



Research

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Atolchelys lepida, a new side-necked turtle from the Early Cretaceous of Brazil and the age of crown Pleurodira

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We report a new pleurodiran turtle from the Barremian Morro do Chaves Formation, Sergipe-Alagoas Basin, Brazil. We tested the phylogenetic position of *Atolchelys lepida* gen. et sp. nov. by including it in a comprehensive cladistic analysis of pleurodires. The new species is a basal member of Bothremydidae and simultaneously the oldest unambiguous crown Pleurodira. The biogeographic and chronostratigraphic significance of the finding has implications for the calibration of molecular clocks studies by pushing back the minimum age of crown Pleurodira by more than 12 Ma (*ca* 125 Ma). The reanalysis of Pelomedusoides relationships provides evidence that the early evolution and relationships among the main lineages of side-necked turtles can be explained, at least partially, by a sequence of vicariance events.

1. Introduction

Side-necked turtles (Pan-Pleurodira) have an extensive fossil record dating back to the Late Jurassic. Regardless of the discussion on the phylogeny of stem turtles [1–8], the Triassic *Proterochersis robusta* has been consistently positioned outside of this clade in recent studies [1,6,8] and the stem lineage is therefore only populated by the clade Platycheilyidae [1–12].

All records of Platycheilyidae range from the Oxfordian (Late Jurassic) to Valangian (Early Cretaceous) [11,13], whereas the oldest unambiguous crown Pleurodira were previously known from the Aptian (Early Cretaceous). The apparent temporal gap during the Early Cretaceous reveals that the early record of Pleurodira is extremely poor. The earliest Pan-Chelidae, one of the two primary branches of Pleurodira, dates from the Albian [1]. A fragmentary podocnemidoid specimen from the Valangian (*ca* 135 Ma) of Colombia, by contrast, has been argued to be the earliest record of crown Pelomedusoides, but we are cautious about this interpretation [14] (see §4). Thus, the oldest unambiguous Pelomedusoides are those from Araripe Basin of Brazil (Aptian–Albian): *Araripemys* (Araripemydidae), *Cearachelys* (Bothremydidae) and *Euraxemys* (Euraxemydidae). Of these three taxa, only the first is confirmed from Aptian localities [15], in addition to more fragmentary material referable to Pan-Podocnemididae [16].

Here, we describe a new species of Pelomedusoides from the Lower Cretaceous (Barremian) of the Sergipe-Alagoas Basin in Brazil. This is not the first record of a turtle from the Morro do Chaves Formation [17], but, it is sufficiently complete to allow testing its phylogenetic relationships, discussing its biogeographic and chronostratigraphic significance, and its impact on molecular calibration studies of turtles.

2. Material and methods

In order to test the phylogenetic position of *Atolchelys lepida* gen. et sp. nov., it was included in the most recent published character/taxon matrix [2], including subsequent additions and modifications proposed [5,11,18]. The cladistic analysis was performed using TNT [19] (details in the electronic supplementary material; characters states coded to *Atolchelys* gen. nov. in data matrix: 1111??0??01??[12]1??00??0000??010??111??0??1110100??????????11110?41101?????020110?????210?11??1?11401?02????????????1????????????2111??1??11??1??1?).

3. Results

(a) Systematic palaeontology

Testudines Linnaeus, 1758

Pleurodira Cope, 1865

Pan-Podocnemididae Joyce *et al.*, 2004

Bothremydidae Baur, 1891

Atolchelys lepida gen. et sp. nov.

(b) Etymology

Atol, from the former name of the type locality (Atol quarry); *chelys*, an ancient Greek tortoise-shell lyre, generally used to designate 'turtle'. *Lepida* (fem.) from Latin: pleasant, charming, witty.

(c) Holotype

Atolchelys lepida gen. et sp. nov. is based on the holotype and only known specimen UERJ.MC 2 housed at the palaeontological collection of the Departamento de Zoologia of the Universidade do Estado do Rio de Janeiro. It is an individual preserved in a carbonate concretion and includes the skull, mandible, a pair of ceratohyals, plastron and some elements of the carapace and the appendicular skeleton (figure 1). The skeleton shows evidence of compression, hindering the visualization of some sutures and foramina. A CT scan was produced in order to visualize internal structures, but density differences were not sufficient to distinguish bony remains from sedimentary matrix. The holotype will be described in more detail in the future.

(d) Locality and horizon

UERJ.MC 2 was recovered from deposits of the Morro do Chaves Formation outcropping in the CIMPOR quarry (former 'Atol quarry') located 6.7 km WNW from the city of São Miguel dos Campos, Alagoas State, Northeastern Brazil (09°45'38" S/36°09'22" W). The Morro do Chaves Formation is dated as Upper Barremian (details in the electronic supplementary material).

(e) Diagnosis

The plastron of *A. lepida* gen. et sp. nov. exhibits the usual 11 bones present in most pleurodires, including a reduced pair of mesoplastra, and no fontanelles. It possesses two cranial characters diagnostic to Pan-Podocnemididae (Podocnemidera *sensu* 2): presence of a wide maxillary triturating surfaces and reduced single vomer. Also, the new species shares two synapomorphies with Podocnemidoidea (*sensu* 2): pterygoid contribution to the anterior margin of the foramen posterius canalis carotici interni and short basioccipital. Features

diagnostic of Bothremydidae (*sensu* 2) are: triturating surfaces moderately wide, cavum pterygoidei absent, prootic partially covered in ventral view, foramen posterius canalis carotici interni not in prootic and basisphenoid-quadrangle contact present. The autapomorphic characters of *A. lepida* gen. et sp. nov. are: longitudinally elongated foramen palatinum posterius, squared opisthotic in ventral view and basioccipital triangular, uneven, with tuberculum and with a broad anterior portion.

(f) Remarks

The phylogenetic analysis resulted in 24 most parsimonious trees of 437 steps and the placement of *A. lepida* gen. et sp. nov. inside the clade Bothremydidae (figure 2 and the electronic supplementary material). The inclusion of *A. lepida* gen. et sp. nov. results in a loss of resolution within Kurmademydini, Cearachelyini and Bothremydini. Another remarkable result of this analysis is the fact that Pelomedusidae is placed as sister-group to all other Pelomedusoides and not only Araripemydidae.

The other specimen from the type locality of *A. lepida* gen. et sp. nov., MCP 4721PV [17], is not referable to this species due to some morphological differences: *A. lepida* gen. et sp. nov. has a more elongated plastron and the pubis and ischium scar are shaped differently. However, MCP 4721PV's small size, loose sutures and strong caudal constriction in the xiphiplastra suggest that it is a juvenile individual [17], hindering conclusive judgements.

4. Discussion

The previously reported putatively oldest crown pleurodires [14,17] are both based on fragmentary shell remains that do not allow an accurate identification. MCP 4721PV [17], from the same locality as *A. lepida* gen. et sp. nov., is clearly a pan-pleurodiran, but lacks diagnostic features for a more accurate identification. Fragmentary material from the Valanginian of Colombia [14] cannot be identified with any confidence either. It was originally described as a podocnemidoid based on the presence of an inguinal buttress that medially extends onto the ventral surface of costal 5, a character that purportedly supports uniting *Teneremys* and Podocnemidoidea, but might be artificial ([2, p. 637], fig. 294). However, this character is highly variable within Pelomedusoides, even within all of Testudines [20], and is therefore not helpful in diagnosing fragmentary material. Thus, it is imprudent to use highly homoplastic apomorphy to support the identification as the oldest crown pleurodire [14] and it is more conservative to consider the Valanginian remains to be an indeterminate Testudines.

The placement of *A. lepida* gen. et sp. nov. within crown Pleurodira has an impact on the minimal age dating of this clade. Until now, the oldest records used to calibrate the Pelomedusoides–Chelidae divergence were Late Aptian records of *Araripemys* and the Albian record of *Prochelandella*, respectively. Therefore, our finding pushes the minimum age of crown Pleurodira back by more than 12 Ma: to the top of the Barremian, at approximately 125 Ma. As a consequence, this node should be updated in future molecular clock analyses, which may consequently retrieve an older calibrated age for crown Pleurodira [7].

The new phylogenetic hypothesis combined with the new minimum age for crown Pleurodira are consistent with the idea that Pelomedusoides originated from an ancestor in northern Gondwana, whereas Chelidae descendant from an

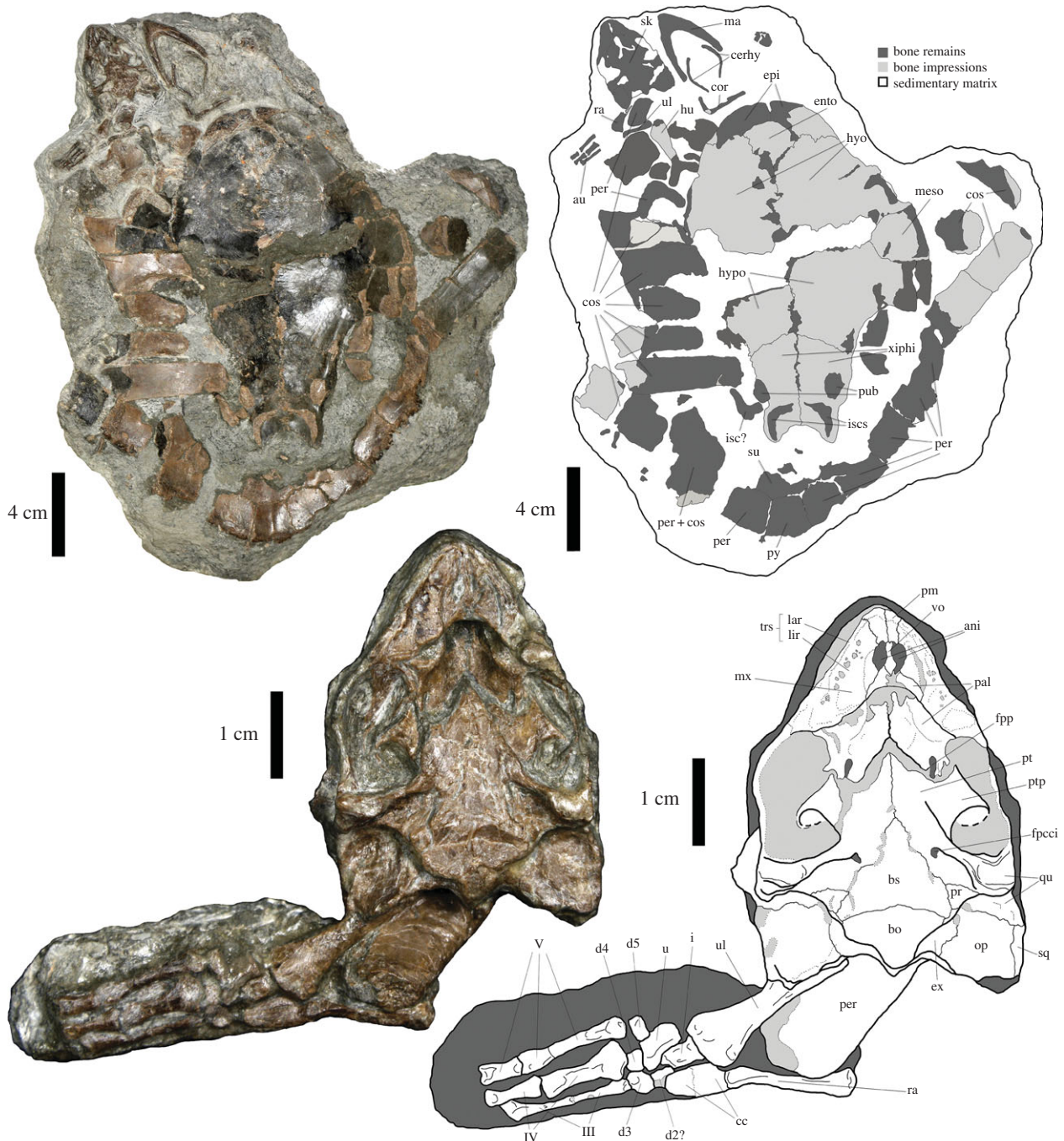


Figure 1. Photograph and line drawing of *A. lepida* gen. et sp. nov. holotype (UERJ.MC 2) (above) and detail of the skull in palatal view and right forelimb after further preparation (below). III–V, digits I–V; ani, apertura narinum interna; au, autopodial elements; bo, basioccipital; bs, basisphenoid; cc, centralia; cerhy, ceratohyals; cor, coracoid; cos, costal bone; d2–5, distal carpalia; epi, epiplastron; ento, entoplastron; ex, exoccipital; fpcci, foramen posterius canalis carotici interni; fpp, foramen palatinum posterius; hu, humerus; hyo, hyoplastron; hypo, hypoplastron; i, intermedium; isc, ischium; iscs, ischium scars; lar, labial ridge; lir, lingual ridge; ma, mandible; mx, maxilla; meso, mesoplastron; op, opisthotic; pal, palatine; per, peripheral bone; pm, premaxilla; pr, prootic; pt, pterygoid; ptp, processus trochlearis pterygoidei; pub, pubis scar; py, pygal; qu, quadrate; ra, radius; sk, skull; sq, squamosal; su, suprapygal; trs, triturating surface; u, ulnare; ul, ulna; vo, vomer; xiphi, xiphiplastron. (Online version in colour.)

ancestor in southern Gondwana. A previous hypothesis [21,22] suggests that the Pelomedusoides–Chelidae split is consistent with a vicariance event that occurred during the Early Cretaceous (figure 2, node I). Following this split, three sister-group relationships can be identified between African and Brazilian Pelomedusoides species (figure 2, nodes II', II'' and II'''), of which two (nodes II' and II'') were not previously recognized [22]. Thus, it is possible to interpret these sister-group relationships as allopatric speciations due to a single vicariance event: the complete opening of the central Atlantic and the separation of Africa from South America. Bothremydidae and Podocnemididae afterwards

greatly expanded their range of distribution but also suffered several lineages extinctions.

After recent progress with respect to knowledge about Pelomedusoides phylogeny and diversity [2,3,5,11,18], our findings indicate that the origin and relationships among the main lineages of side-necked turtles is even more complex than previously reported.

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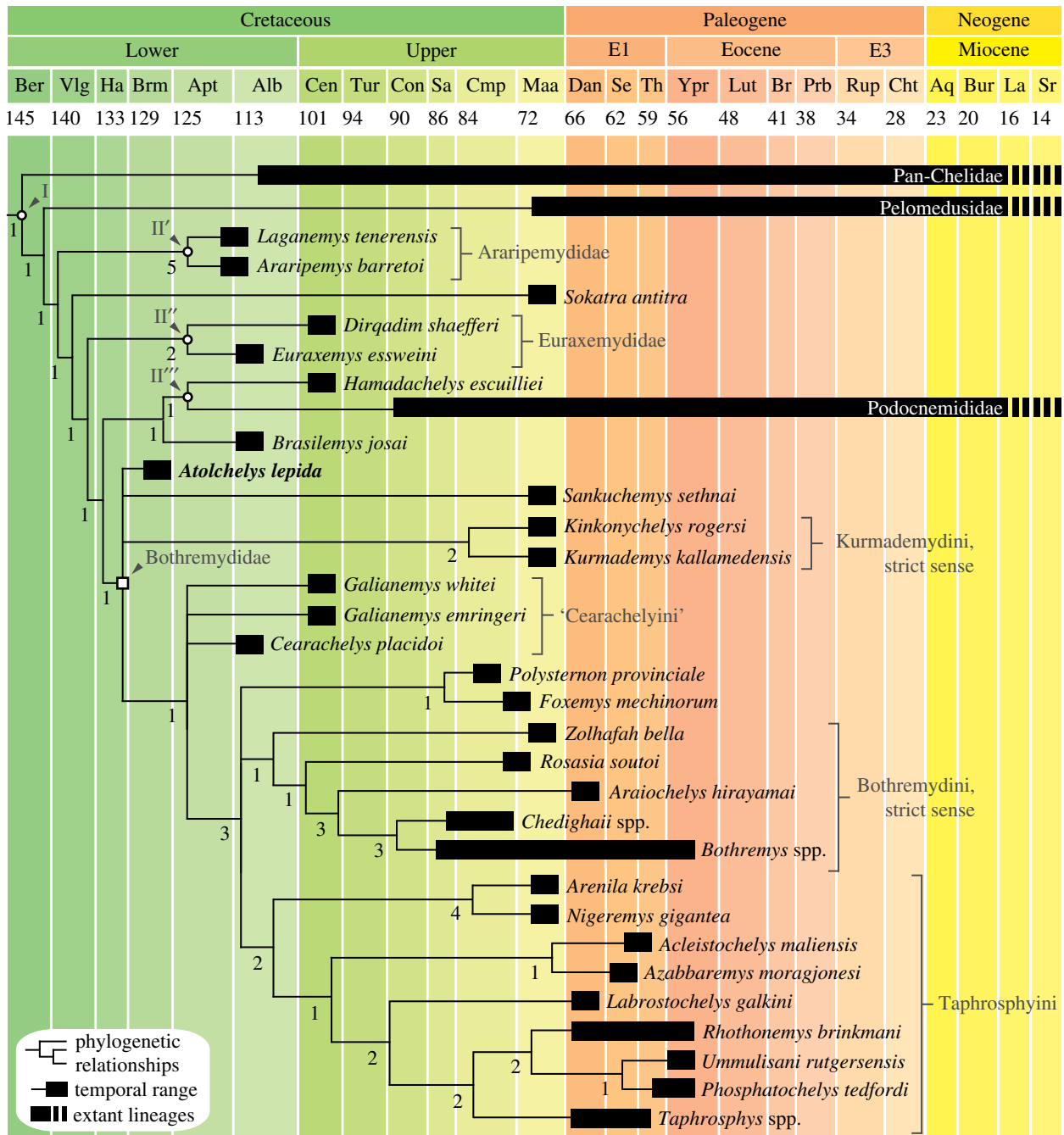


Figure 2. Phylogenetic tree of crown pleurodiran based on the strict consensus of 24 most parsimonious trees of 437 steps superimposed on a geological timescale. Bremer supports are indicated in Arabic numerals. Geochronology ages (in Ma) and abbreviations based on 2013' ICS Chart. Nodes I and II represent vicariance events (see S4). Complete tree is available in the electronic supplementary material. (Online version in colour.)

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Data accessibility. The electronic supplementary material was deposited in the Dryad repository: doi:10.5061/dryad.f2h6r. The matrix was deposited in Morphobank (Project no. 1194).

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