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Palaeontology

A new, nearly complete stem turtle from the Jurassic of South America with implications for turtle evolution

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Turtles have been known since the Upper Triassic (210 Myr old); however, fossils recording the first steps of turtle evolution are scarce and often fragmentary. As a consequence, one of the main questions is whether living turtles (Testudines) originated during the Late Triassic (210 Myr old) or during the Middle to Late Jurassic (*ca* 160 Myr old). The discovery of the new fossil turtle, *Condorchelys antiqua* gen. et sp. nov., from the Middle to Upper Jurassic (*ca* 160–146 Myr old) of South America (Patagonia, Argentina), presented here sheds new light on early turtle evolution. An updated cladistic analysis of turtles shows that *C. antiqua* and other fossil turtles are not crown turtles, but stem turtles. This cladistic analysis also shows that stem turtles were more diverse than previously thought, and that until the Middle to Upper Jurassic there were turtles without the modern jaw closure mechanism.

Keywords: Testudinata; anatomy; phylogeny; Cañadón Asfalto Formation; Cerro Cóndor

1. INTRODUCTION

Although the oldest undoubted turtles are known from the Upper Triassic (Baur 1887; Fraas 1913; Broin 1985; Jenkins *et al.* 1994; Rougier *et al.* 1995), the turtle record until the Upper Jurassic is fragmentary and sparse, with only few known species spread around the world (Gaffney *et al.* 1987; Datta *et al.* 2000; Sukhanov 2000, 2006; Tong *et al.* 2002; Matzke *et al.* 2004). On the other hand, the Jurassic period is a key time for turtle evolution, as is shown by the two main hypotheses of turtle evolution. Gaffney's hypothesis (Gaffney *et al.* 2007 and references therein) suggests that all fossils and extant turtles (with the exception of *Proganochelys quenstedti*, *Palaeochersis talampayensis* and *Australochelys africanus*) are part of the turtle crown group (=Testudines *sensu* Joyce *et al.* 2004), and thus belong to either of the two primary living clades of turtles, Pleurodira or Cryptodira. As a consequence of this phylogeny, the turtle crown is estimated to have originated in the Late Triassic, as soon as turtles appeared in the fossil record. On the contrary, the other hypotheses (Rougier *et al.* 1995; Sukhanov 2006; Joyce 2007) suggest that numerous Mesozoic turtles should rather be considered as a part of the turtle stem group, and that the crown group Testudines originated in the uppermost part of the Middle Jurassic. It is in this context that this new, nearly complete turtle from the Middle to Upper Jurassic Cañadón Asfalto Formation from Patagonia, Argentina, becomes important, giving new insights into this controversy. A revised phylogenetic analysis of turtles, including this taxon, is also presented here.

2. MATERIAL AND METHODS

The new Jurassic turtle, *Condorchelys antiqua* gen. et sp. nov. (figure 1*a*–*d*), was included in a dataset of 74 taxa and 150 characters. Although this dataset is based on the matrix of Joyce (2007), several changes were undertaken, in particular the addition of 14 characters as well as seven taxa, including *C. antiqua* (see the electronic supplementary material). Moreover, the coding of several taxa, and the definition of 11 characters, were modified (see the electronic supplementary material). The hypothetical ancestor used in the phylogenetic analysis of Joyce (2007) was replaced by four real out-groups (*Sphenodon punctatus*, *Simosaurus gaillardoti*, *Owenetta kitchingorum* and *Anthodon serrarius*). The cladistic analysis was performed using the phylogenetic program TNT (Goloboff *et al.* 2003). All characters were treated as unordered and of the same weight. A tree bisection–reconnection (TBR) algorithm with 500 replicates and saving 50 trees per cycle followed by a second cycle of TBR to all the trees found in the first cycle was used to find the most parsimonious trees. A strict consensus tree was calculated from 285 most parsimonious trees of 448 steps (figure 2). The tree consistency index, the tree retention index and other measures of clade support (jackknifing, bootstrap and symmetric resampling) were calculated using TNT (see the electronic supplementary material).

3. SYSTEMATIC PALAEONTOLOGY

Testudinata Klein 1760 (*sensu* Joyce *et al.* 2004)
Condorchelys antiqua gen. et sp. nov.

(a) *Etymology*

Condor from Cerro Cóndor Village; *chelys* from the Greek word for turtle; and *antiqua* from the Latin word for old, ancient.

(b) *Holotype and referred material*

The holotype MPEF-PV1152 (Museo Paleontológico Egidio Feruglio, Trelew, Chubut, Argentina) is represented by a basicranium (figure 1*a*,*b*). The specimens MPEF-PV 1783A and B (fossil and mould of a neural series, costal bones and thoracic vertebrae in visceral view), MPEF-PV 1998 (basicranium), MPEF-PV 3131 (basicranium with skull roof), MPEF-PV 3132 (an almost complete carapace, only lacking the anterior part; figure 1*c*,*d*), MPEF-PV 3133 (pectoral girdle), MPEF-PV 3134 (entoplastron), MPEF-PV 3135 (pelvic girdle) and MPEF-PV 3136 (left hyoplastron) are referred to the species *C. antiqua*.

(c) *Locality and horizon*

All specimens were recovered from the Queso Rallado locality (Rauhut *et al.* 2002), 5.5 km from the west of Cerro Cóndor Village, Chubut Province, Argentina. Queso Rallado is located in outcrops of the Cañadón Asfalto Formation (Stipanicic *et al.* 1968), which is considered to be Middle to Upper Jurassic (Tasch & Volkheimer 1970; Nullo & Proserpio 1975).

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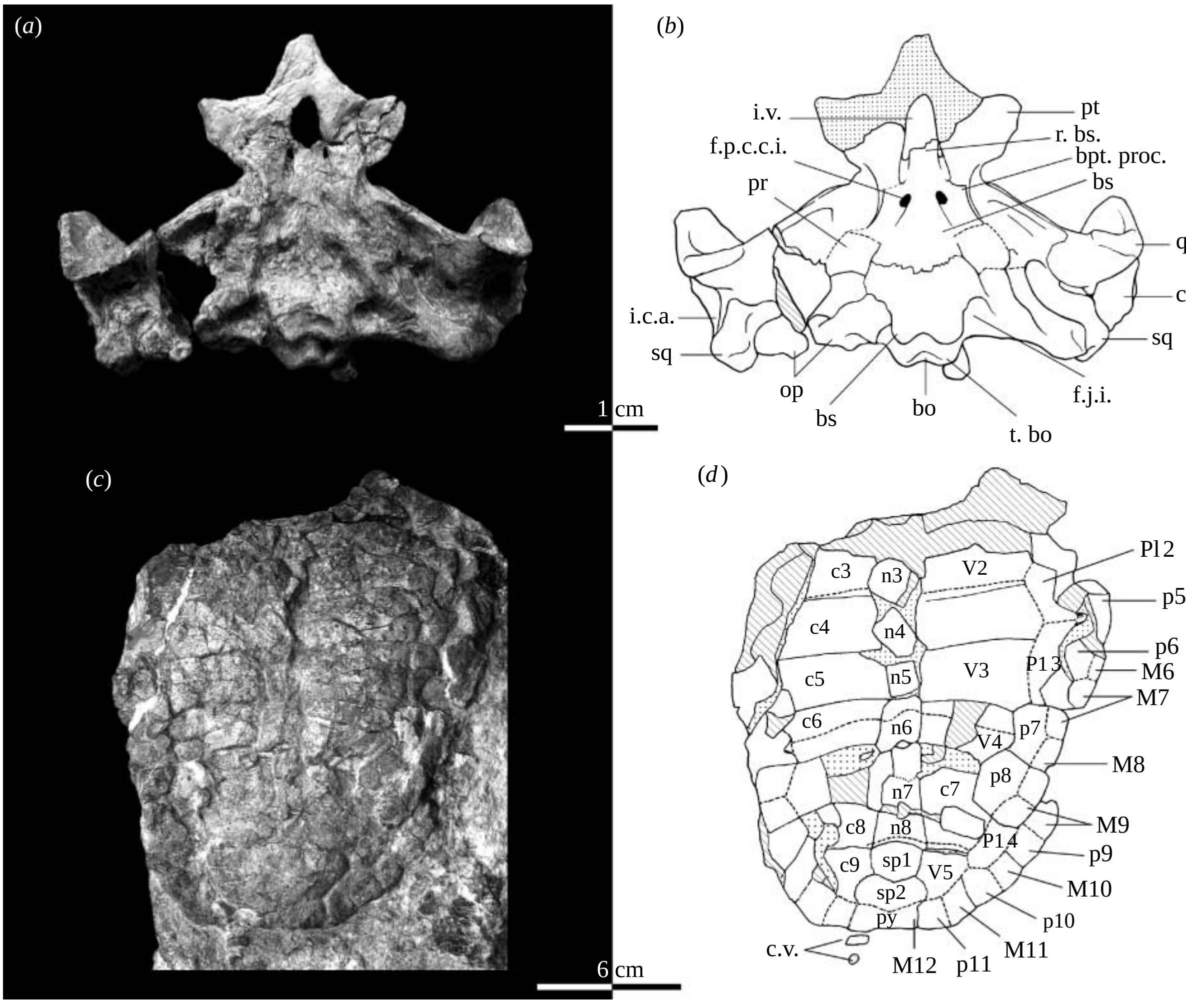

Figure 1. *Condorchelys antiqua* gen. et sp. nov. (*a*) Photograph of the ventral view of the skull MPEF-PV 1152 (holotype). (*b*) Schematic drawing of the ventral view of the skull MPEF-PV 1152 (holotype). (*c*) Photograph of the dorsal view of the carapace MPEF-PV 3132. (*d*) Schematic drawing of the dorsal view of the carapace MPEF-PV 3132. bo, basioccipital; bpt. proc., basipterygoid process; bs, basisphenoid; c, costal plate; c.t., cavum tympani; c.v. caudal vertebrae; f.j.i., foramen jugulare intermedium; f.p.c.c.i., foramen posterius canalis carotici interni; i.c.a., incisura columella auris; i.v., interpterygoid vacuity; M, marginal scute; n, neural plate; op, opisthotic; p, peripheral plate; Pl, pleural scute; pr, prootic; pt, pterygoid; py, pygal plate; qu, quadrate; r. bs., rostrum basisphenoidale; sp, suprapygal plate; sq, squamosal; t. bo, tubera basioccipitalis; V, vertebral scute.

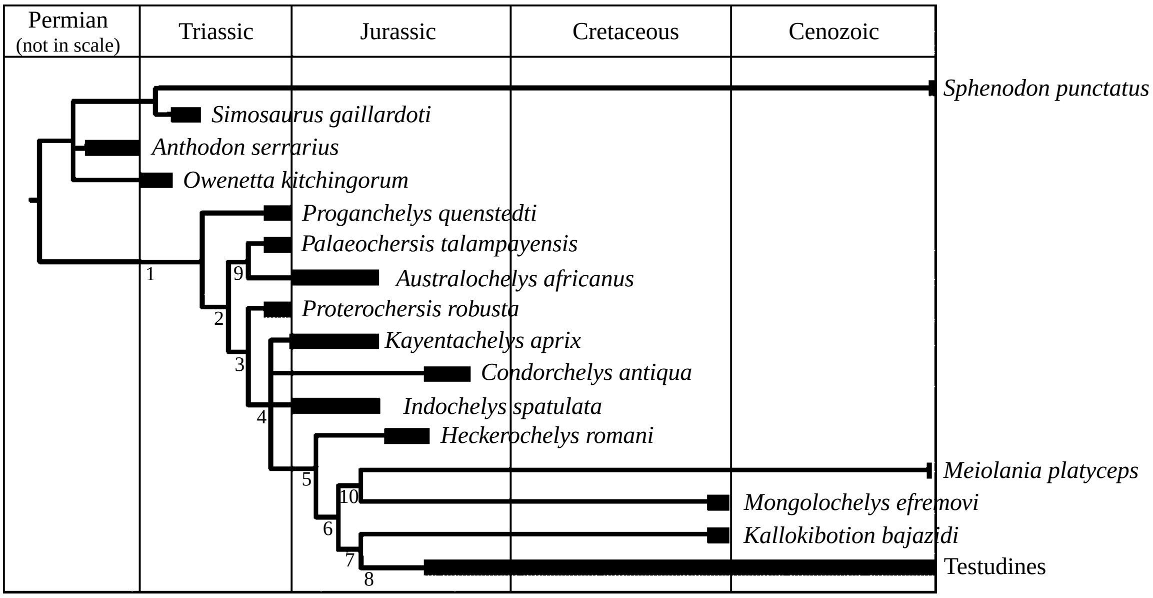

Figure 2. Strict consensus cladogram of 285 trees of 448 steps each, showing the phylogenetic relationships of turtles. CI, 0.353; RI, 0.697. The numbers under the nodes indicate the node number (see the electronic supplementary material).

(d) *Diagnosis*

The characters shared among *C. antiqua* and Triassic and Early Jurassic turtles were as follows: the presence of an interpterygoid vacuity; canalis cavernosus not completely floored; the floor of the cavum cranii thick; the presence of a pair of basioccipital tubera; prootic not covered by the pterygoid; the presence of basipterygoid process; the presence of basisphenoid pits; foramen posterius canalis carotici interni formed entirely by the basisphenoid; the presence of foramen jugulare intermedius; the absence of processus trochlearis oticum or pterygoidei; vertebral scutes broader than pleurals; sulcus between vertebral 3 and 4 located on neural 6; entoplastron with anterior process separating, at least partially, the medial contact of the epiplastra; long posterior process of the entoplastron; and long epipubic process.

The characters shared between *C. antiqua* and more derived turtles (turtles above node 5 in figure 2) were as follows: pterygoid covering at least part of the canalis cavernosus; cavum tympani well developed with an incipient antrum postoticum; the absence of pterygoid teeth; and 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 suprapygal 2.

4. DISCUSSION

The importance of *C. antiqua* lies in two main points: the filling of a gap in the Jurassic fossil turtle record, and the position of this taxon in turtle phylogeny, consequently changing our ideas about the evolution of some features. Although the continental Jurassic turtle record is very scarce and fragmentary, it is interesting to note that all discoveries are widespread around the world (southern Africa, southern South America, North America, Europe, India, and Central Asia). Unfortunately, the vast majority of Early to Middle Jurassic findings are isolated skulls or carapaces, with the exception of three species: *K. aprix* from the Early Jurassic of North America (Gaffney *et al.* 1987); *Heckerochelys romani* from the Middle Jurassic of Russia (Sukhanov 2006); and the turtle presented here, *C. antiqua*. As the main hypotheses about turtle evolution differ, among other things, in the tempo and the mode of origin of the modern groups of turtles, all Jurassic turtles are key fossils that allow further testing of both hypotheses. It is in this context that the detailed description of the Early Jurassic *K. aprix* (Joyce *et al.* 2006; Sterli & Joyce 2007), combined with the discovery of additional Early to Middle Jurassic turtles, such as *C. antiqua*, may shed new light on the anatomy of the first moments of turtle evolution. The data gathered from these studies are also useful to research on one of the most intriguing themes in amniote evolution, the origin of turtles.

The updated cladistic analysis presented here (figure 2) generally supports the topology obtained by Joyce (2007) confirming the basal placement of *K. aprix*, as well as *C. antiqua* and all other Triassic to Middle Jurassic turtles included in this analysis. *Indochelys spatulata* is assessed within a cladistic context for the first time and is hypothesized not to be a cryptodiran turtle as was proposed by Datta *et al.* (2000), but rather a stem turtle. The phylogenetic position of *H. romani* is also somewhat different in this analysis from that originally proposed by the cladistic analysis of Sukhanov (2006). In the present phylogeny, *H. romani* is considered a stem turtle located above the unresolved '*K. aprix*, *C. antiqua* and *I. spatulata*'. Sukhanov (2006), by contrast, suggested that this Russian turtle was placed more basal than *K. aprix* relative to the turtle crown.

Since Gaffney (1975) performed the first cladistic analysis of turtle evolution, the two living clades of turtles were supported by several synapomorphies that have not been questioned until the recent papers of Joyce (2007) and Sterli & Joyce (2007). The presence of a pulley system for the jaw closure in the otic region was suggested by Gaffney (1975) as a synapomorphy of Cryptodira (the most diverse group of living turtles including tortoises, marine turtles and some kinds of fresh water turtles, among others). However, as it was suggested by Joyce (2007) and is shown in the present cladistic analysis of turtles, the presence of this character is a synapomorphy of a more inclusive clade (node 6 in the tree shown in figure 2 and the electronic supplementary material). The evidence available at present, and the discovery of *C. antiqua* from the Middle to Upper Jurassic of Patagonia, show that until that time there were turtles that did not develop a specialized jaw closure mechanism (the absence of processus trochlearis). This finding, together with the new interpretation of the otic area of *K. aprix* (Sterli & Joyce 2007), suggests that the origin of the pulley systems in turtles is at least 60 Myr younger than that previously thought (Gaffney *et al.* 1987). It is also interesting to note that during the same time, Middle to Upper Jurassic (160–146 Myr old), there were turtles with and without a pulley system, and that the evolution of turtles is far more complex than that previously thought.

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Baur, G. 1887 Über den Ursprung der Extremitäten de Ichthyopterygia. *Jahrbr. Mitt. Oberhein Geol. Verein* **20**, 17–20.

Broin, F. de 1985 *Proganochelys ruchae* n.sp., chélonien du Trias supérieur de Thaïlande. *Stud. Geol. Salman. Stud. Palaeoch.* **1**, 87–97.

Datta, P. M., Manna, P., Ghosh, S. C. & Das, D. P. 2000 The first Jurassic turtle from India. *Palaeontology* **43**, 99–109. (doi:10.1111/1475-4983.00120)

Fraas, E. 1913 *Proterochersis*, eine pleurodire Schildkröte aus dem Keuper. *Jahr. Ges. Nat. Württemberg* **69**, 13–90.

Gaffney, E. S. 1975 A phylogeny and classification of the higher categories of turtles. *Bull. Am. Mus. Nat. Hist.* **155**, 389–436.

Gaffney, E. S., Hutchison, J. H., Jenkins, F. A. & Meeker, L. J. 1987 Modern turtle origins: the oldest known cryptodire. *Science* **237**, 289–291. (doi:10.1126/science.237.4812.289)

Gaffney, E. S., Rich, T. H., Vickers-Rich, P., Constantine, A., Vacca, R. & Kool, L. 2007 *Chubutemys*, a new eucryptodiran turtle from the Early Cretaceous of Argentina, and the relationships of the Meiolaniidae. *Am. Mus. Nov.* **3599**, 1–35. (doi:10.1206/0003-0082(2007)3599[1:CANETF]2.0.CO;2)

Goloboff, P. A., Farris, J. S. & Nixon, K. C. 2003 *T.N.T.: tree analysis using new technology*. Program and documentation. See www.zmuc.dk/public/phylogeny.

Jenkins Jr, F. A. *et al.* 1994 Late Triassic continental vertebrates and depositional environments of the Fleming Fjord Formation, Jameson Land, East Greenland. *Medd. Grønland, Geosci.* **32**, 3–25.

Joyce, W. G. 2007 Phylogenetic relationships of Mesozoic turtles. *Bull. Peabody Mus. Nat. Hist.* **48**, 3–102. (doi:10.3374/0079-032X(2007)48[3:PROMT]2.0.CO;2)

Joyce, W. G., Parham, J. F. & Gauthier, J. A. 2004 Developing a protocol for the conversion of rank-based taxon names to phylogenetically defined clade names, as exemplified by turtles. *J. Paleontol.* **78**, 989–1013. (doi:10.1666/0022-3360(2004)078<0989:DAPFTC>2.0.CO;2)

Joyce, W. G., Jenkins, F. A. & Rowe, T. 2006 The presence of cleithra in the basal turtle *K. aprix*. In *Fossil turtle research*, vol. 1 (eds I. G. Danilov & J. F. Parham), *Russ. J. Herpetol.* **13**(Suppl.), 93–103.

Klein, I. T. 1760 *Klassification und kurze Geschichte der Vierfüßigen Thiere* (transl. by F. D. Behn). Lübeck, Germany: Jonas Schmidt.

Matzke, A., Maisch, M. W., Sun, G., Pfretzschner, H.-U. & Stöhr, H. 2004 A new Xinjiangchelyid turtle (Testudines; Eucryptodira) from the Jurassic Qigu formation of the southern Junggar Basin, Xinjiang, North-West China. *Palaeontology* **47**, 1267–1299. (doi:10.1111/j.0031-0239.2004.00410.x)

Nullo, E. F. & Proserpio, C. 1975 La Formación Taquetrén en Cañadón del Zaino (Chubut) y sus relaciones estratigráficas en el ámbito de la Patagonia, de acuerdo a la flora, República Argentina. *Rev. Asoc. Geol. Argent.* **30**, 133–150.

Rauhut, O., Martin, T., Ortiz-Jaureguizar, E. & Puerta, P. 2002 A Jurassic mammal from South America. *Nature* **416**, 165–168. (doi:10.1038/416165a)

Rougier, G. W., de la Fuente, M. S. & Arcucci, A. B. 1995 Late Triassic turtles from South America. *Science* **268**, 855–858. (doi:10.1126/science.268.5212.855)

Sterli, J. & Joyce, W. G. 2007 Skull anatomy of the Lower Jurassic turtle *Kayentachelys aprix*. *Acta Palaeontol. Pol.* **52**, 675–694.

Stipanicic, P. N., Rodrigo, F., Baulíes, O. L. & Martínez, C. G. 1968 Las formaciones presenonianas en el denominado macizo Nordpatagónico y regiones adyacentes. *Rev. Asoc. Geol. Argent.* **23**, 67–98.

Sukhanov, V. B. 2000 Mesozoic turtles of Middle and Central Asia. In *The age of dinosaurs in Russia and Mongolia* (eds M. J. Benton, M. A. Shishikin, D. M. Unwin & E. N. Kurochkin), pp. 309–367. Cambridge, UK: Cambridge University Press.

Sukhanov, V. B. 2006 An archaic turtle, *Heckerochelys romani* gen. et sp. nov., from the Middle Jurassic of Moscow region, Russia. In *Fossil turtle research*, vol. 1 (eds I. G. Danilov & J. F. Parham), *Russ. J. Herpetol.* **13**(Suppl.), 112–118.

Tasch, P. & Volkheimer, W. 1970 Jurassic conchostracans from Patagonia. *Univ. Kansas, Paleontol. Contrib.* **50**, 1–23.

Tong, H., Buffetaut, E. & Suteerthorn, V. 2002 Middle Jurassic turtles from Thailand. *Geol. Mag.* **139**, 687–697. (doi:10.1017/S0016756802006805)