



# Giant fossil tortoise and freshwater chelid turtle remains from the middle Miocene, Quebrada Honda, Bolivia: Evidence for lower paleoelevations for the southern Altiplano



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## ARTICLE INFO

### Article history:

Received 13 August 2015

Received in revised form

14 October 2015

Accepted 18 October 2015

Available online 27 October 2015

### Keywords:

Bolivia

Turtles

Miocene

Chelidae

Testudinidae

Paleoelevation

Altiplano

## ABSTRACT

We describe the first Miocene turtle remains from Bolivia, which were collected from the late middle Miocene (13.18–13.03 Ma) of Quebrada Honda, southern Bolivia. This material includes a large scapula-acromion and fragmentary shell elements conferred to the genus *Chelonoidis* (Testudinidae), and a left xiphiplastron from a pleurodire or side-necked turtle, conferred to *Acanthochelys* (Chelidae). The occurrence of a giant tortoise and a freshwater turtle suggests that the paleoelevation of the region when the fossils were deposited was lower than has been estimated by stable isotope proxies, with a maximum elevation probably less than 1000 m. At a greater elevation, cool temperatures would have been beyond the tolerable physiological limits for these turtles and other giant ectotherm reptiles.

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## 1. Introduction

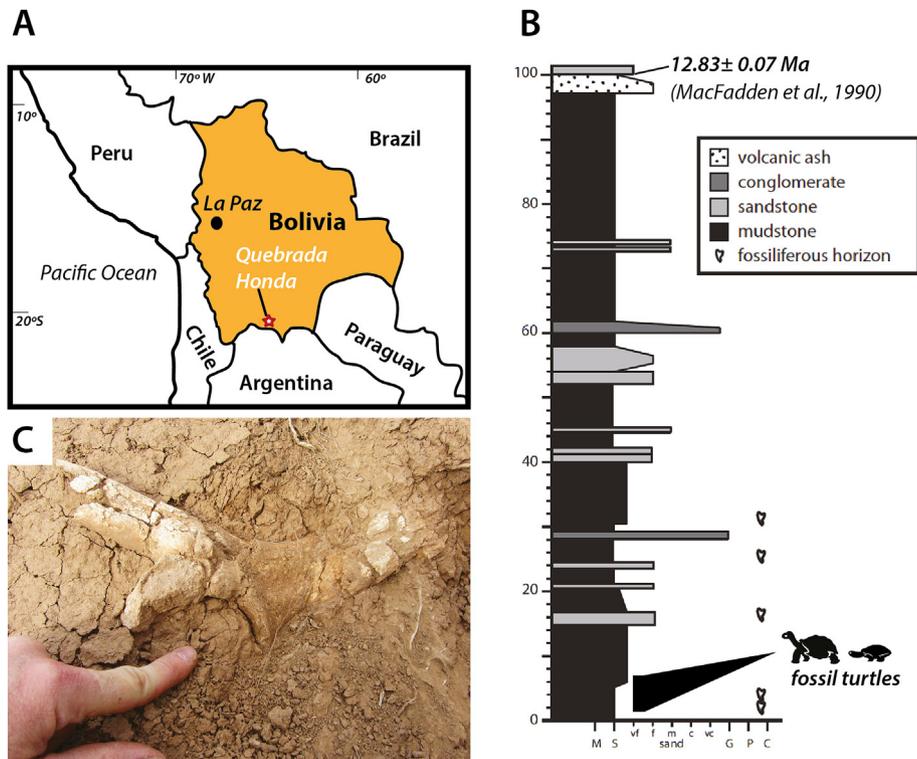
The Bolivian fossil record of turtles is restricted to four Cenozoic localities. The oldest turtle remains are Paleocene in age and come from the Vilavila locality in the El Molino Formation, department of Cochabamba. These specimens pertain to a single species of pleurodire (side-necked turtle; family Podocnemididae), *Lapparentemys vilavilensis* Broin, 1971 (sensu Gaffney et al., 2011). Two late Oligocene (Deseadan South American Land Mammal “Age” or SALMA) localities have produced turtle remains. Specimens from Quebrada Saguayo in the Petaca Formation of the department of Santa Cruz pertain to a cryptodire or hidden-necked turtle, family Testudinidae (tortoises), cf. *Chelonoidis*. Undetermined podocnemidids have been reported from the “Estratos de Salla” of the Salla locality in the department of La Paz (Broin, 1991). The fourth locality is the late Pleistocene section of the Ñuapua Formation at the Quebrada de Ñuapua, Chuquisaca department, which has produced

remains of giant tortoises (*Chelonoidis* sp.) and undetermined pleurodires (Broin, 1991).

Quebrada Honda is located in the Eastern Cordillera of the Tarija department of southern Bolivia, close to the border with Argentina (S 21° 57' 23.4", W. 65° 9' 3.9"), at an elevation of ~3500 m (Fig. 1). The locality has a stratigraphic sequence of fluvial channels, floodplain and overbank deposits that belong to an unnamed formation of the Honda Group (MacFadden and Wolff, 1981; Croft et al., 2011). Quebrada Honda fossils primarily come from two fossil-producing areas that are separated by approximately 6 km: one near the town of Quebrada Honda and another near the town of Río Rosario. Based on radiometric dates and paleomagnetic correlations, the fossils collected near the town of Quebrada Honda (i.e., those comprising the Quebrada Honda Local Fauna sensu Croft, 2007) are late middle Miocene in age, approximately 13.0–12.7 million years old (MacFadden et al., 1990; but see refined age estimates below). The outcrops in both areas have produced abundant fossil mammals, principally rodents, notoungulates, and xenarthrans, that pertain to the Laventan SALMA (Croft, 2007; Croft et al., 2011). Fossil bird remains and ichnofossils have also been identified through recent field investigations (Croft et al., 2013).

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**Fig. 1.** Location and stratigraphic framework. A, location of Quebrada Honda, southern Altiplano, Bolivia. B, stratigraphic interval where the fossil tortoise and chelid specimens were found (modified from a version courtesy of D. Auerbach). C, UATF-V-001867 scapula-acromion in situ, illustrating the surrounding rock matrix.

Despite the abundant fossil remains that have been collected at Quebrada Honda, its climate, vegetation, and elevation during the middle Miocene have been poorly constrained. Determining the paleoelevation, in particular, is not straightforward (e.g., Gregory-Wodzicki, 2000) and generally must rely on using paleotemperature as a proxy. A recent paper by Garzione et al. (2014) used a soil temperature proxy (clumped isotope paleothermometry of pedogenic carbonates) to estimate the paleoelevation of Quebrada Honda at  $2.6 \pm 0.6$  km. This suggests that the southern Altiplano rose 1.2–2.6 km during the 3 million years preceding deposition of the Honda Group and that uplift of the southern Altiplano preceded that of the northern Altiplano by 3–11 million years. This, in turn, has important implications for tectonic modeling of Central Andean uplift as well modeling of middle Miocene climates and weather patterns.

Here we describe the first occurrences of fossil turtles at Quebrada Honda, which also constitute the only Miocene turtle remains from Bolivia and the first fossil chelids reported for the country. Although the fossil material is fragmentary, it preserves enough characteristics to be identified as belonging to two taxa: (1) a giant tortoise of the genus *Chelonoidis*, the most abundant extant and fossil South American tortoise genus (de la Fuente et al., 2014); and (2) a taxon conferred to *Acanthochelys*, a chelid genus with abundant current distribution in southern South America (de la Fuente et al., 2014; van Dijk et al., 2014). In addition to describing this material, we discuss the implications these fossils have for assessing the paleoelevation of Quebrada Honda.

## 2. Materials and methods

One of the fossil tortoise specimens described here consists of a right scapula-acromion element (UATF-V-001867). A three-dimensional surface model of this specimen was acquired using a

Hexagon Metrology ROMER Absolute Arm 7-Axis SI 3D scanner with 0.040 mm dimensional scan accuracy at think[box] Institute for Collaboration and Innovation at Case Western Reserve University. A video of the surface mesh model is available as Supplementary Data 1. The internal angle between the scapula and the acromion processes was measured using ImageJ (Abramoff et al., 2004) angle tool. Shell fragments correspond to a left epiplastron associated with the scapula-acromion and two fragments of a costal bone collected elsewhere (UATF-V-00964).

Supplementary data related to this article can be found online at <http://dx.doi.org/10.1016/j.jsames.2015.10.013>.

Altitude and geographical data for three extant species of *Chelonoidis* (*Ch. carbonaria*, *Ch. denticulata*, *Ch. nigra* and *Ch. chilensis*) and for nine species of chelids (*Chelus fimbriata*, *Phrynops geoffroanus*, *P. tuberosus*, *P. hilarii*, *Platemys platycephala*, *Mesolemmys gibba*, *Hydromedusa maximiliani*, *H. tectifera*, and *Acanthochelys pallidipectoris*) were obtained from the Global Biodiversity Information Facility (GBIF, 2015), for records with geographical information but without altitude data, we use Google Earth 7.1.5.1557 to establish their corresponding altitude. Species with just one or two geographical points were included in the Supplementary Data 1, but excluded from the elevation plots, these include: *P. williamsi*, *M. raniceps*, *M. vanderhaegei*, *M. dahlia*, *M. heliostemma*, and *A. spixii*.

**Institutional abbreviations** – AMNH, American Museum of Natural History, Herpetological collection, New York, USA; ICN, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia; MNHN, Muséum national d'Histoire naturelle, Paris, France; MNMW, Naturhistorisches Museum Wien, Vienna, Austria; MTKD, Senckenberg Natural History Collections, Dresden, Germany; UATF-V, Universidad Autónoma Tomás Frías, Potosí, Bolivia; USMN, United States National Museum, Washington, USA.

### 3. Systematic paleontology

TESTUDINES Batsch, 1788.  
 CRYPTODIRA Cope, 1868.  
 TESTUDINIDAE Gray, 1825.  
*Chelonoidis* Fitzinger, 1835.  
 cf. *Chelonoidis*.  
 Figs. 2 and 3.

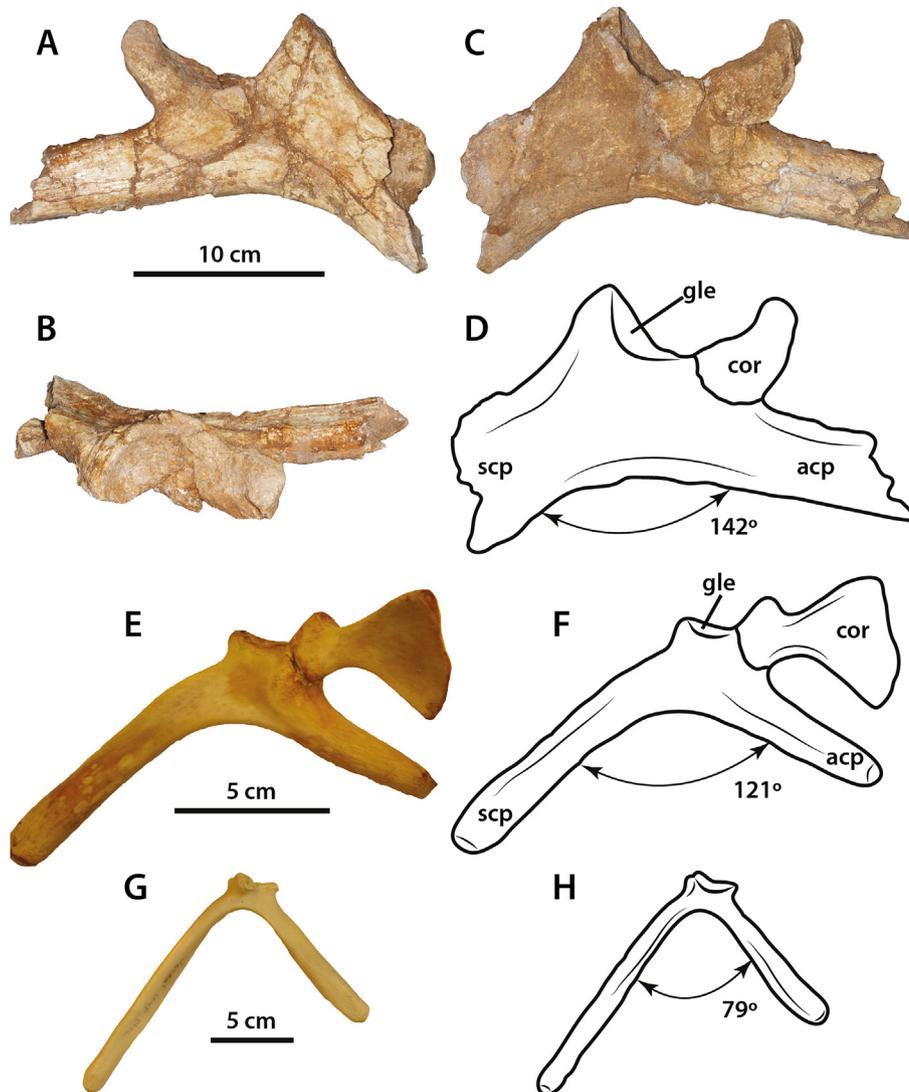
*Referred material* – UATF-V-001867 (scapula-acromion and left epiplastron), UATF-V-00964 (costal bone fragments) and UATF-V-001778 (right xiphiplastron).

*Locality and geological age* – The specimens described here were collected near the base of the stratigraphic section, which corresponds to Unit 2, lower Quebrada Honda section of MacFadden and Wolff (1981). Based on ongoing stratigraphic and paleomagnetic studies at the site (Croft et al., 2013), this level is within local magnetic polarity zone N1. According to MacFadden et al. (1990), this zone correlates to polarity chron C5AAn, which is presently estimated to span 13.18–13.03 Ma (Ogg, 2012).

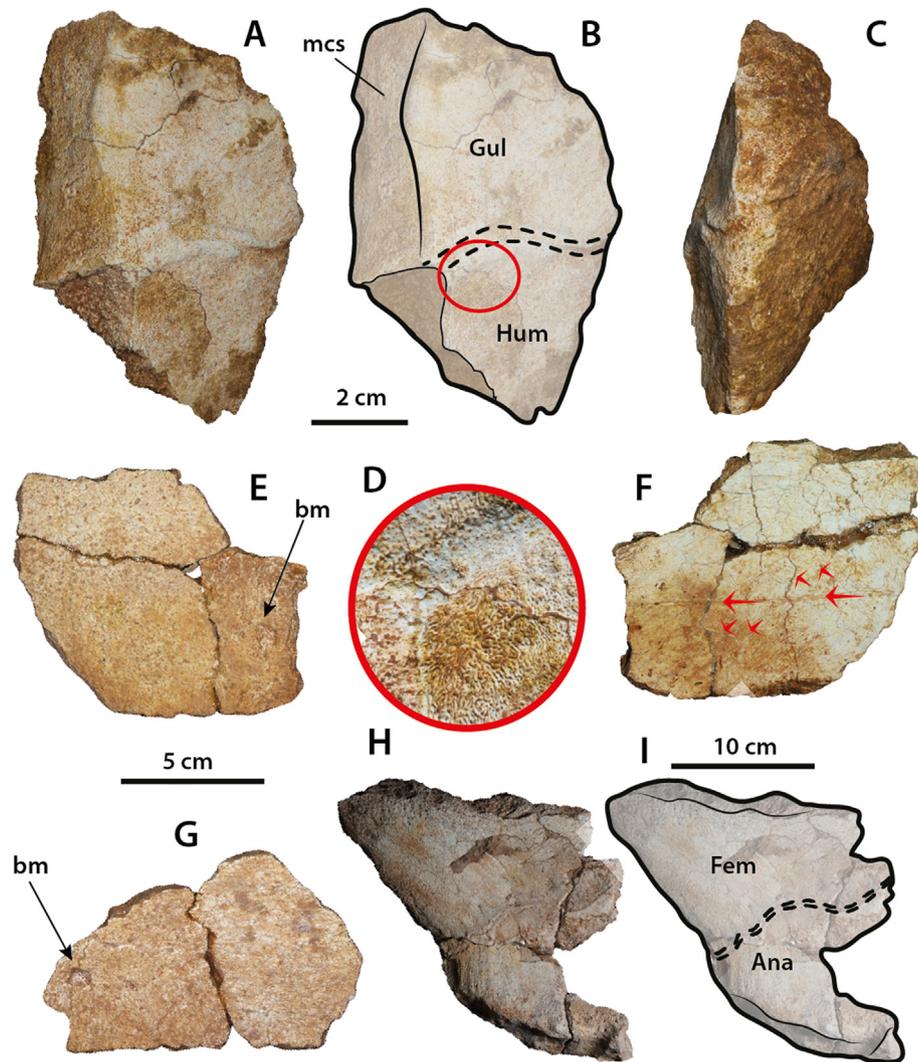
*Description and comparisons* – UATF-V-001867 is a scapula-

acromion bone, moderately affected by crushing, missing the most distal portions of both processes and having a total width as preserved of 23 cm (Fig. 2A–D). The most proximal portion of the coracoid is also preserved, articulated to the scapula-acromion. The glenoid cavity is large and deep as in extant and fossil giant tortoises, and the internal angle between the scapula-acromion processes is  $142^\circ$ . Very wide internal angles between scapula-acromion processes are characteristic of terrestrial turtles (tortoises), whereas freshwater and some marine turtles have more acute angles (Depecker et al., 2006). For example, this angle measures  $121^\circ$  in a specimen of the Galapagos giant tortoise *Chelonoidis nigra* (USMN 015192; Fig. 2E–F) but only  $79^\circ$  in the freshwater *Podocnemis expansa* (AMNH 62947; Fig. 2G–H).

A left epiplastron (UATF-V-001867; Fig. 3A–D) found associated with the scapula-acromion is considered here as belonging to the same individual. As in all other giant *Chelonoidis* spp., the epiplastron is a very thick bone (3.5 cm), lacking of a strong sutural medial contact with the right epiplastron. On the ventral surface there is a well defined gular-humeral sulcus that exhibits the characteristic testudinid shape: similar to a canal with high lateral walls (Fig. 3C)



**Fig. 2.** UATF-V-001867 scapula-acromion of cf. *Chelonoidis*. A, lateral view; B, glenoid in posterior view; C–D, medial view; E–F, pectoral girdle (scapula-acromion, and coracoid) in medial view of the extant tortoise *Chelonoidis nigra* (USMN 015192); G–H, scapula-coracoid in medial view of the extant freshwater turtle *Podocnemis expansa* (AMNH 62947). Abbreviations: acp, acromial process; cor, coracoid; gle, glenoid capsule; scp, scapular process.



**Fig. 3.** Shell fragments of cf. *Chelonoidis*. A–D, UATF-V-001867, left epiplastron. A–B, ventromedial view; C, lateral view; D, close-up of the red circle in B, showing the vermiculated sculpturing. E–H, UATF-V-00964, two costal bone fragments. E, fragment 1, dorsal view; F, ventral view, red arrows indicate different direction of bone tissue; G, fragment 2, dorsal view. H–I, UATF-V-001778, right xiphiplastron in ventral view. Abbreviations: Ana, anal scute; bm, bite marks (possible); Fem, femoral scute; Gul, gular scute; Hum, humeral scute; mcs, medial contact surface. Scale bar of 2 cm applies for A–C, 5 cm for E–G, and 10 cm for H–I. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

and a highly dense vermiculated bone surface (Fig. 3D).

UATF-V-00964 (Fig. 3E–G) includes two fragments of costal bones, potentially belonging to the same costal. Unfortunately, neither of the fragments preserves indicative sulci. However, on the ventral surface of one of the fragments, there are changes in the orientation of the bone tissue, with a “sulcus-like” separation of the patterns (Fig. 3F, red arrows), similar to that present in a recently described middle Miocene tortoise from the Castilletes Formation of northern Colombia (Cadena and Jaramillo, in 2015, fig. 6.6). On the dorsal surface of both costal fragments there is possible evidence of bite-marks represented by a rounded-circular and slightly deep pit, one in each bone. However, considering that no crocodile fossils have yet been discovered at Quebrada Honda, these pits could have been caused by bioerosion or another taphonomic process.

UATF-V-001778 (Fig. 3H–I) corresponds to a right xiphiplastron, missing its most anteromedial portion. On the ventral surface, there is a clearly defined sulcus between the anal and the femoral scutes. The most posterior tip of the xiphiplastron has a relatively flat facet, evidencing a very robust anal scute tip.

**Remarks** – The morphology of the scapula-acromion described here and its large size resemble the pectoral girdle elements of both the extant Galapagos giant tortoise *Chelonoidis nigra* and fossils representatives of the genus such as *Ch. lutzae* (Zacarias et al., 2013) from the late Pleistocene of Argentina. The turtle shell elements from Quebrada Honda also resemble other fossil tortoises from South America such as the early to middle Miocene tortoise from the Castilletes Formation of Colombia (Cadena and Jaramillo, 2015). Nevertheless, there are no undisputable diagnostic features that permit genera of tortoises (Testudinidae) to be distinguished based only on pectoral girdle elements and shell fragments. A major obstacle to understanding the evolution of tortoises in South America is the lack of complete articulated skeletons with associated cranial and postcranial elements. Such remains would make it possible to determine whether all of these fossils truly belong to a single genus or to several genera of which only one is still alive today.

TESTUDINES Batsch, 1788.

PANPLEURODIRA sensu Cadena and Joyce, 2015.

CHELIDAE Lindholm, 1929.

*Acanthochelys* Gray, 1873.

cf. *Acanthochelys*.

Fig. 4.

Referred material – UATF-V-001850 (left xiphiplastron).

Locality and geological age – same as for cf. *Chelonoidis*, mentioned above.

Description and comparisons – UATF-V-001850 is a left xiphiplastron bone, missing a portion of its medial and lateral margins at the femoro-anal sulcus level, having a maximum width as preserved of 3.6 cm and maximum length as preserved of 4.5 cm, indicating a juvenile turtle (Fig. 4A–D). In dorsal view (Fig. 4A and B), the pubis scar is oval in shape and the ischium scar is triangular elongated in shape, projected medially. A relatively wide and positive relief surface (lip) that runs almost parallel to the lateral margin of the bone indicates the area that was covered by the anal and femoral scutes; it is limited medially by a moderate step before the visceral surface. The contact between the anal and the femoral scutes is indicated a moderate notch on the lateral margin of the xiphiplastron. The anal notch has a wide V-shape. In all these aspects, UATF-V-001850 resembles the xiphiplastra of species of

*Acanthochelys* (see Fig. 5 for comparisons among chelid genera).

The xiphiplastra of *Acanthochelys* spp., including UATF-V-001850, can be distinguished from those of all other South American chelids as detailed below based on our observations of at least one species of each extant genus. *Mesoclemmys* (*M. dahlia*) lacks a wide, continuous lip for the anal and femoral scutes and has a more posteriorly projecting ischium scar. *Platemys* (*P. platycephala*) exhibits a shallower anal notch, which has a wide U-shape in some cases, and has a narrower lip for the anal and femoral scutes. *Phrynops* (*P. geoffroanus*) has an ischium scar that projects more horizontally toward the midline of the plastron and is narrower medially; *Phrynops* also lacks a wide, continuous lip for the anal and femoral scutes, and in some cases exhibits a deeper lateral notch. Xiphiplastra of *Hydromedusa* (*H. tectifera*) differ in having a very narrow ischium scar that is closely positioned to margin of the anal notch margin, which is always very deep, exhibiting either a U (mostly males) or V (mostly females) shape. Because of this deep anal notch, the ischium scar is positioned very close to it and is very narrow along its entire length. Additionally, the lip for the anal and femoral scutes is very narrow in *Hydromedusa*, and the anterior

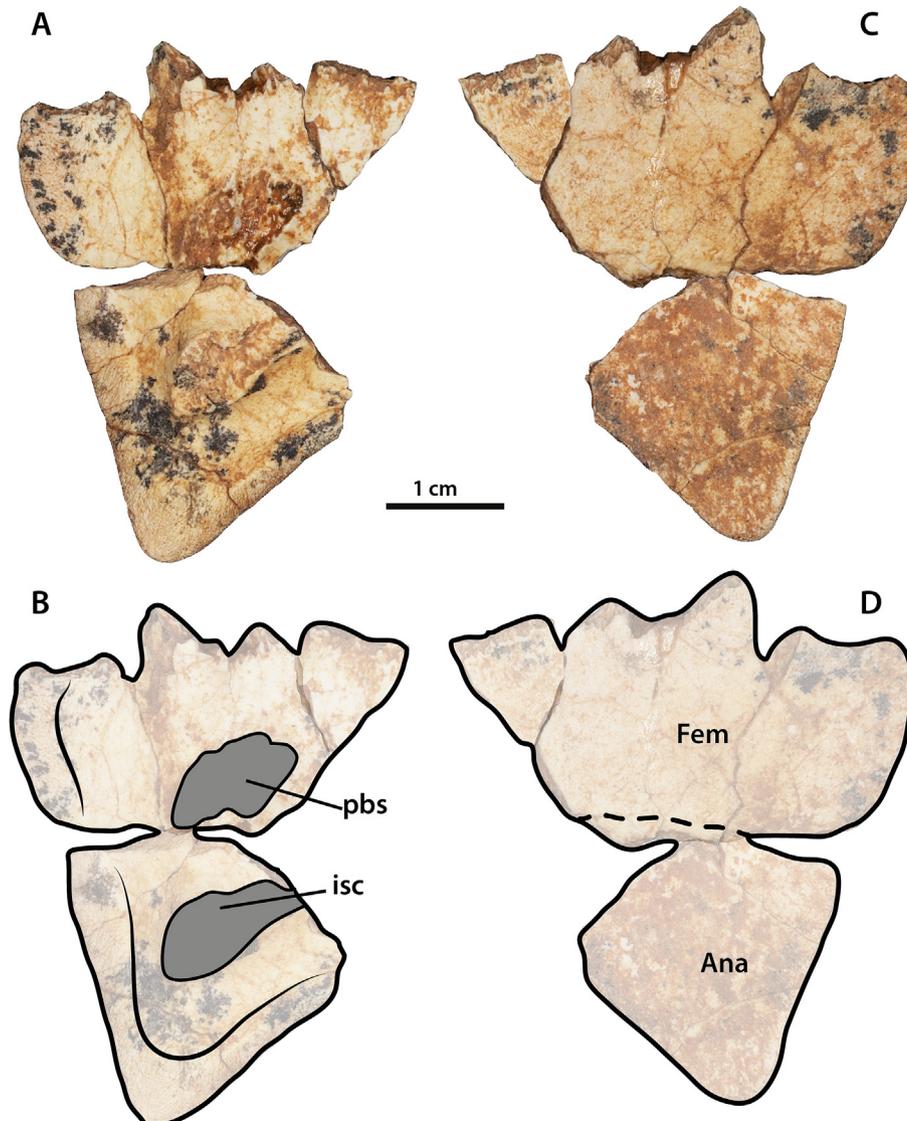
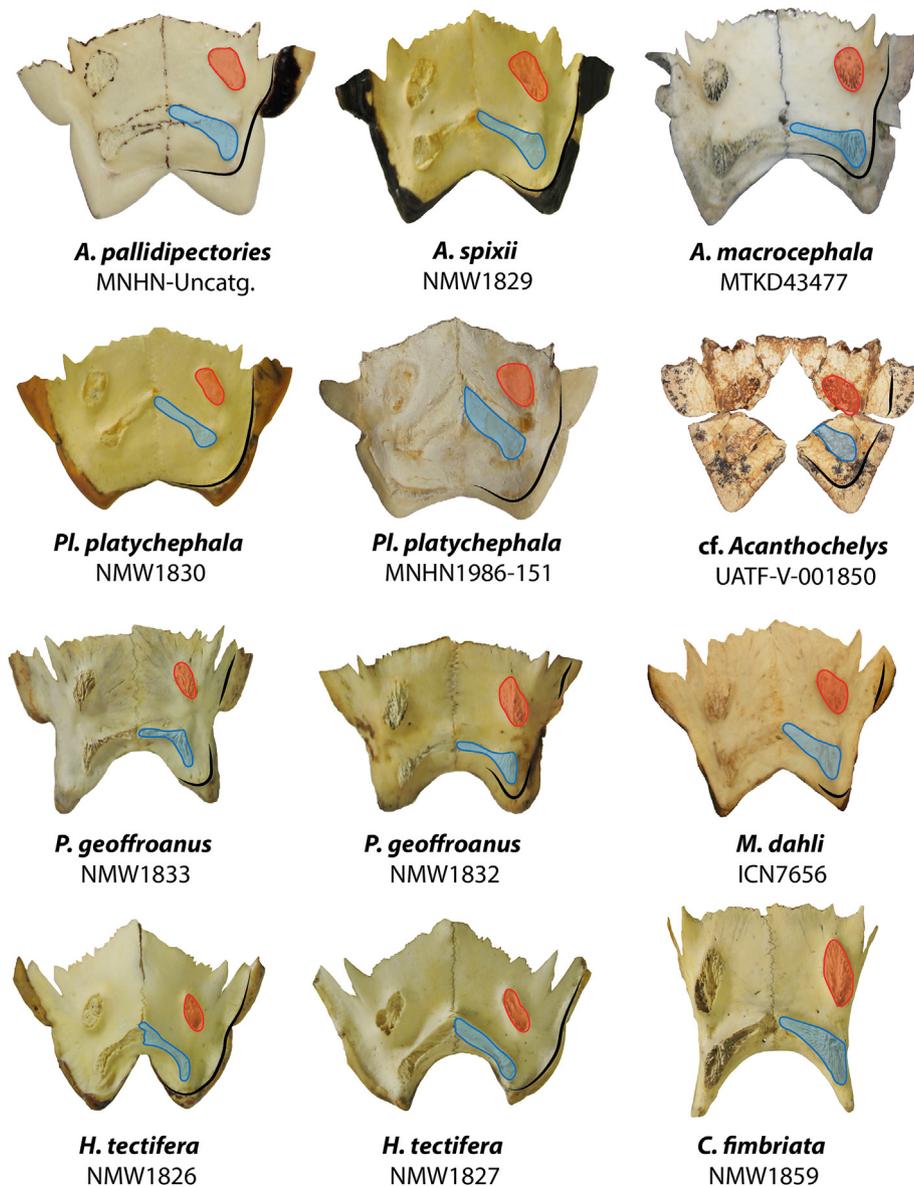


Fig. 4. Left xiphiplastron of cf. *Acanthochelys*. UATF-V-001850. A, B, dorsal view. C, D, ventral view. Abbreviations: Ana, anal scute; Fem, femoral scute; isc, ischium scar; pbs, pubis scar.



**Fig. 5.** Xiphiplastra of extant South American chelids, including at least one species of each extant genus, only juveniles to adult specimens included. Red shadow marks pubis scar, blue shadow marks ischium scar, and black line marks boundary of the lip between anal and femoral scutes. Abbreviations: *A.* *Acanthochelys*; *C.* *Chelus*; *H.* *Hydromedusa*; *M.* *Mesoclemmys*; *P.* *Phrynops*; *Pl.* *Platemys*. Specimens are all to same scale. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

margin of both xiphiplastra (left and right) is very oblique, forming a tapering acute tip medially. *Chelus* (*C. fimbriata*) has: a very wide U-shaped anal notch with long, narrow posterior tips; a ischium scar that almost matches the anal notch in outline and is located very close to it; a pubis scar almost parallel to the midline axis of xiphiplastra; and no well-defined lip for the anal and femoral scutes.

**Remarks** – The xiphiplastron from Quebrada Honda represents a panpleurodire based on the strong suture between the pelvis and the plastron (see Cadena and Joyce, 2015) as evidenced by the pubis and ischium scars. In general, the xiphiplastra of chelids differ from all other pancryptodires, particularly from the south american extant genera *Podocnemis* and *Peltocephalus* in having a deeper lateral notch at the femoroanal sulcus, as well as more inclined (tapering) lateral margins (except *Chelus*), and pubic scar that is oval but less elongated (wider).

## 4. Discussion

### 4.1. Paleobiogeographical implications

The occurrence of giant tortoises at Quebrada Honda, in the Eastern Cordillera of southern Bolivia, expands the paleogeographical distribution of Miocene South American tortoises, which now includes records from: Honda Group, La Venta, Colombia (Wood, 1997); Castilletes Formation, Alta Guajira Peninsula, Colombia (Cadena and Jaramillo, 2015); Gaiman and Sarmiento formations, Chubut Valley (Chubut province) and Andalhualá Formation, (Catamarca province), Argentina (de la Fuente et al., 2014 and references therein); and Quebrada Honda, Bolivia (this study). Although the turtle material described here is too fragmentary to allow its inclusion in a phylogenetic study, its closer proximity to Argentina than to the northern South American

localities suggests that it may be related to the tortoises that inhabited southeastern South America during the Miocene such as *Chelonoidis gringorum* (Simpson, 1942) and ?*Ch. gallardoii* (Rovereto, 1914) or even the smaller tortoises from late Oligocene, Petaca Formation of Bolivia (Broin, 1991). Other vertebrates from Quebrada Honda are known to show such a pattern. Quebrada Honda mammals are more similar to those of Miocene sites in Argentina than those of La Venta (Croft, 2007). Similarly, phorusrhacid “terror birds” are known from Quebrada Honda (Croft et al., 2013) and many sites in Argentina but have yet to be reported from northern South America (Alvarenga and Höfling, 2003; Tambussi and DeGrange, 2013).

Currently, five genera of chelid turtles inhabit the lowland fluvial systems of Bolivia (van Dijk et al., 2014): *Chelus*, *Mesochemmys*, *Phrynops*, *Platemys*, and *Acanthochelys*. Thus, the occurrence of cf. *Acanthochelys* in the middle Miocene Quebrada Honda is not surprising from a biogeographical standpoint. Nevertheless, this discovery is very important because represents the first record of fossil chelids in Bolivia as well as the potential earliest occurrence of the genus *Acanthochelys* in South America. Additionally, the occurrence of cf. *Acanthochelys* in the late middle Miocene of Bolivia significantly shortens the ghost lineage for this genus; a recent phylogenetic hypothesis considered *Chelus* and *Acanthochelys* to be sister genera that diverged from one another prior to the early Miocene (see Maniel and de la Fuente, in press).

#### 4.2. Implications for the paleoelevation of the southern Altiplano

Generally turtles are ectotherms, which means they rely on environmental heat sources for normal physiological and metabolic functions (Angilleta and Dunham, 2003). Environmental temperature mainly varies according to latitude and elevation (i.e., higher latitudes and elevations typically experience lower temperatures) (Ashton and Feldman, 2003). Extant tortoises are globally distributed and inhabit a wide range of latitudes spanning tropical to temperate zones in all continents except Australia (Rhodin et al., 2010). However, in terms of elevation or altitude in meters above sea level, they tend to be restricted to areas of low elevation: 0 to ~1200 m in the case of North American tortoises (Morafka et al., 1989; Nussear et al., 2009), 0 to ~1800 m for Asian, European, and African tortoises (Stubbs, 1989; Broadley, 1989), and only 0–~950 m for South American *Chelonoidis* (Fig. 6A) (GBIF, 2015; see Supplementary Data 2). There is no evidence of any large, sustainable population of extant South American continental tortoises living at elevations higher than 900 m, at least not that has been scientifically confirmed by coordinates and precise elevation data. This could be due to the challenges any ectotherm must face when living at very high elevation, including hypoxia, cold temperatures, and intense UV radiation (Yang et al., 2015). Giant tortoises in continental areas such as the one described here may have been more resilient than smaller tortoises and behaved like endotherms during basking by increasing their body temperature (Barrick et al., 1999; references there in) and retaining heat better in cooler areas. However, we consider it unlikely that the giant tortoise from Quebrada Honda could have developed and completed metabolic and physiological requirements at Quebrada Honda if the site were located at elevations between 2000 and 3200 m, as estimated from isotopic analyses (Garziona et al., 2014). At these high elevations, the mean annual temperature can be below the critical temperature not only for the existence of adult tortoises, but also for the incubation of eggs (<10 °C; Huey, 1982). Indeed, Garziona et al. (2014) estimated the mean annual air temperature (MAAT) at Quebrada Honda at 4–13 °C. A low paleoelevation, probably below 1000 m, is further supported by the occurrence of a freshwater chelid (cf. *Acanthochelys*) at Quebrada Honda. Extant chelids

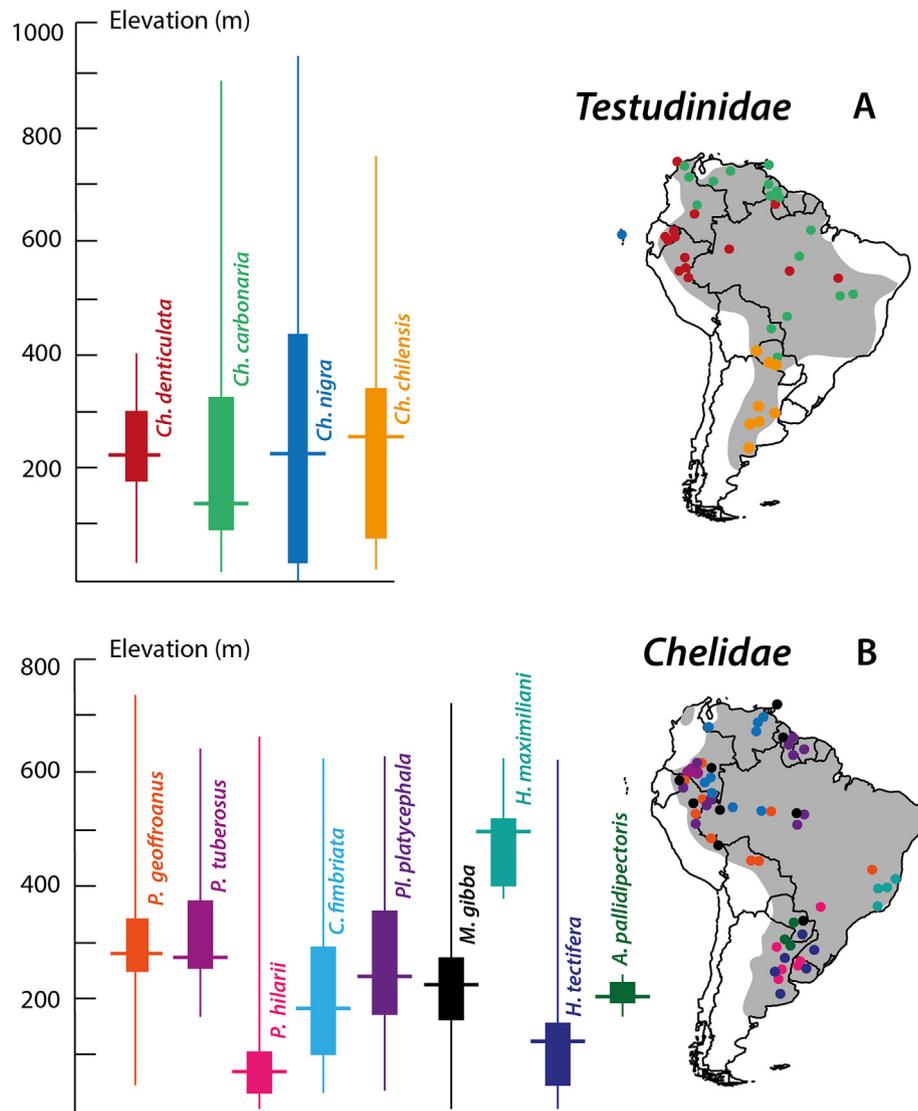
presently do not inhabit elevations higher than ~800 m, (see Fig. 6B, and Supplementary Data 2), and are restricted to fluvial systems, mostly in lowlands.

The hypothesis of a lower paleoelevation for this particular region of the southern Altiplano is also supported by the discovery of a large fossil snake in the same stratigraphic levels as the tortoise and chelid specimens described here (J. Head, personal communication). Several groups of Quebrada Honda mammals, including astrapotheres (Astrapotheria: Astrapotheriidae) and palaeothentid marsupials (Paucituberculata), may also indicate a lower paleoelevation. Astrapotheres and palaeothentids were widespread in South America through the early middle Miocene, became restricted to tropical latitudes during the late middle Miocene, and apparently went extinct by the late Miocene (Bown and Fleagle, 1993; Dumont and Bown, 1997; Johnson and Madden, 1997; Goillot et al., 2011; Vallejo-Pareja et al., 2015). This Miocene biogeographic pattern parallels that of platyrrhine primates and porcupines (Rodentia: Erethizontidae), mammals that today are restricted to tropical to subtropical, generally forested habitats. The most likely explanation for these changes is that they are associated with the contraction of warm, humid habitats concomitant with global cooling following the middle Miocene Climatic Optimum (MMCO) (e.g., Pascual et al., 1996; Ortiz-Jaureguizar, 2003). Thus, the presence of an astrapothere and several species of palaeothentids at Quebrada Honda suggests late middle Miocene environmental conditions similar to tropical lowlands (i.e., northern South America) rather than temperate latitudes and/or higher elevations (i.e., southern South America). The same may be true of the rodents *Mesoprocta hypsodus* (family Dasyproctidae), *Quebradachondomys potosiensis* (family Echimyidae), and *Acarechimys* sp. (superfamily Octodontoidea) (see Croft et al., 2011). The recent discovery of astrapothere remains at the early middle Miocene site of Cerdas, Bolivia (Croft, in prep), further argues against a significant elevation difference between these two sites; the paleoelevation of Cerdas was estimated by Garziona et al. (2014) at 400–1800 m.

Although no plant fossils have been identified from Quebrada Honda, paleoelevation estimates for two other Miocene sites in Bolivia based on foliar physiognomy suggest that the Altiplano experienced MAATs of roughly 16–24 °C and likely had an elevation <1600 m ( $\pm 1000$  m) through the early late Miocene (Gregory-Wodzicki et al., 1998; Gregory-Wodzicki, 2002). These estimates are concordant with those based on clumped isotopes for Cerdas but are lower than clumped isotope estimates for Quebrada Honda. The faunal data reported here support estimates based on plant physiognomy and suggest that clumped isotope data may overestimate paleoelevation in the case of Quebrada Honda. In this regard, Garziona et al. (2014:179) note that their method “results in a minimum MAAT estimate that would tend to over-predict paleoelevations” and that “this method is most accurate for paleosols that formed at higher elevations.” The discrepancy between these lines of evidence could result from high levels of precipitation at Quebrada Honda and/or greater depth of carbonate formation, both of which could result in lower apparent soil temperatures and therefore greater apparent elevation estimates (Garziona et al., 2014).

#### 4.3. Taphonomic and possible reworking considerations

We exclude a potential reworking event of these fossils from older sequences for two reasons. First, from a taphonomic standpoint, the bone preservation resembles that of other, more complete fossils found at the site, principally mammals, which include complete skulls and partial skeletons. The occurrence of articulated bones such as the coracoid and scapula-acromion also argue



**Fig. 6.** Box plots of altitudinal ranges for the four extant species of *Chelonoidis* and nine species of chelids, obtained from GBIF (2015). A, box plot for elevation in meters (m), for *Chelonoidis denticulata*, *Ch. carbonaria*, *Ch. nigra* and *Ch. chilensis*. B, box plot for elevation in meters (m), for *Phrynops geoffroanus*, *P. tuberosus*, *P. hiliarii*, *Chelus fimbriata*, *Platemys platycephala*, *Mesoclemmys gibba*, *Hydromedusa maximiliani*, *H. tectifera*, and *Acanthochelys pallidipectoris* (raw data in Supplementary Data 2). Median values are designated by horizontal bars and the range is designated by the vertical line. The upper and lower edges of the box are the 25th and 75th percentiles. The locations of the specimens are shown in the South America map. Gray shadow represents the composite total geographic distribution for Testudinidae and Chelidae in South America based on van Dijk et al. (2014).

against reworking, as does the absence of extreme abrasion-erosion of the bone surface. Nevertheless, it is possible that the bones went through some transport inside the fluvial-floodplain system before final burial. Second, the Miocene sequence at Quebrada Honda is underlain by partly metamorphosed Paleozoic strata. No fossil bones have been reported from these levels, and turtles of this age have never been reported.

## 5. Conclusion

The discrepancies among paleoelevation estimates for the middle Miocene of Quebrada Honda based on fossil tortoise and chelid remains (this study) and stable isotopes (Garzzone et al., 2014) demonstrate the importance of additional sampling of these and other types of proxies in this section as well as in other sedimentary sequences in the area (e.g., Río Rosario). This will permit a more refined understanding of the distribution of isotopic values within the section as well as factors independent of

temperature that could affect isotope-based paleotemperature estimates. Similarly, additional sampling of the fossil record may reveal additional middle Miocene herpetofauna including other elevation/temperature-limited lineages such as crocodiles and freshwater turtles.

## Acknowledgments

We thank D. Auerbach, M. de la Fuente, C. Garzzone, L. Gibert, C. Jaramillo, and B. Saylor for helpful discussions of topics addressed in this contribution; T. Matson and R. Mulheim (Cleveland Museum of Natural History); B. Carroll and D. Chapman (Cleveland Museum of Natural History) for assistance with fossil preparation and specimen curation; D. Auerbach, P. Cabrera, A. Carlini, P. Carlini, A. Catena, R. Chavez, M. Ciancio, J. Conrad, A. Deino, N. Drew, C. Garzzone, L. Gibert, P. Higgins, B. MacFadden, G. Mendez, B. Saylor, and J. Smith for assistance in the field; R. Krajci of think[box] at Case Western Reserve University for assistance with scanning UATF-V-

001867. We also that the Facultad de Ingeniería Geológica of the Universidad Autónoma Tomás Frías for supporting fieldwork at Quebrada Honda. Funding for this research was provided by the National Geographic Society Committee for Research and Exploration (NGS 8115-06 to D. Croft), the National Science Foundation (EAR 0958733 to D. Croft), and Alexander Von Humboldt Foundation (Georg Forster Fellowship), Germany. Special thanks to the three reviewers of the manuscript.

## Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jsames.2015.10.013>.

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