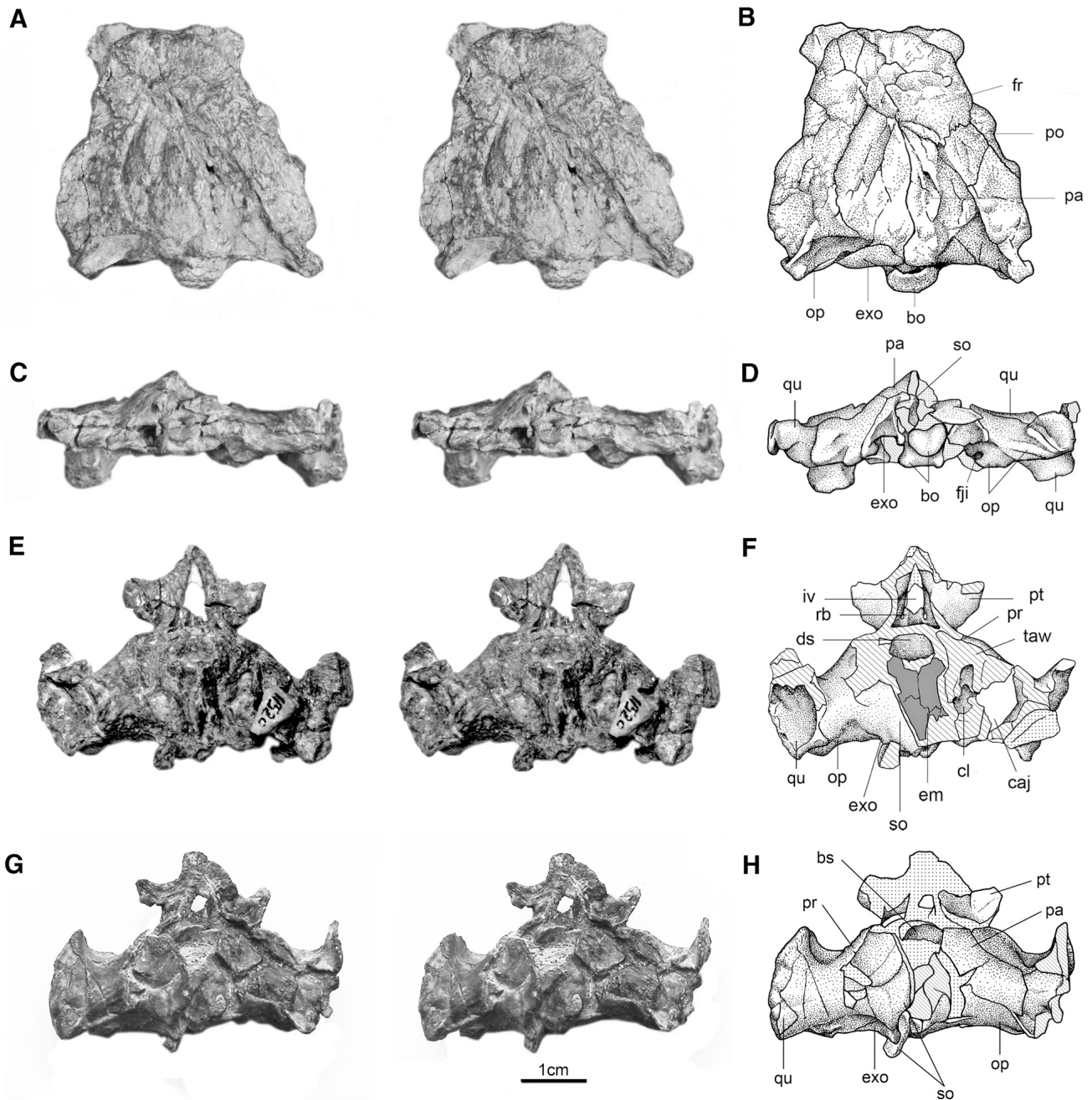


FIGURE 2. Skull of *Condorchelys antiqua*. **A**, stereophotographs and **B**, drawing of MPEF-PV 3131 in dorsal view. **C**, stereophotographs and **D**, drawing of MPEF-PV 1998 in posterior view. **E**, stereophotographs and **F**, drawing of MPEF-PV 1152 in dorsal view. **G**, stereophotographs and **H**, drawing of MPEF-PV 1998 in dorsal view.

DESCRIPTION

Skull

Four skulls of *Condorchelys antiqua* are preserved three-dimensionally. Three of them (MPEF-PV 1152, 1875A and B, and 1998) are basicrania that have lost the skull roof and the anterior region. The skull roof is known only in MPEF 3131 (Fig. 2A, B). This specimen exhibits ornamentation formed by ridges and grooves, arranged in a random pattern and similar to that found in *Kayentachelys aprix* (Sterli and Joyce, 2007). A dorsal scale pattern, if there was any, is not apparent from the available specimens.

Dermal Skull Roof—Unfortunately, none of the nasal, prefrontal, frontal, jugal, quadratojugal, or postorbital could be identified in the available material due to poor preservation. The horizontal plate of the parietal bone (MPEF-PV 1152, 1998, and 3131) forms part of the skull roof (Fig. 2A–B, G–H) and does not indicate so much as a hint of a temporal emargination, as in many turtles, including *Pr. quenstedti*, *Pa. talampayensis*, *K. aprix*, and *Chubutemys copelloi* (Gaffney et al., 1987; Gaffney, 1990; Rougier et al., 1995; Gaffney et al., 2007; Sterli et al., 2007; Sterli and Joyce, 2007). The processus inferior parietalis contacts the supraoccipital posteriorly, the quadrate laterally, and the prootic anterolaterally

(Fig. 2C, D). Given the fragmentary nature of the available skull remains, it is not possible to determine the anterior extension of the processus inferior parietalis or whether it enclosed the foramen nervi trigemini. The squamosal (MPEF-PV 1152 and 1998) contacts the processus paraoccipitalis of the opisthotic ventromedially, which is the only well-preserved contact of that bone. It is likely that the squamosal precluded the lateral exposition of the opisthotic (as it seen in all turtles except *Pr. quenstedti*) and that the squamosal contacted the quadrate ventrally and anteriorly. Furthermore, it is hard to establish whether the squamosal contributed to the formation of the cavum tympani and of the antrum postoticum, and whether a supratemporal bone was present (as in *Pr. quenstedti* and *Pa. talampayensis*) or not (as in all the remaining turtles).

Palate—No palatal elements (premaxilla, maxilla, vomer, and palatine) were found among the available specimens.

Palatoquadrate—The quadrate is preserved in MPEF-PV 1152 and 1998 (Figs. 2C–H, 3A–D). As in all turtles, the quadrate is C-shaped. It contacts the pterygoid anteromedially and the opisthotic posterolaterally, and contacts the prootic medially and the opisthotic posteriorly. The contact with the pterygoid is completely vertical and is formed by the vertical quadrate ramus of the pterygoid and the pterygoid ramus of the quadrate. The contacts with squamosal or the quadratojugal are not preserved in any specimen.

The quadrate forms many structures of the skull, including the anterior wall of the middle ear, the condylus mandibularis, and the cavum tympani. The anterior wall of the middle ear is formed in *C. antiqua* by the vertical contact between the quadrate and the pterygoid. These bones also form the posterior wall of the fossa temporalis inferior. The quadrate exhibits an anteroventral processus mandibularis, which ends in the condylus mandibularis. The condylus mandibularis is divided in two portions, both of which are flat or slightly concave. The cavum tympani in *C. antiqua* is well developed, deep, and funnel-shaped (Fig. 3C, D, I, J), as in most turtles except *Pr. quenstedti*, *Pa. talampayensis*, and *A. africanus*. Ventrally the quadrate forms the incisura columella auris, which is open as in many fossil and extant turtles.

The anterior wall of the inner ear of *C. antiqua* is thicker than in *Pr. quenstedti*, *Pa. talampayensis*, and *A. africanus*, and is similar to the condition seen in *K. aprix*. There is no development of a processus trochlearis oticum, however, as is the case in many pancryptodiran turtles, or a roughened area, as in *Meiolania platyceps* and *Mongolochelys efremovi* (Gaffney, 1983; Sukhanov, 2000) (Fig. 4A–D; see discussion in Joyce, 2007; Sterli and Joyce, 2007).

There are no preserved epipterygoid remains in any available specimens of *C. antiqua*. However, in the dorsal portion of the pterygoid (MPEF-PV 1152), there is a contact or broken surface that could have been produced by a dorsal contact either with an epipterygoid, through an ossification of the orbital cartilage and the pila antotica ('pleurosphenoid' of Gaffney, 1990), or with a well developed processus inferior parietalis.

The pterygoid (MPEF-PV 1152 and 1998) contacts the basisphenoid posteriorly and the quadrate laterally. In general morphology, it resembles that of *Kayentachelys aprix* and turtles more basal than node B (Fig. 1A). The pterygoid has an anteriorly directed palatine process, a laterally directed transverse process, and a posterolaterally directed quadrate process (Fig. 3A–D). The pterygoids meet each other along the midline. This medial contact is reduced as in *Pr. quenstedti* and less extensive as in *K. aprix*. *Condorchelys antiqua* has an open interpterygoid vacuity as in *Pr. quenstedti*, *Pa. talampayensis*, *A. africanus*, *K. aprix*, and *Heckerochelys romani*. In all remaining turtles (all turtles above node B in Fig. 1A), this vacuity is closed by the medial contact of both pterygoids and the development of the basisphenoid (or parabasisphenoid, see Discussion). The transverse process of the pterygoid is thick and well developed laterally, but

it does not bear a posterior process, vertical flange, or processus trochlearis pterygoidei. The quadrate ramus is directed posterolaterally and a horizontal plate is directed posteriorly. At the place where these two structures diverge, there is a tear-shaped concavity into which the pterygoid muscles may have inserted (Brinkman and Wu, 1999). This concavity is also present in turtles such as *K. aprix*, *Dracocheilus bicuspidis*, *Hangaiemys hobuensis*, and some baenids (Gaffney, 1982; Gaffney and Ye, 1992; Sterli and Joyce, 2007). The quadrate ramus is a vertical flange, as in more basal turtles than node B (Fig. 1A), and contacts the pterygoid ramus of the quadrate posteriorly through a vertical contact (Fig. 3A–D). This contact extends laterally almost to the condylus mandibularis. The posterior extension of the horizontal plate of the pterygoid cannot be established with confidence because of the poor preservation. As a result of the lack of broken surfaces in the quadrate ramus of the pterygoid, it is likely that if the plate was developed, it was not extensive. The morphology of this area resembles that of *K. aprix* where there is a posteriorly directed horizontal plate that encloses, at least partially, the canalis cavernosus. All of the available specimens show that there are no pterygoid teeth in *C. antiqua*, differing from *Pr. quenstedti* and *K. aprix*.

Braincase—The supraoccipital (MPEF-PV 1998 and 3131) contacts the opisthotic ventrolaterally, the exoccipital ventromedially, and the parietal anteriorly (Fig. 2C, D). Given that these specimens are highly deformed, it is not possible to establish the participation of the supraoccipital in the foramen magnum. The crista supraoccipitalis does not extend posteriorly to the foramen magnum. The exoccipital (MPEF-PV 1152, 1998, and 3131) contacts the opisthotic laterally, the supraoccipital dorsally, and the basioccipital ventrally (Fig. 2C, D). This last contact is not clearly seen in any of the specimens, possibly because the exoccipitals and the basioccipital are fused, as in the condylus occipitalis of many turtles (Siebenrock, 1897). The exoccipital forms the lateral border of the foramen magnum, but the morphology of this foramen cannot be determined because the surrounding bones collapsed during compaction. In posterior and ventral view, a large foramen is seen between the exoccipital, the opisthotic, and the basioccipital, but neither is a ventral process of the exoccipital and/or the opisthotic developed nor is the processus interferenstalis of the opisthotic reduced in size (Fig. 3G, H). The morphology of these structures resembles those of *K. aprix* and turtles more basal than node B (Fig. 1A) and the foramen is interpreted as the foramen jugulare intermedium (Sterli and Joyce, 2007; 'foramen metoticum' of Rieppel, 1980). The vena jugulare and cranial nerves X and XI exited the skull through this foramen. In the exoccipital of MPEF-PV 3131, only one foramen is apparent for the exit of cranial nerve XII. The basioccipital (MPEF-PV 1152, 1875A and B, 1998, and 3131) contacts the exoccipital dorsally, the opisthotic laterally, and the basisphenoid anteriorly (Fig. 2C, D). The contact with the prootic is not clearly seen. As described above, it is likely that the basioccipital forms part of the condylus occipitalis, but the suture with the exoccipital is not apparent. In the middle of the basioccipital, a pair of posteriorly directed tubera basioccipitalis is seen in ventral view (Fig. 3A–F), as in *Pa. talampayensis* and *K. aprix*, which could have served as attachment sites for the neck musculature (Gaffney, 1979). Between these tubera there is an anteriorly directed, semilunar concavity, which also may have served for muscle attachment. Although the basioccipital and the basisphenoid of *C. antiqua* are thick elements, as in *K. aprix*, they are not as thick as in Triassic turtles or as thin as in crown-group turtles. The morphology found in *C. antiqua*, *K. aprix*, and *Eileanchelys waldmani* seems to be intermediate between both conditions. Although the prootic is preserved in several specimens (MPEF-PV 1152, 1875A and B, and 1998), its margins are hard to establish (Fig. 3A–D). The contact with the opisthotic can be inferred in MPEF-PV 3131 in the right fenestra ovalis, because this fenestra is surrounded

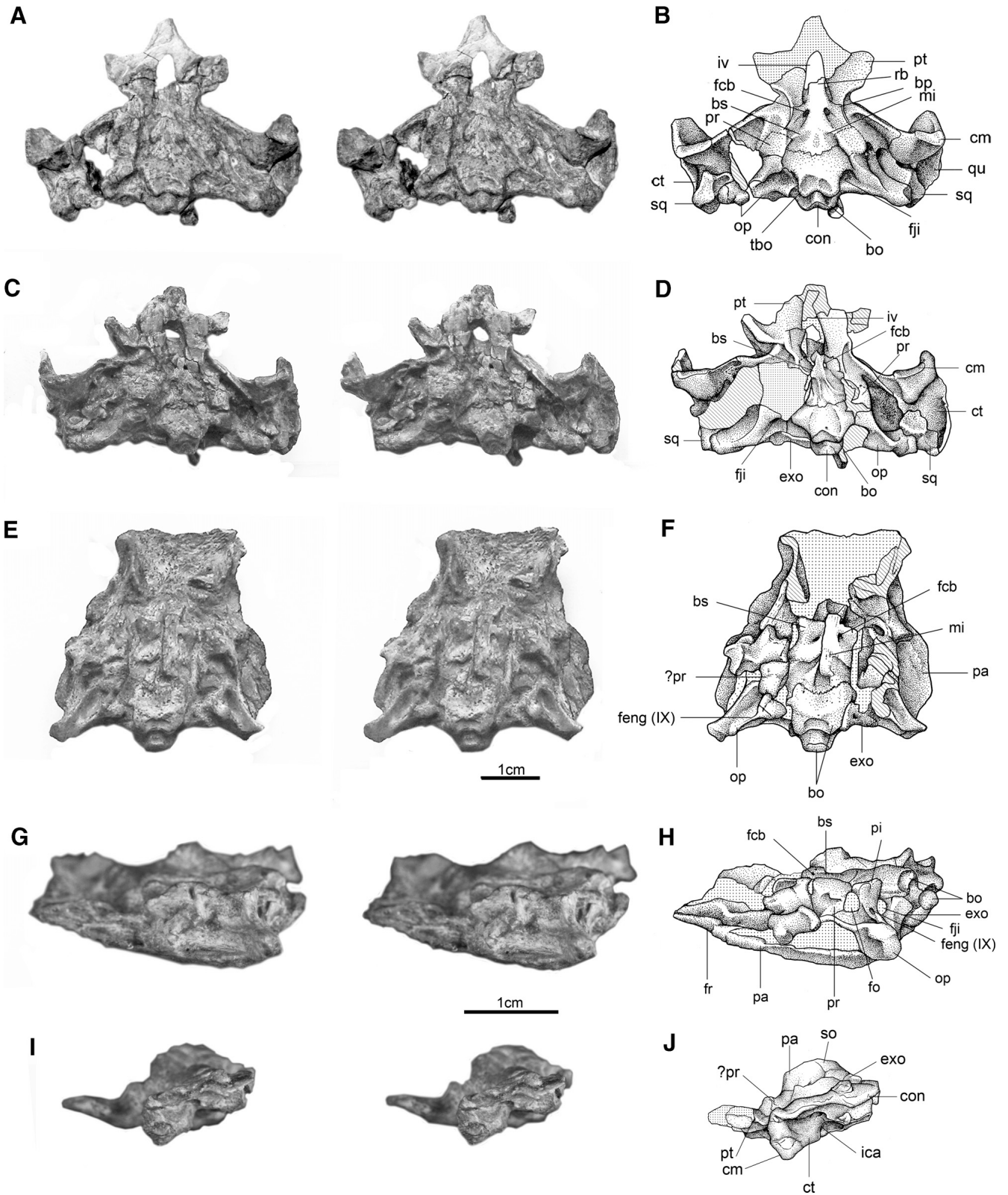


FIGURE 3. Skull of *Condorchelys antiqua*. **A**, stereophotographs and **B**, drawing of MPEF-PV 1152 in ventral view. **C**, stereophotographs and **D**, drawing of MPEF-PV 1998 in ventral view. **E**, stereophotographs and **F**, drawing of MPEF-PV 3131 in ventral view. **G**, stereophotographs and **H**, drawing of MPEF-PV 3131 in oblique ventrolateral view. **I**, stereophotographs and **J**, drawing of MPEF-PV 1998 in left lateral view.

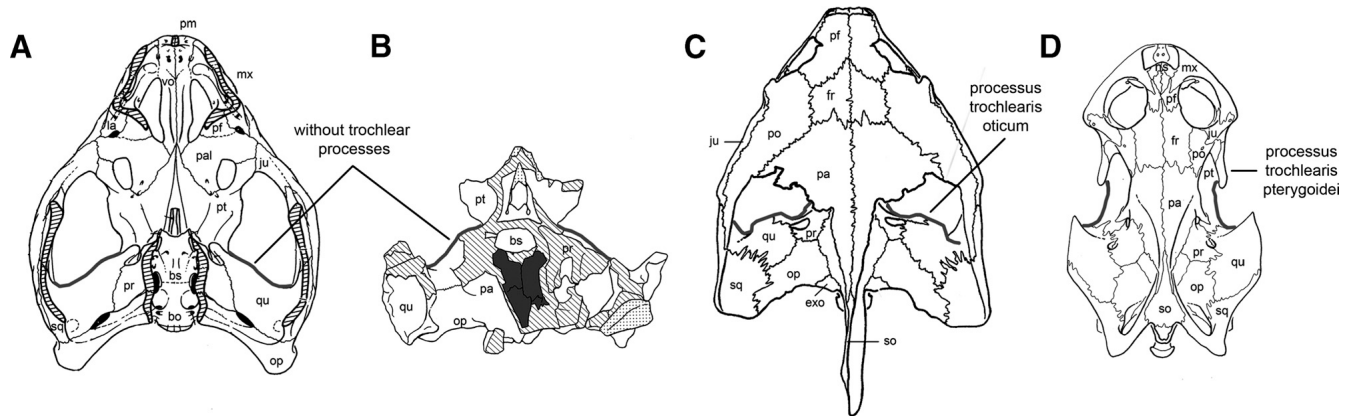


FIGURE 4. Comparison of the inferior temporal fenestra in turtles. **A**, *Proganochelys quenstedtii* (modified from Gaffney, 1990); **B**, *Condorchelys antiqua* (MPEF-PV 1152); **C**, *Chelydra serpentina* (modified from Gaffney, 1979); **D**, *Hydromedusa tectifera* (modified from Gaffney, 1977).

by the prootic and the opisthotic in all turtles (Gaffney, 1979). As mentioned before, the anterior wall of the prootic and the quadrate is thicker than in *Pr. quenstedtii* and *Pa. talampayensis*, but there is no development of a processus trochlearis oticum (Fig. 2E–H, 3A–D). In anterodorsal view of MPEF-PV 1998, it is apparent that the prootic and the pterygoid form the ossified canalis cavernosus dorsally and ventrally, respectively.

The opisthotic (MPEF-PV 1152, 1875A and B, 1998, and 3131) contacts the basioccipital medially, the exoccipital dorsomedially, the prootic anteromedially, the quadrate anteriorly, and the squamosal laterally (Figs. 2A–D, 3A–D). The posterior part of the opisthotic develops an incipient ventral process that partially encloses the recessus scalae tympani, as in *Pr. quenstedtii*, *Pa. talampayensis*, *A. africanus*, and *K. aprix*. In many pancryptodiran turtles this ventral process is well developed and forms, together with the development of the exoccipital, the enclosed recessus scalae tympani and the foramen jugulare posterius. In panpleurodiran turtles, the posterior wall of the recessus scalae tympani remains mainly cartilaginous. Another feature present in the opisthotic is the processus interfenestralis of the opisthotic, which is a robust structure in *C. antiqua* as in turtles more basal than *Heckerochelys romani*. This process is identified by the presence of the foramen for the nervi glossopharyngei (IX) that is seen in MPEF-PV 3131. In turtles crownwards of *H. romani*, this process is reduced. As it was described above, the opisthotic together with the exoccipital and the basioccipital forms the border of the foramen jugulare intermedium.

The basisphenoid (MPEF-PV 1152, 1875A and B, 1998, and 3131) contacts the pterygoid anterolaterally, the prootic laterally, and the basioccipital posteriorly (Fig. 3A–F). This last contact is not clearly seen and both bones may be fused, as in *K. aprix*. The basisphenoid has a pentagonal shape in ventral view and is longer than wide, although its length cannot be precisely determined because the rostrum basisphenoidale is broken. In the anterior part of the main body of the basisphenoid, there is a pair of ventral basitrabecular (basiterygoid) processes. In *Pr. quenstedtii*, the basitrabecular processes are present but not sutured to the pterygoid. In *Condorchelys antiqua*, each process is tightly sutured to the pterygoid, as seen in *Pa. talampayensis*, *A. africanus*, *K. aprix*, and *Ordosemys* sp. Based on personal observations, the basitrabecular process of *Pleurosternon bullockii* (UMZC-T1041), identified by Evans and Kemp (1975), is reinterpreted here as absent. In more derived turtles (node B in Fig. 1A), there are no remains of this process and the basisphenoid and the pterygoid are sutured along all their entire contact (i.e., the interpterygoid vacuity is closed). In ventral view, there is a pair of foramina caroticum basisphenoidale (see Discussion)

that are located anteriorly between the basitrabecular processes. This condition is also present in *Pr. quenstedtii*, *K. aprix*, and *H. romani* (Gaffney, 1990; Gaffney et al., 1987; Sukhanov, 2006). Posterolateral to each foramen there is a groove that could represent the path of the cerebral artery before entering the skull. As the interpterygoid vacuity remains open in *Condorchelys antiqua* and there is no evidence of the presence of other foramina in the ventral view, it is likely that the palatine artery entered the skull through the interpterygoid vacuity and not through an enclosed foramen caroticum lateralis (Gaffney and Meylan, 1992). Posterior to the foramen caroticum basisphenoidale there are two teardrop-like scars, which could have served as muscle attachment as was proposed for *Ordosemys liaoxiensis* and *Judithemys sukhanovi* (Parham and Hutchison, 2003; Tong et al., 2004).

Mandible

The only jaw element preserved is a left dentary (MPEF-PV 1785A) that bears a moderately developed coronoid process posteriorly. Various nutritive foramina are present in the form of small pores to elongated grooves.

Carapace

The description of the carapace is primarily based on MPEF-PV 3132, although additional information is obtained from MPEF-PV 3147, 1783A and B, and 3160 (Fig. 5A–D). The general shape of the carapace cannot be established with certitude because the anterior part is missing, but it is clear that the outline is not serrated as in *Pr. quenstedtii* or *Platycheilus oberndorferi* (Fig. 5A, B). The length of the carapace could have attained 20 cm. The carapace exhibits a fine ornamentation of small pits and a central ridge that begins at neural 4 and ends in neural 8.

Bony Plates—The nuchal is not preserved in any of the available specimens. Neural 1 (MPEF-PV 3147) contacts neural 2 posteriorly through a concave posterior border, and contacts costals 1 and 2 through a convex lateral border. Neural 2 (MPEF-PV 3147) is the smallest element of the series and is rectangular, being longer than wide. It contacts costal 2 laterally via a straight border and neural 3 posteriorly via a convex border (Fig. 5A–D). Neural 3 (MPEF-PV 3132 and 3147) has a hexagonal shape and is longer than wide. It contacts costals 2 and 3 laterally and neural 4 posteriorly. Neural 4 (MPEF-PV 3132 and 3147) has a hexagonal shape and is slightly longer than wide. It contacts costals 3 and 4 laterally and neural 5 posteriorly. Neural 5 (MPEF-PV 3132 and 3147) is also hexagonal and

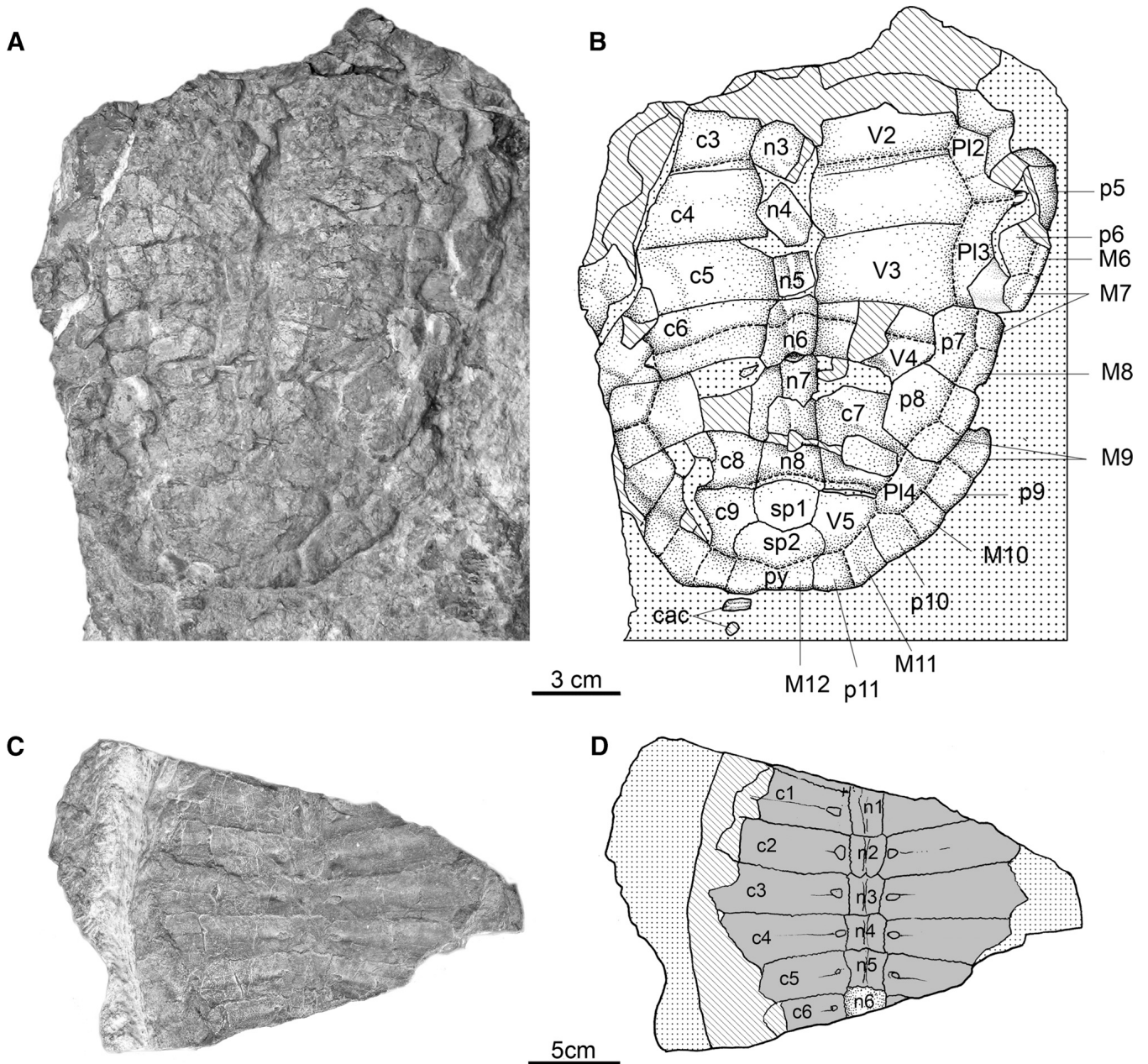


FIGURE 5. Carapace of *Condorchelys antiqua*. **A**, photograph and **B**, drawing of MPEF-PV 3132 in dorsal view. **C**, photograph and **D**, drawing of MPEF-PV 3147 in ventral view.

is as long as wide. It contacts through convex borders costals 4 and 5 laterally and neural 6 posteriorly. Neural 6 (MPEF-PV 3132 and 3147) has a rectangular shape, being longer than wide, and contacts costals 5 and 6 laterally and neural 7 posteriorly. Neural 7 (MPEF-PV 3132 and 3147) is not well preserved and its shape cannot be discerned. It contacts costals 6 and 7 laterally, but its contact with neural 8 is not seen in any specimen. Neural 8 (MPEF-PV 3132 and 3160) is rectangular, being wider than long, and contacts suprapygal 1 posteriorly and costal 8 laterally. In specimen MPEF-PV 3132, there are two medial elements posteriorly to neural 8, identified here as suprapygals 1 and 2. Suprapygal 1 is rectangular (wider than long) and contacts suprapygal 2 posteriorly, and laterally makes contact

with an element that is located posteriorly to costal 8 that could perhaps be the costal 9. Suprapygal 2 has a trapezoidal shape and is wider than long. It contacts the peripheral 11 and the pygal posteriorly. The costal series is almost complete in MPEF-PV 1783A, 3132, and 3147, and lacks only the anterior part of costal 1. The presence of a ninth pair of costals in *C. antiqua* is unique among turtles (Fig. 5A–D). Gaffney et al. (1987) mentioned the presence of a ninth costal in *K. aprix*, but it is not corroborated by Joyce and Sterli (unpubl. data). The contacts of the costals with the peripherals are described below. Each costal contacts the preceding costal anteriorly and the following costal posteriorly. Costals 1–4 curve slightly anteriorly, whereas the more posterior costals curve slightly posteriorly. All costals are wider than long, except

the last one, which is as wide as long. The peg-like distal rib end of costal 4 indicates that the costals likely inserted into sockets formed by the peripherals.

The peripheral series (Fig. 5A–B) is incompletely preserved with only peripherals 5–11 being available in MPEF-PV 3132. Peripherals 5–8 are displaced from their natural position. For this reason, the contacts of these peripherals with costals are somewhat speculative. The anterior part of peripheral 5 is missing, but it is likely that it contacted costal 3 and perhaps also costal 4 medially. Posteriorly, peripheral 5 contacted peripheral 6. The anterior portions of peripherals 6–8 are wider than their posterior portions. These elements produce a sinuous medial contact with the costals. Peripheral 6 contacted costals 4 and 5 medially and peripheral 7 posteriorly. Peripheral 7 contacted costals 5 and 6 medially and peripheral 8 posteriorly. Peripheral 8 likely contacted costals 6 and 7 medially and peripheral 9 posteriorly. Peripheral 9 would contact costals 7 and 8 medially and peripheral 10 posteriorly. Peripheral 10 contacts costals 8 and 9 medially and peripheral 11 posteriorly. Peripheral 11 contacts costal 9 anteriorly, pygal medially, and suprapygal 2 anteromedially.

Scales—The scale pattern is preserved almost completely in MPEF-PV 3132 (Fig. 5A–B). Only the cervical, vertebral 1, pleural 1, and marginals 1–5 are not present. Vertebral scales are wider than long, as in stem turtles. Vertebral 2 contacts at least pleural 2 laterally and vertebral 3 posteriorly. The sulcus between vertebrals 2 and 3 is located on the posterior part of costal 3 and perhaps it crossed neural 3. Vertebral 3 contacts pleurals 2 and 3 laterally and vertebral 4 posteriorly. The sulcus between vertebrals 3 and 4 is located on the middle of costal 6 and neural 6. Vertebral 4 laterally contacts pleural 4 and maybe pleural 3 and vertebral 5 posteriorly. The sulcus between vertebrals 4 and 5 is located on the posterior part of costal 8 and neural 8. Vertebral 5 contacts pleural 4 and marginals 10 and 11. Pleural scales are longer than wide, which is correlated with broad vertebral scales. Pleurals 2–4 are preserved, but the anterior part of pleural 2 is missing. Unfortunately, the lateral contacts of pleurals 2 and 3 cannot be determined with confidence because of poor preservation. It is apparent, however, that the sulcus between this scale and pleural 3 is located on costal 4. Pleural 4 contacts marginals 9–11 laterally. Marginals 1–5 are missing. The remaining marginals are longer than wide and located only on the peripherals. Marginals 6–8 are very narrow and resemble the marginals 5–6 of *K. aprix* and 4–8 of *Sichuanchelys chowi*. The sulcus between marginals 6 and 7 is located on peripheral 6. Marginal 7 is located on peripherals 6 and 7 and the sulcus between this scale and marginal 8 is located on peripheral 7. Marginal 8 is located on peripherals 7 and 8 and the sulcus between this scale and marginal 9 is located on peripheral 8. Marginal 9 is located on peripherals 8 and 9, and marginal 10 is located on peripherals 9 and 10. Marginal 11 is located on peripherals 10 and 11, and marginal 12 is located on peripheral 11 and the pygal. The medial contact between both marginals 12 is not preserved.

Plastron

Bony Plates—No complete plastron was found. As suggested by the dentate morphology of the contact area of the available specimens, the sutures between plastral elements were weak. The ornamentation is formed by pits that in some places are enlarged forming small randomly arranged grooves (MPEF-PV 3136). The entoplastron (MPEF-PV 3134) is almost complete and only lacks its ends. It is cruciform and twice as long as wide (Fig. 6A, B). The entoplastron has a well-developed anterior process that hinders, partially or completely, the medial contact between both epiplastra. This anterior process is also present in *Pr. quenstedtii*, *Pa. talampayensis*, *K. aprix*, and *I. spatulata*. The entoplastron also has a well-developed and narrow posterior process that

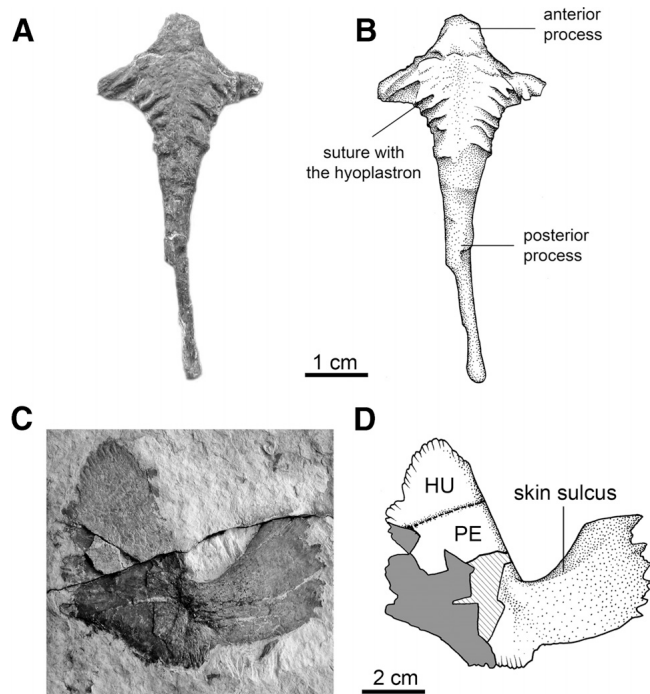


FIGURE 6. Plastron of *Condorchelys antiqua*. **A**, photograph and **B**, drawing of entoplastron of MPEF-PV 3134 in ventral view. **C**, photograph and **D**, drawing of left hyoplastron of MPEF-PV 3136 in ventral view.

resembles that of *Pr. quenstedtii* and *Pa. talampayensis*. A posterolateral process is present. Posterolaterally, the entoplastron contacts the hyoplastron along an interdigitated suture, which is oblique, resulting in the entoplastron appearing smaller in ventral view than in visceral view. The suture with the epiplastra seems to be straight and is not oblique. In visceral view, the entoplastron shows a roughened area, which could represent the articulation with the cleithrum as proposed by Joyce et al. (2006) for *K. aprix*, following Jaekel's (1915) ideas. The hyoplastron (MPEF-PV 3136) can be divided as in all turtles into a horizontal medial plate and a lateral plate that is part of the bridge (Fig. 6C, D). The contacts of the hyoplastron with the epiplastron and the entoplastron are interdigitated. The presence of a straight border and a thinner plate in the medial part of the hyoplastron could be the result of a remnant medial plastral fenestra. In the right hyoplastron MPEF-PV 1783C, a foramen for the musk ducts (Rathke's glands) is seen in the anterior part of the axillar bridge. The foramen for the musk ducts of *C. antiqua* is included in the plastron, as in *Siamochelys peninsularis*, but in the latter, the foramina are present in the mesoplastron and in the hypoplastron as well (Tong et al., 2002). In other Jurassic turtles, such as *K. aprix*, *Xinjiangchelys latimarginalis*, and *Platychelys oberndorferi*, these foramina are located between the plastron and the peripherals (Peng and Brinkman, 1993; Weldon and Gaffney, 1998).

Scales—The only preserved sulcus is on the hyoplastron of MPEF-PV 3136. This sulcus represents the limit between humeral and pectoral scales and is almost perpendicular to the plastral midline.

Vertebral Column

All available cervical vertebrae were found isolated and for this reason their position in the cervical column cannot be established with confidence. There are four specimens that could be identified as cervical vertebrae (MPEF-PV 3155, 3156, 3157, and

3159). All of them are amphicoelous, as in stem turtles in general. The anterior central articulation of MPEF-PV 3155 (Fig. 7A–J) is circular, whereas the posterior articular surface is more triangular. Ventrally it bears a short keel that is more developed posteriorly. The transverse process is located laterally in the middle of the vertebral body. Anteroventrally to the transverse process, there is a convexity that represents the ventral articulation with the double-headed cervical ribs. It cannot be established, however, if the ribs were fused or not, as in the posterior cervical vertebrae of *Pr. quenstedti*. The neural arch is well developed and is taller than the vertebral body. The development of the neural arch and the position of transverse process of this vertebra are similar to that found in the sixth or seventh cervical vertebra of *Pr. quenstedti* and *Pa. talampayensis*. For these reasons, MPEF-PV 3155 is recognized tentatively as a sixth or seventh cervical vertebrae. The remaining vertebrae are similar to MPEF-PV 3155, but the transverse processes are missing, which makes it difficult to establish their position in the cervical column.

The description of the thoracic vertebrae and ribs is based on MPEF-PV 1783A. Only the fifth to tenth thoracic vertebrae and second to ninth ribs are preserved. The thoracic vertebrae have an hourglass-shape, their anterior and posterior ends are flat, and they decrease in size posteriorly. At least the last five vertebrae contact only one pair of thoracic ribs (Fig. 8A, B), as in *Pa. talampayensis* (Sterli et al., 2007: fig. 8A, B), but contrary to the condition found in most other turtles, each vertebra contacts two pairs of ribs (Gaffney, 1990). No sacral vertebrae are preserved. Caudal vertebrae are seen in MPEF-PV 3132 and 3158 (Fig. 7K–N). The anterior ends of the vertebral bodies are flat, circular, and bear a long transverse process and short neural arch. The presence or absence of an articulation with chevron bones cannot be determined.

Pectoral Girdle

The pectoral girdle of *Condorchelys antiqua* (MPEF-PV 3133) is triradiate as it is in modern and some stem turtles (e.g., *Kayentachelys aprix*), but contrary to the condition found in Triassic turtles. The dorsal process of the scapula is long and decreases in size towards the dorsal end. The acromion process is broken. The coracoid (MPEF-PV 3133 and 3148) has a rod-like proximal end and flat distal end, and is expanded laterally.

Pelvic Girdle

The description of the pelvic girdle is based on the specimen MPEF-PV 3135 (Fig. 9A, B). As in many turtles, except in Panpleurodira, *Pa. talampayensis*, and *P. robusta*, the pelvic girdle of *Condorchelys antiqua* is not sutured to the carapace. The ilium is so fragmentary that its description is not possible. The ischium contacts the pubis anteriorly and the other ischium medially, but the contact with the ilium is not preserved. Between the ischium and the pubis, the thyroid fenestra is developed. The thyroid fenestrae do not contact one another along the midline because the ischium and the pubis contact each other, as in *Pr. quenstedti* and some testudinids (e.g., *Chelonoidis chilensis*). Posteromedially, there is a long process similar to that found in *X. qiguensis* (Matzke et al., 2004). This structure could be a posteromedial process of the ischium or could be a residual hypischium. The hypischium is a paired or odd-numbered structure found in Triassic turtles that articulates with the ischium. Posterolaterally, the ischium develops a triangular process (posterolateral process) that narrows distally. This process is similar to that found in *K. aprix* and modern cryptodires. The pubes contact each other along the midline, whereas the contact with the ilium is not preserved. Anteromedially, the pubis develops an ossified epipubic process, as exhibited by *Pr. quenstedti*, *Pa. talampayensis*, *K. aprix*, *X. latimarginalis*, and baenids. Anterolaterally

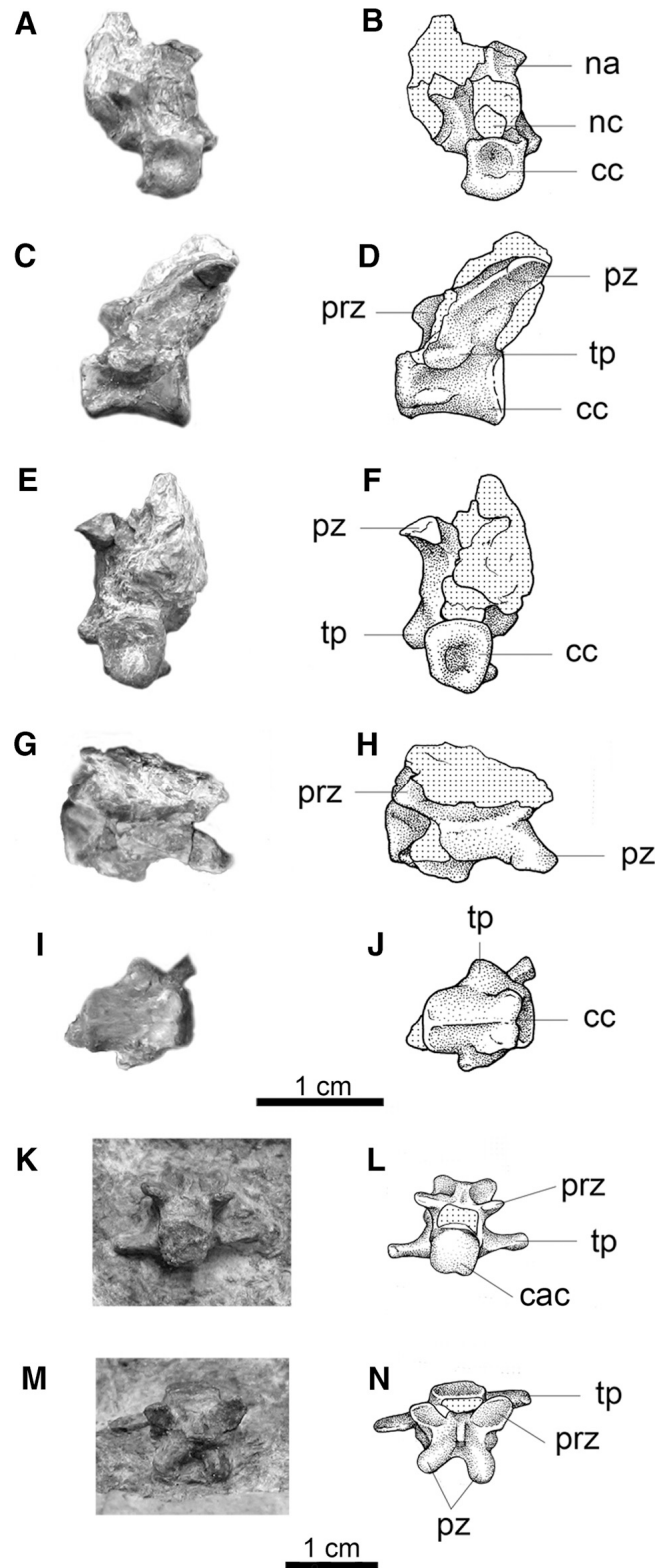


FIGURE 7. Cervical and caudal vertebrae of *Condorchelys antiqua*. **A**, photograph and **B**, drawing of a cervical vertebra of MPEF-PV 3155 in anterior view. **C**, photograph and **D**, drawing of MPEF-PV 3155 in left lateral view. **E**, photograph and **F**, drawing of MPEF-PV 3155 in posterior view. **G**, photograph and **H**, drawing of MPEF-PV 3155 in dorsal view. **I**, photograph and **J**, drawing of MPEF-PV 3155 in ventral view. **K**, photograph and **L**, drawing of a caudal vertebra of MPEF-PV 3158 in anterior view. **M**, photograph and **N**, drawing of MPEF-PV 3158 in dorsal view.

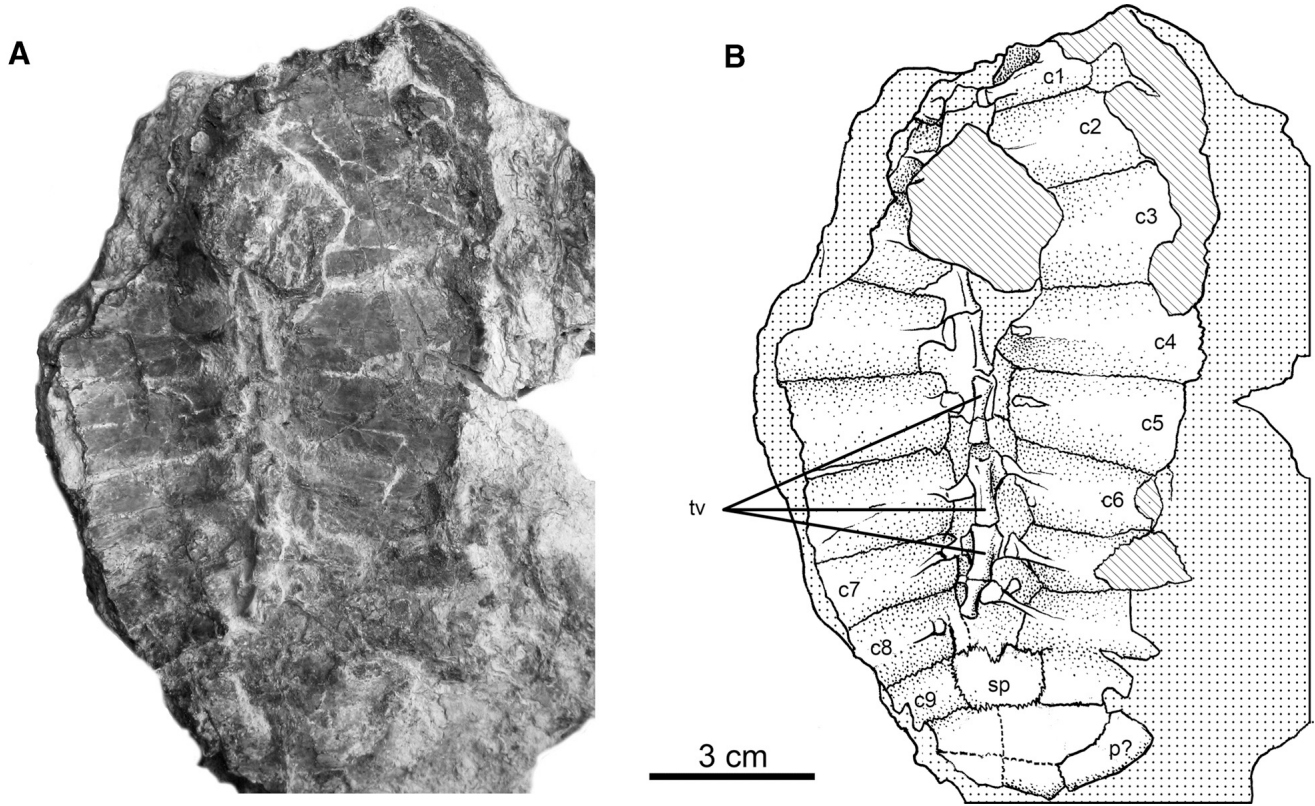


FIGURE 8. Carapace and thoracic vertebrae of *Condorchelys antiqua*. **A**, photograph and **B**, drawing of MPEF-PV 1783A in ventral view.

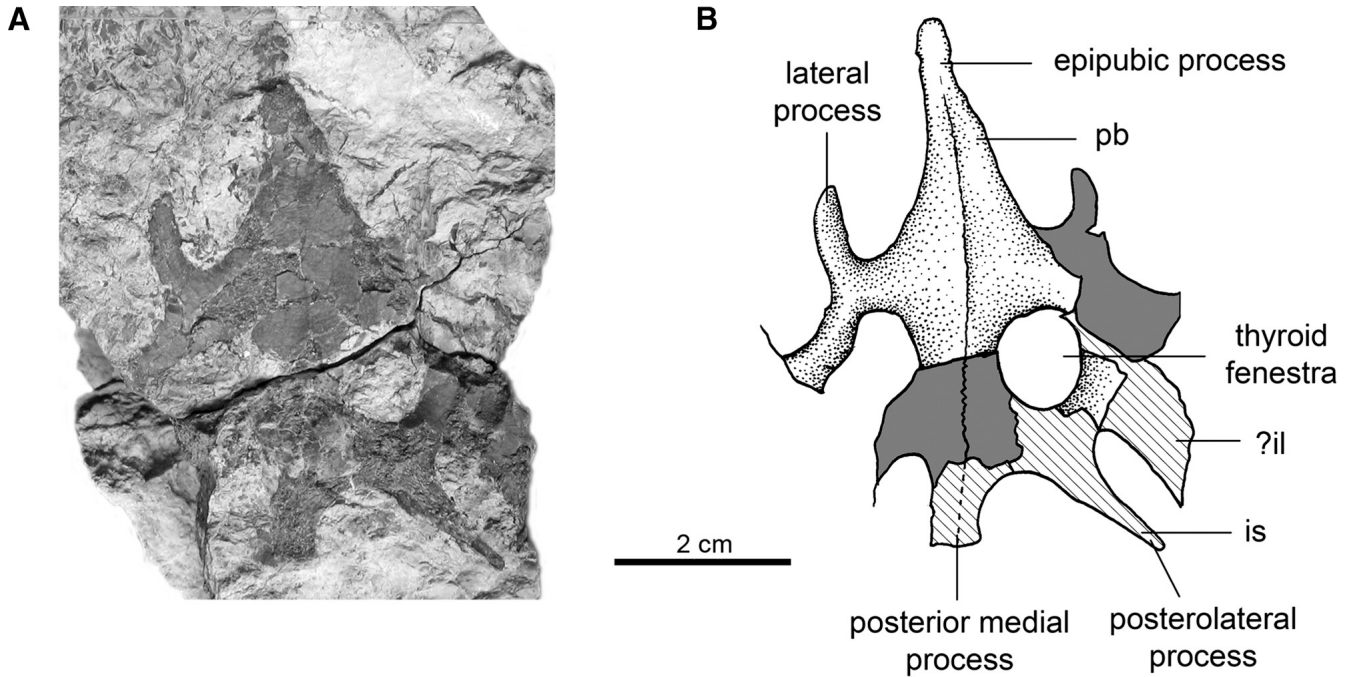


FIGURE 9. Pelvic girdle of *Condorchelys antiqua*. **A**, photograph and **B**, drawing of MPEF-PV 3135 in dorsal view.

the pubis bears a lateral process that is one-third shorter than the epipubic process.

Forelimb

Only a few humeri are preserved (MPEF-PV 1784, 3149, 3150, and 3153). The general shape resembles that of *K. aprix*, being intermediate between the robust humeri of Triassic turtles and the slender humeri of modern taxa. Both ends of the humerus are expanded. The proximal end forms the articular head with the shoulder girdle, the medial process, the lateral process, and the small shoulder or shelf (Gaffney, 1990:fig. 149). The distal end is less expanded than the proximal end and has the trochlear and capitular processes developed. A groove is seen in the ectepicondyle that ends in an ectepicondylar foramen. This foramen is also found *Pr. quenstedti*, *Pa. talampayensis*, and *K. aprix*.

Hind Limb

Only two proximal femoral ends (MPEF-PV 3151 and 3152) and one tibia (MPEF-PV 3154) were found. The articular head of the femur is developed proximodistally and it is continuous with the trochanter major. The trochanter minor is well developed and is located ventral and posterior to the articular head. The proximal end of the tibia is more expanded laterally and anteroposteriorly than the distal end. The ridge for the patellar tendon is well developed. The distal end of the tibia bears a convex medial area and a flat lateral area that articulates with the astragalocalcaneum.

DISCUSSION

During the last few years, one of the main topics in turtle evolution has been the timing of the origin of crown-group turtles (= Testudines sensu Joyce et al. 2004). Two main hypotheses can be discussed in a cladistic framework.

The first cladistic analysis was performed by Gaffney (1975) and developed by the same author in a series of later contributions (Gaffney et al., 2007, and references therein). Gaffney's hypothesis suggests that all turtles, with the exception of *Pr. quenstedti*, *Pa. talampayensis*, and *A. africanus*, are members of one of the two main groups of modern turtles, Cryptodira or Pleurodira. According to this hypothesis, the origin of crown-group turtles occurred during the Upper Triassic, coincident with the first appearance of turtles, which is based on the interpretation that *Proterochersis robusta*, from the Late Triassic, is a stem pleurodire. The alternative hypothesis, as proposed by Joyce (2007) and expanded upon by Sterli (2008), suggests that many fossil turtles previously considered to be crown-group turtles are instead stem-group turtles. Examples of these turtles are *K. aprix* and *P. robusta* (the position of the last taxon outside of Pleurodira was proposed previously by Rougier et al., 1995). This hypothesis suggests that the origin of crown-group turtles was more recent, during the Middle to Late Jurassic, as was suggested and discussed by Danilov and Parham (2008, and literature therein cited) and Anquetin et al. (2009).

Another difference between these hypotheses pertains to the evolution of some key characters, mainly those that were originally considered to be synapomorphies of Cryptodira and Pleurodira. The synapomorphies of Cryptodira proposed by Gaffney (1975) include the presence of a processus trochlearis oticum, a vertical flange on the transverse process of the pterygoid, and the presence of an epipterygoid. The alternative view (Joyce, 2007; Sterli and Joyce, 2007) suggests that the presence of a vertical flange on the pterygoid and the presence of an epipterygoid should instead be considered symplesiomorphies for turtles. Moreover, the presence of a processus trochlearis oticum would be a synapomorphy of a more inclusive clade than Cryptodira (Joyce, 2007).

It is in this context that the detailed study of the cranial anatomy of *Kayentachelys aprix* and *Condorchelys antiqua*, both from the Jurassic, provides new insights about turtle evolution. *Kayentachelys aprix* was originally proposed as the oldest pancryptodiran turtle by Gaffney et al. (1987) because of the presence of a processus trochlearis oticum, among other characters. However, Sterli and Joyce (2007) disagreed and pointed out that the anterior wall of the otic region of *K. aprix* is thicker than in *Pr. quenstedti*, but does not develop a processus trochlearis oticum per se. The same morphology present in *K. aprix* is also found in *C. antiqua* (Fig. 4A–C). The cladistic analysis performed by Sterli (2008) suggests that this new taxon from the Jurassic of Patagonia is phylogenetically close to *K. aprix*. Consequently, the discovery of new fossil turtle taxa from the Triassic and Jurassic, for example *C. antiqua*, gives new information about the first steps in turtle evolution and it allows us to reinterpret some characters and to test the competing hypotheses about turtle evolution.

The following discussion is divided into three sections. The first two are related to the evolution of two particular cranial features: the processus interfenestralis of opisthotic and the arterial pattern. The third item relates to the distribution and evolution of the trochlear process. In the last, we suggest that several structures found in the turtle skull could be related with the development of the processus trochlearis.

Evolution of the Processus Interfenestralis of the Opisthotic

The morphology of the processus interfenestralis of the opisthotic in most basal turtles differs from that seen in more derived ones. In *Condorchelys antiqua* node and more basal turtles, the process is a robust structure that is seen in ventral and posterior views, recognizable because it is pierced by the foramen for the glossopharyngeal nerve (IX). In these turtles there is no development of a posterior ventral process of the exoccipital or opisthotic, and consequently the posterior part of the recessus scalae tympani is not ossified (Fig. 10A); the foramen that communicates between the unossified recessus scalae tympani and both the cavum cranii and the cavum labyrinthicum is the foramen jugulare intermedium (Sterli and Joyce, 2007). In all the turtles crownwards of *H. romani* (clade B in Fig. 1A), including the recently described *E. waldmani*, the processus interfenestralis of the opisthotic is reduced in size and becomes a smaller process that projects ventrally from the roof of the middle ear (Gaffney, 1979; Rieppel, 1980). However, two main morphologies can be identified among these turtles. In some basal turtles and some more derived turtles (e.g., the pleurodires, *Plesiochelys etalloni*, *Kallokibotion bajazidi*, *E. waldmani*), there is no development of the posterior wall of the opisthotic, and the exoccipital and the recessus scalae tympani remains unossified (Fig. 10B). On the contrary, in the cryptodiran lineage (Gaffney, 1979), the posterior wall of the recessus scalae tympani ossifies and encloses the recessus scalae tympani in bone posteriorly, thus delimiting the fenestra postotica and the foramen jugulare posterius (except in cheloniid turtles) (Fig. 10C).

Evolution of the Arterial Pattern

The recent discoveries of fossil taxa have shown that the history of the cranial arterial pattern is far more complex than previously thought. We provide here a summary of the main patterns. Turtles exhibit two broad forms of carotid circulation. The first group includes those turtles in which the split between the cerebral and palatine arteries is floored by bone and consequently situated inside the skull (Fig. 11A, B). The second group includes those turtles where this bifurcation is not covered ventrally by bone (Fig. 11C–E).

Inside the first group, three main variations in the arterial pattern can be identified. The first, termed here pattern I, is characterized by a closed interpterygoid vacuity, and a posterior

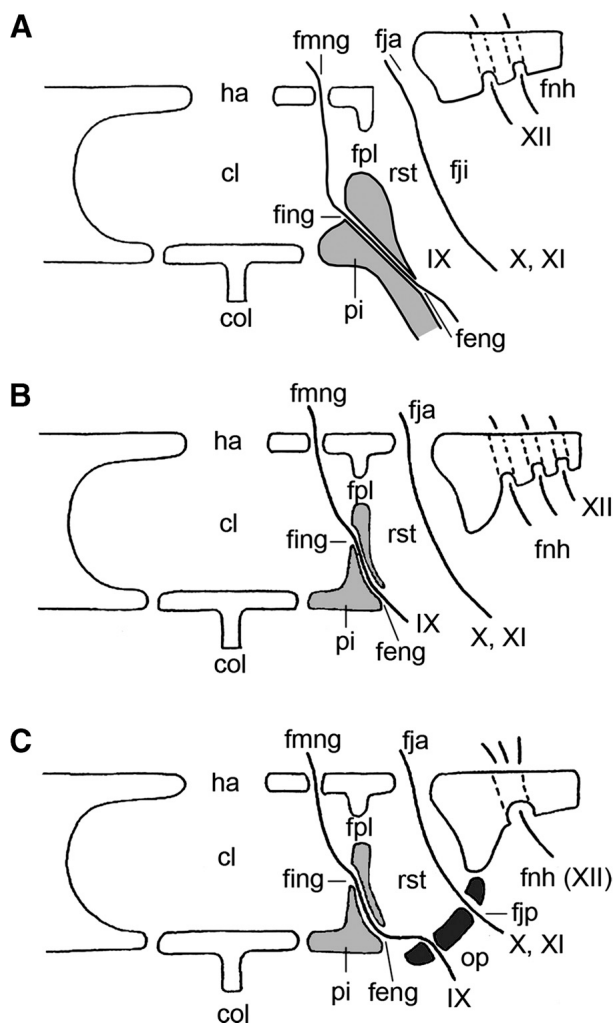


FIGURE 10. Comparison of the recessus scalae tympani of different turtles in horizontal section. **A**, condition in Late Triassic and Early to Middle Jurassic turtles; **B**, condition in Late Jurassic turtles from Europe, e.g., *Thalassemys marina* (modified from Rieppel, 1980); **C**, condition in modern turtles (modified from Rieppel, 1980).

extension of the pterygoid, and an entrance of the internal carotid that is located at the far posterior end of the pterygoid (Fig. 11A). This pattern is seen in crown Cryptodira and in some closely related fossil turtles (e.g., plesiochelyids). Although the arterial pattern of extant non-marine cryptodiran turtles is variable (Jamniczky and Russell, 2007; Jamniczky, 2008), the differences are not as radical as they are between the different groups of fossil turtles. Pattern II comprises turtles with the foramen posterior canalis carotici interni formed midway along the basisphenoid-ptyergoid suture. This kind of arterial circulation is found in baenids (Fig. 11B). The last kind of arterial pattern of the first group, pattern III, is seen in pleurodiran turtles, in which the foramen posterior canalis carotici interni is formed by the basisphenoid and the prootic.

Inside the second group, in which the division between the cerebral and palatine artery is not floored by bone, there are three main variations. The first, termed here pattern IV (Fig. 11C), is found in those Jurassic to Paleogene turtles from Asia and North America known as 'sinemyids' and 'macrobaenids.' In these turtles, the pterygoid expands posteriorly and the posterior foramen for the entrance of the internal carotid

inside the skull (foramen posterior canalis carotici interni) is located in the posterior part of the pterygoid. Although the pterygoid is well developed posteriorly, the floor of the canalis carotici interni is thin and, in some regions of the bone, is not complete. In addition, because the interptyergoid vacuity is closed by the pterygoid and the basisphenoid (or parabasisphenoid, see below), two pairs of foramina are seen in ventral view. The foramina located in the basisphenoid are called foramen caroticus basisphenoidale (Gaffney, 1983), and are interpreted as the entrance of the cerebral and maxillary artery to the skull, whereas the foramina formed by the pterygoid and the basisphenoid are interpreted as the posterior opening of the canalis caroticum lateralis through which the palatine artery runs (Brinkman and Nicholls, 1993; Brinkman and Wu, 1999). The next pattern in the second group, termed here pattern V, is found in *Kallokibotion bajazidi* and *Mongolochelys efremovi* (Fig. 11D) and it differs from pattern IV in that there is no foramen posterior canalis carotici interni; there are only the foramen caroticum basisphenoidale and foramen caroticum lateralis. The final pattern (VI) is found in *Proganochelys quenstedti*, *Kayentachelys aprix*, *Heckerochelys romani*, and *Condorchelys antiqua*, and presumably in *Pa. talampayensis* and *A. africanus*. In these taxa, there is a pair of foramina in the ventral surface of the endochondral basisphenoid and the interptyergoid vacuity is open (Fig. 11E). We reinterpret both foramina present in the basisphenoid of Triassic and Early–Middle Jurassic turtles as non-homologous with the foramina posterior canalis carotici interni of other turtles (as it was interpreted by Gaffney et al., 1987, 2007; Sterli and Joyce, 2007; Sterli, 2008), but the foramen caroticum basisphenoidale of 'sinemyids' and 'macrobaenids.' We postulate that the cerebral and the maxillary arteries (medial branch of the internal carotid) could have entered the skull through these foramina, whereas the palatal artery (lateral branch of the internal carotid) could have entered the skull via the interptyergoid vacuity (Gaffney and Meylan, 1992).

Evolution of Cranial Features Related to the Processus Trochlearis

As a result of important discoveries of Mesozoic turtles during the last 20 years and the development of cladistic methodology, we suggest that the presence of the pulley system for the jaw closure mechanism in modern turtles is accompanied by modification of several cranial features. In the following paragraphs, we present several changes in skull morphology that could have caused a more rigid skull.

Interptyergoid Vacuity—The interptyergoid vacuity is closed in all turtles except *Proganochelys quenstedti*, *Palaeochersis talampayensis*, *Australochelys africanus*, *Kayentachelys aprix*, *Condorchelys antiqua*, and *Heckerochelys romani*. The interptyergoid vacuity is closed in later turtles by a more extensive contact between both pterygoids and by the anterior development of the basisphenoid (or parabasisphenoid). During the embryological development of modern cryptodires, the basisphenoid is formed by endochondral bone (basisphenoid sensu stricto) and the dermal parasphenoid, resulting in a composite bone called the parabasisphenoid (Sheil, 2003, 2005; Sheil and Greenbaum, 2005). Personal observations on some fossil turtles (*Plesiochelys etalloni* [MH 435] and *Pleurosternon bullockii* [UMZC-T1041]) suggest to us that two different bones are fused in the basisphenoid region. Similar observations have been made on other tetrapods (Shishkin, 1968; Rieppel, 1993). We suggest that it is the more extensive ossification of the parasphenoid that could have closed the interptyergoid vacuity and that could have trapped the internal carotid between this bone and the basisphenoid, producing, together with the posterior expansion of the pterygoid, the various kinds of arterial patterns described above.

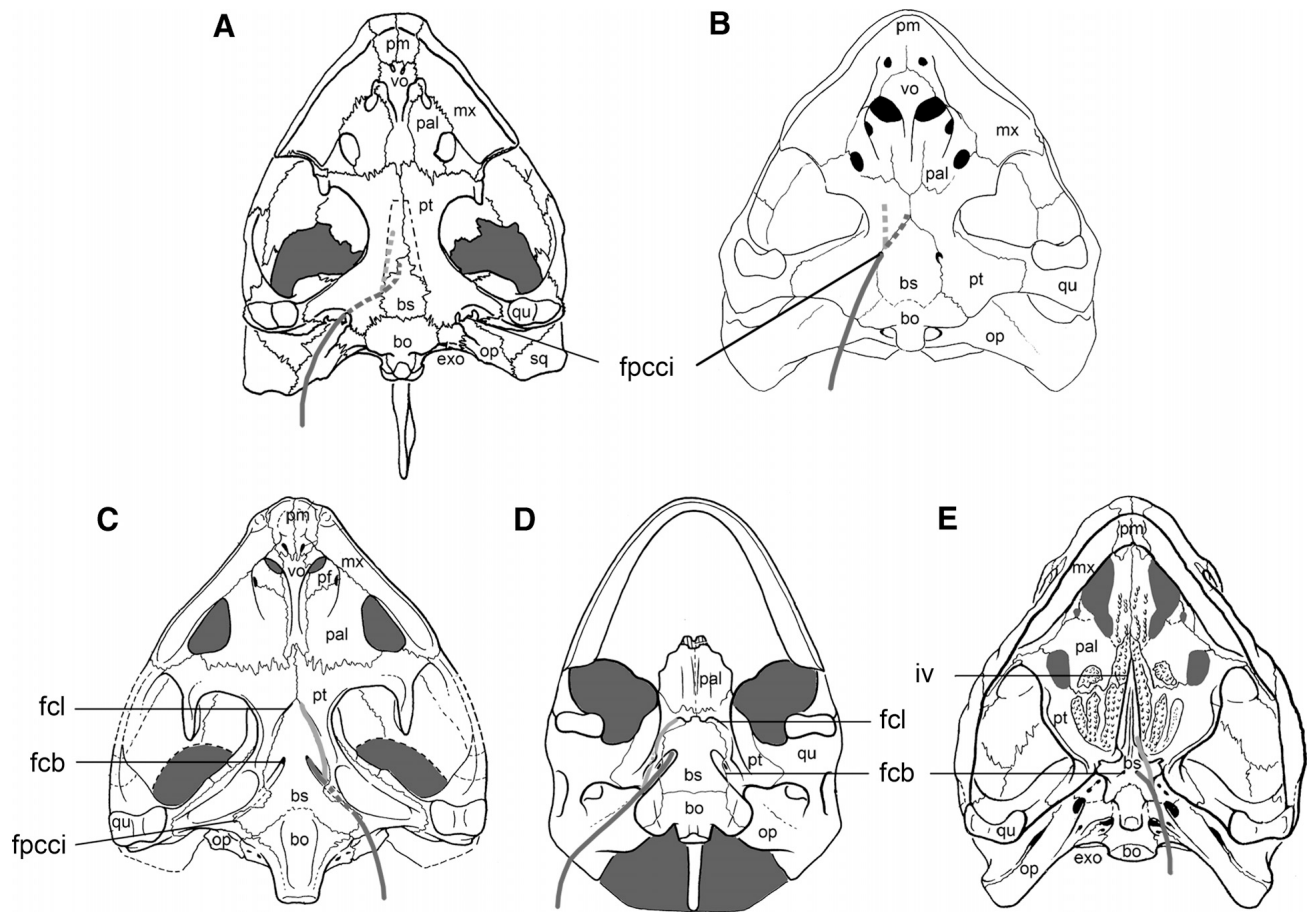


FIGURE 11. Comparison of the arterial skull pattern in turtles. **A**, pattern I, exemplified by *Chelydra serpentina* (modified from Gaffney, 1979); **B**, pattern II, exemplified by *Baena arenosa* (modified from Gaffney, 1972); **C**, pattern IV, exemplified by *Dracochelys bicuspis* (modified from Gaffney and Ye, 1992); **D**, pattern V, exemplified by *Kallokiboton bajazidi* (modified from Gaffney and Meylan, 1992); **E**, pattern VI, exemplified by *Proganochelys quenstedtii* (modified from Gaffney, 1990).

The closure of the interpterygoid vacuity allows a more extensive contact between an element of the braincase (basisphenoid) and one of the palate (pterygoid), reducing the relative movement between the bones and increasing the strength of the skull. This feature is directly correlated with the reduction of the basitrabecular processes of the basisphenoid (see below).

Basipterygoid Articulation—Another important change during turtle evolution resulting in strengthening of the skull is the closure of the basipterygoid articulation (Gaffney, 1975) and the reduction of the basitrabecular process. In turtles more basal than node B (Fig. 1A), there are a paired basitrabecular (basipterygoid) processes in the anterior region of the basisphenoid body. Each basitrabecular process fits into a pocket in the pterygoid. In all turtles, except *Proganochelys quenstedtii*, the basipterygoid articulation is closed, producing an akinetic skull. In turtles above node B in Figure 1A, the processes are lost and the remnants of the basipterygoid articulation disappear completely.

Correlated with this feature are the posterior extension of the pterygoid in pancryptodiran and some stem turtles and the development of the extensive suture between the prootic and the quadrate in pleurodiran turtles. In turtles more basal than node B (Fig. 1A) and in *E. waldmani*, the quadrate ramus of the pterygoid is a vertical plate that is sutured to the quadrate anteriorly. In these turtles, the canalis cavernosus is partially covered ventrally by the pterygoid. In more derived turtles, there

are two kinds of closure of the canalis cavernosus that stabilize the relationship between the elements of the neurocranium (basisphenoid, basioccipital, prootic) and the palate and the palatoquadrate (pterygoid, quadrate). In pleurodiran turtles, the quadrate and the prootic contact each other through a large suture flooring the canalis cavernosus (Gaffney, 1979). In pancryptodiran turtles, robustness is gained by the development of a horizontal plate of the pterygoid between its quadrate ramus and its main body (Gaffney, 1979). This horizontal plate contacts the basisphenoid medially, and in some taxa it extends further posteriorly contacting the basioccipital and even the exoccipital (e.g., *Solnhofia parsonsi*).

Extensive Contact Between the Skull Roof and the Basicranium—A more extensive contact between the elements of the skull roof (parietal, postorbital, squamosal) and the basicranium and palate (prootic, opisthotic, epipterygoid, pterygoid) is obtained in turtles in several ways. One way is the tight suture between the opisthotic and the squamosal in all turtles, except *Proganochelys quenstedtii* (Gaffney, 1990). Another way is the development of the secondary lateral wall in the braincase. A cavum epiptericum enclosed by a secondary lateral braincase wall is characteristic of a few amniote groups (e.g., mammals, some squamate groups, and turtles). The secondary lateral wall is formed in modern turtles by the descending process of the parietal and the laminar epipterygoid (in Cryptodira) or by the

former only (in Pleurodira). In the basalmost known turtles, the ventral process of the parietal does not extend anteriorly further than the foramen prooticum. The epipterygoid in these turtles is rod-like and is not attached dorsally to the skull roof (Gaffney, 1990; Sterli and Joyce, 2007). As a result, the cavum epipticum (or secondary brain cavity) is open (Gaffney, 1990).

In addition to the secondary wall of the braincase, the contact between the basicranium and the skull roof in pleurodiran turtles is reinforced by a contact between the pterygoid and the postorbital. This contact allows the pterygoid to be firmly braced against the skull roof and to support the processus trochlearis pterygoidei (Joyce, 2007).

The modern morphology of the braincase wall found in more derived turtles not only results in the closure of the cavum epipticum, but also in an akinetic skull.

Development of Temporal Emargination and the Crista Supraoccipitalis—The presence of temporal emargination and/or a posteriorly developed crista supraoccipitalis in turtles is generally correlated with the development of the adductor jaw musculature (Schumacher, 1973). The development of the trochlea and the shift in the orientation of the muscle fibers is related to a hypertrophy of the otic chamber in turtles (Schumacher, 1973; Gaffney, 1975; Joyce, 2007). In those turtles with a posteriorly directed crista supraoccipitalis, the adductor musculature originating from the crista produces a horizontal force that is changed into a vertical force (away from the coronoid process of the lower jaw) at the trochlea (Schumacher, 1973). The development of temporal emargination provides more space for increasing muscle volume. In some fossil turtles and in modern turtles, it is frequently found that some of these two traits are present or even both together (e.g., *Chelydra serpentina*, *Elseya latisternum*). For example, in *Glyptops plicatus* and in *Pleurosternon bullockii*, there is a temporal emargination, but the crista supraoccipitalis is not developed, whereas in *Meiolania platyceps*, *Mongolochelys efremovi*, and cheloniids, the skull roof has no temporal emargination, but a well-developed crista supraoccipitalis is present. It is interesting to note that turtles below node B (Fig. 1A) do not show either temporal emargination or a posterior development of the crista supraoccipitalis. In addition, in these turtles the otic chamber is not in the way of the adductor musculature and they do not have a processus trochlearis (Sterli and Joyce, 2007). Consequently, it is inferred that in these turtles the adductor musculature of the jaw is not as developed as in modern turtles.

Development of the Pulley System—Many of the features listed above (i.e., the tight suture between the opisthotic and the squamosal, closure of the interpterygoid vacuity, loss of the basitrabecular processes, posterior development of the pterygoid, and more extensive contact between the skull roof elements and the neurocranium) generally strengthen the skull, prohibit skull kinesis, and firmly brace those elements that support the trochlea (quadrate and prootic in pancryptodires, pterygoid in pleurodires) against the rest of the skull. On the other hand, the posterior development of the crista supraoccipitalis and of the temporal emarginations are related to an expansion (in volume) of the adductor muscle. Consequently, increasing strength of the skull is accompanied by the appearance of certain structures that allow a larger volume of adductor musculature to be developed.

The majority of the changes listed above occurred between the origin of the turtle Bauplan (Late Triassic) and node B (Fig. 1A), which can be dated to the Middle to Late Jurassic, and it appears to have resulted in a more rigid skull. It is interesting to note that in turtles with an open interpterygoid vacuity, basitrabecular process, short connection between the skull roof, posterior extension of the pterygoid, and the basicranium, and a relatively poorly developed otic chamber, no processus trochlearis is developed. This basal morphology is found in *Proganochelys*

quenstedti, *Palaeochersis talampayensis*, *Australochelys africanus*, *Kayentachelys aprix*, *Condorchelys antiqua*, and *Heckerochelys romani*. The closure of the interpterygoid vacuity, the fusion of the basiptyergoid joint and the reduction of basitrabecular process, the posterior extension of the pterygoid, the presence of temporal fenestration and/or the posterior development of the crista supraoccipitalis, and the more extensive contact between the skull roof and the basicranium through the development of the descending process of the parietal and, in some cases, the incorporation of the epipterygoid produce a more robust skull. As it turns out, all of these structures could be related to the appearance of the processus trochlearis. As shown in the Sterli (2008) and Gaffney et al. (2007) phylogenies (Fig. 1), these features optimize at the same node as the appearance of the processus trochlearis, independent of which phylogenetic hypothesis of turtle evolution is preferred. This could suggest that the apparent correlation among those characters may actually be independent of the phylogenetic hypothesis, giving support to the fact that those characters could be correlated to the acquisition of trochlear processes and not to the preferred hypothesis. Although the optimization of those characters in both phylogenies (Fig. 1) is at the same node as the optimization of the presence of the processus trochlearis, the optimization in Sterli's (2008) phylogeny (Fig. 1A) is more parsimonious than in Gaffney et al.'s (2007) phylogeny (Fig. 1B). It is interesting to note that, if the relationship among those characters is functionally correlated, the independence of those characters should be evaluated more carefully in future cladistic analysis.

As mentioned above, the processus trochlearis is related to the adductor muscles and, in turn, adductor muscles are related to feeding. The increase in volume of the adductor muscles and all related changes in the skull could have resulted in more efficient processing of food and bite performance. Improvements in bite performance could have allowed turtles to invade new niches or expand their range of diets (see Herrel et al., 2002, and references therein). As evidence in support of the idea that evolutionary radiations could have followed the acquisition of anatomical innovations (Carroll, 1997), we suggest that the appearance of this new structure (the processus trochlearis) could have aided the rapid radiation shown by molecular (Shaffer et al., 1997) and morphological (Parham and Hutchison, 2003; Danilov and Parham, 2006) phylogenetic analyses of turtle evolution. The oldest turtles involved in the radiation are from the Middle to Upper Jurassic, dating the radiation to no later than the Upper Jurassic. Moreover, the oldest turtles with an unequivocal processus trochlearis come from the Upper Jurassic. All currently available evidence suggests that the Jurassic period is very important for understanding the origin and evolution of modern turtles.

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