

CRANIAL VARIATION IN *BAIRDEMYS* TURTLES (PODOCNEMIDIDAE: MIOCENE OF THE CARIBBEAN REGION) AND DESCRIPTION OF NEW MATERIAL FROM URUMACO, VENEZUELA

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SYNOPSIS Four new skulls referable to *Bairdemys*, from the Late Miocene Urumaco Formation in Venezuela, are described and compared with other specimens allocated to this genus. Several characters previously used to distinguish *B. hartsteini* (Cibao Formation, middle Miocene of Bayamon, Puerto Rico) from *B. venezuelensis* (Urumaco Formation) are present in the new Urumaco specimens, which show a mosaic of features from both species as originally diagnosed. Features of another *Bairdemys* skull from the Castillo Formation in the early Miocene of Lara State, Venezuela are unique, suggesting this is a new species, but poor preservation of known specimens prevents a formal diagnosis. In *Bairdemys* from Castillo the ventral surface of the secondary palate is proportionally larger in size, correlated with a smaller width of the internal nares and the distance between the foramina palatinae is relatively shorter. The ventral position of the quadrate in relation to the basisphenoid is far more posterior in the Castillo *Bairdemys* than in any other known specimen of this genus.

The lower jaw of a *Bairdemys* specimen from Urumaco is described for the first time and compared to that of several Recent and fossil *Pelomedusoides* taxa. The specimen from Urumaco has a relatively large triturating surface, a large and wide dorsal opening of the fossa meckelii, a curved tomial ridge that slopes dorsally, a curved labial ridge that is less acute than in *Podocnemis* and no obvious accessory ridges comparable to ridges in *Podocnemididae*. Several shared features separate *Bairdemys* and *Stereogenys* from other fossil and Recent *Podocnemididae*.

KEY WORDS Pleurodira, *Podocnemididae*, taxonomy, Neogene, Caribbean, skull, jaw

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INTRODUCTION

The turtle fauna from the Urumaco Formation in Venezuela is remarkable because of singular occurrences and exceptional species (Sánchez-Villagra *et al.* 2003; Aguilera 2004). These include the world's largest extinct turtle (Wood 1976a), the first reliable reported occurrence of a trionychid in South America (Wood & Patterson 1973), and a fossil species of the matamata turtle (Wood 1976b; Bocquentin-Villanueva 1988; Sánchez-Villagra *et al.* 1995). But the most common turtle in Urumaco is the podocnemidid *Bairdemys venezuelensis*, described originally by Wood & Díaz de Gamero (1971) as a new species of *Podocnemis* and recently placed in the newly erected genus, which also includes the extinct *B. hartsteini* from the middle Miocene of Puerto Rico (Gaffney & Wood 2002). In the original species description only the carapace was reported. Later discoveries were the basis of the recent revision of Gaffney & Wood (2002) of skull material associated with carapaces. *Bairdemys* has also been reported from the early Miocene of the Castillo Formation in Venezuela (Sánchez-Villagra *et al.* 2000, 2004).

Here we present an analysis and comparison of *Bairdemys* skulls based on the study of new material and a revision of previously described specimens from Urumaco as well as a description of the first known lower jaw in this species. Our aim is to provide new anatomical and morphometric information for the genus and discuss its taxonomic implications.

The anatomy of the lower jaw in Pelomedusoides has been described only in a few species. The lower jaw of *Podocnemis expansa* was described in detail by Fuchs (1931). Additional data and comparisons have been provided in contributions describing fossil Pelomedusoides (e.g. Broin 1971, 1991; Tong *et al.* 1998; Lapparent de Broin 2000; Gaffney & Forster 2003).

The genus *Bairdemys* has a cavum pterygoideus and belongs to the Podocnemididae (Gaffney & Wood 2002). Its relation to the *Shweboemys* Group (Gaffney & Wood 2002) is based on a secondary palate, which is well developed in this genus. According to Gaffney & Wood (2002), five features characterise only *Bairdemys*: (1) triturating surface is ventrally more convex than in all other species of the *Shweboemys* Group, (2) bone separates the Eustachian tube from the rest of the fenestra postotica, (3) small and slit-like antrum postoticum, (4) dorsal surface of frontal and prefrontal is extremely convex and (5) palatine does not contact parietal due to the jugal-ptyergoid contact. Four additional characters with diagnostic importance within the *Shweboemys* Group are (1) *Bairdemys* and '*Shweboemys*' *gaffneyi* have a shorter secondary palate, (2) *Bairdemys* and '*Shweboemys*' *gaffneyi* have curved medial edges of the palatine, (3) basisphenoid of *Bairdemys* and '*Shweboemys*' *antiqua* is separated from palatines by pterygoids which contact medially, (4) *Bairdemys* and *Shweboemys pilgrimi* have a longer basioccipital (Gaffney & Wood 2002).

Institutional abbreviations used in the text are: AMNH, American Museum of Natural History, New York; CURS, Colección Alcaldía de Urumaco, Rodolfo Sánchez; LACM,

Los Angeles County Museum of Natural History; MBLUZ-P, Museo de Biología de la Universidad del Zulia, Paleontología; MCNC, Museo de Ciencias Naturales de Caracas; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge; NHM, Natural History Museum, London.

MATERIALS AND METHODS

Four new skulls belonging to *Bairdemys* were examined: CURS 98, CURS 96, CURS 97 and CURS 99, the first very well preserved specimens. In addition, the following previously described specimens were studied: MCNC-Pal-21-10708 (MCNC-Pal-0001 of Gaffney & Wood 2002) and MCNC-Pal-21-10707 (MCNC-Pal-0002 of Gaffney & Wood 2002). All these skulls were collected in Urumaco (see below). We also studied *Bairdemys* reported from the early Miocene of the Castillo Formation in Venezuela, represented by an almost complete skull, AMNH 30000, a cast, MBLUZ-P-1887 (Sánchez-Villagra *et al.* 2000), and a large cranial portion, MBLUZ-P-5045 (Sánchez-Villagra *et al.* 2004).

Thirteen skull characters were examined, 10 of which are new. Characters 1 (snout shape), 2 (premaxillary notch) and 11 (palatal depressions) are taken from Gaffney & Wood (2002). Our own observations were carried out on the specimens listed above and characters were also coded for every specimen figured in Gaffney & Wood (2002). Different degrees of preservation meant that not every character could be detected or measured in all specimens examined. Skull terminology follows Gaffney (1972).

Skull measurements were taken following Gaffney & Wood (2002), with some modifications (Fig. 1; Table 1). In order to describe skull proportions several ratios were created, including: (1) maximum width of skull/midline length (see Fig. 1: measurements 2/1), (2) skull height at occipital condyle/midline length, (3) width between orbits/maximum width of skull (Fig. 1: measurements 3/2).

A lower jaw belonging to the *Bairdemys* specimen MCNC-Pal-21-10708 is also described. Measurements taken and features described are based, for the most part, on Gaffney *et al.* (1998), where a description of the lower jaw of an unnamed Podocnemididae is provided. Comparisons with other Recent and fossil Pelomedusoides are based on data in the literature and on observations of the following specimens: *Podocnemis unifilis* NHM 60.4.16.10, NHM 72.4.29.9, NHM 60.4.16.9; *Podocnemis expansa* NHM 72.4.29.8; *Pelomedusa subrufa* NHM 87.3.11.10; *Pelusios gabonensis* NHM 87.3.11.10; *Pelusios niger* NHM 1974.3.01.2, NHM 1974.2.47.8; *Pelusios subniger* NHM 70.5.5.4.

The only known preserved jaw of another member of the *Shweboemys* Group is that of *Stereogenys cromeri* from the middle Eocene of Fayum, Egypt, which is depicted in Andrews (1906: plate 25, figs 3–4). The lower jaw of *Erymnochelys*, Recent and from the upper part of the late Cretaceous Maevarano Formation, Madagascar and *Roxochelys*, from the early Paleocene Santa Lucía Formation, Bolivia, are described in Gaffney & Forster (2003) and Broin (1991),

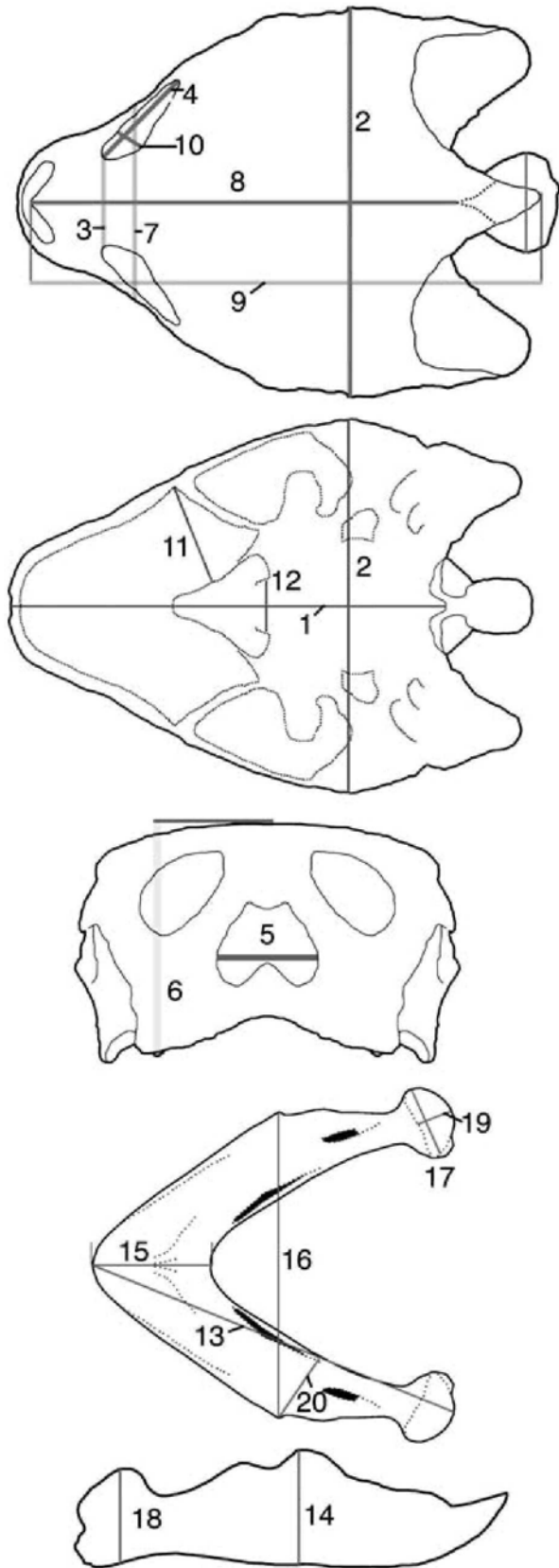


Figure 1 Sketches of skull and lower jaw measurements listed in Tables 1 and 4. Sketch of skull based on idealised specimen CURS 98, sketch of lower jaw based on idealised Podocnemididae. Measurements 1, 2, 4–8, 10 and 11 taken from Gaffney & Wood (2002), measurements 3 and 9 have been modified. Measurements 13–20

respectively. Following Meylan (1996) *Erymnochelys* and *Roxochelys* are close relatives of the *Shweboemys* Group.

Locality data

CURS 96–99 were found approximately 2 km North of El Picache, North of the town of Urumaco ($11^{\circ} 14' 40''$ N, $70^{\circ} 14' 44''$ E), Municipio Urumaco, Estado Falcón (*contra* Aguilera 2004: 83, who stated that they were found in the El Hatillo locality). The fossil-bearing rocks are from the upper member of the Urumaco Formation, stratigraphically below the ‘capa de huesos’ of Corralito (Díaz de Gamero & Linares 1989). Specimens were collected by Rodolfo Sánchez and Daryl Domning in 2002. CURS 98 was associated with a carapace, which was left in situ (R. Sánchez, pers. comm.).

The lower jaw was found in Corralito, 8 km North of Urumaco, $11^{\circ} 14' 56''$ N, $70^{\circ} 16' 10''$ W (Aguilera 2004: 81). Stratigraphically, the sediments belong to the Upper Member of the Urumaco Formation (Díaz de Gamero & Linares 1989). This lower jaw is associated with the skull MCNC-Pal-21-10708 (MCNC-Pal-0001 of Gaffney & Wood 2002; Aguilera 2004: 81), which was attributed to *Bairdemys venezuelensis* by Gaffney & Wood (2002).

RESULTS

Description and comparison of skull characters

Table 2 summarises the information presented in the character descriptions of the new material (Figs 2 & 3) and in the discussion on the Castillo specimen (Fig. 4) that follows, excluding characters 12 and 13 which do not relate to the material from Urumaco. For comparison, characters 1–11 below were also coded for the Castillo specimen. The distribution of character states listed in Table 2 was summarised graphically for several *Bairdemys* specimens (Fig. 5). Fig. 6 illustrates CURS 98 with partially reconstructed sutures.

Character 1. Snout shape. Gaffney & Wood (2002: figs 6 & 12) figure *B. hartsteini* as having a pinched snout and *B. venezuelensis* as having a straight one. Gaffney & Wood’s (2002: fig. 4) reconstruction of *B. venezuelensis* was reportedly based on several specimens (MCZ 9417, MCZ 9418, MCNC-Pal-21-10707, MCNC-Pal-10708). The condition in that reconstruction is different to the

relate to the lower jaw. 1, midline length as preserved; 2, maximum width; 3, width between orbits; 4, width of right orbit; 5, width of external nares; 6, maximum height at quadrate; 7, width of skull at middle of orbits; 8, length from anterior margin of prefrontals to posterior margin of parietals; 9, length from the anterior margin of prefrontals to posterior margin of supraoccipitals; 10, height of right orbit; 11, anterior width of left triturating surface; 12, width between foraminae palatini posterius; 13, total length along long axis of jaw; 14, height of jaw at processus coronoideus; 15, length of triturating surface at symphysis; 16, width of jaw at processus coronoideus; 17, width of area articularis mandibularis; 18, maximum height at area articularis; 19, length of area articularis mandibularis; 20, width of rami at processus coronoideus.

Table 1 Skull measurements (in mm) from specimens of *Bairdemys* spp.

Measurement no. in Fig. 1	Skull measurements	CURS 96	CURS 97	CURS 98	CURS 99	AMNH 30000
1	Midline length as preserved	82 [†]	111.2	115.8	97.5 [†]	92.6 [†]
2	Maximum width	88	82.4	101.5	92.4 [†]	88.1
3	Width between orbits	18.4	17.9	22.3	–	22
–	Width of left orbit	21.4	27.1	28.9	–	21.2
4	Width of right orbit	23.1	27.4	27.7	–	22.4
5	Width of external nares	23.7	15.3 [‡]	24.5	20.1	17.5
–	Width of internal nares	6	–	5.3	6.4	5.1
6	Maximum height at quadrate	44.7 [†]	46.2 [†]	60.8	52.9	55
7	Width of skull at middle of orbits	52.9	45.5	54.4	56.5 [†]	52.9
8	Length from anterior margin of prefrontals to posterior margin of parietals	94.8	–	113.8	–	80.8 [‡]
9	Length from the anterior margin of prefrontals to posterior margin of supraoccipitals [§]	103.3	–	132.6	–	88.2 [‡]
–	Height of left orbit	20.3	20.7	24	–	21
10	Height of right orbit	22.6	21.1	22	–	20
–	Skull height at occipital condyle	38.9	41.4 [‡]	44.5	42.8	40.2 [‡]
11	Anterior width of left triturating surface [§]	25.8	–	30.3	26.2	32.1
–	Anterior width of right triturating surface	27.5	–	30.1	28.4	31.6
–	Posterior width of left triturating surface [§]	–	–	19.1	20.8	27
–	Posterior width of right triturating surface	20.4	–	22.1	21.9	24
12	Width between foraminae palatini posterius [§]	19	–	23.9	22.5	17.6 [‡]
–	Length from front of skull to median anterior edge of condylus articularis [§]	–	84.7	95.5	–	56.6 [‡]

See the text and Fig. 1 for explanations.

[†]Damaged.

[‡]Estimated.

[§]Modified measurements from Gaffney & Wood (2002).

Bairdemys specimen depicted in fig. 11 in Gaffney & Wood (2002) and in CURS 98 (Fig. 2). The snout shape in fig. 2 of Gaffney & Wood (2002) is illustrated as being straight, but the snout of specimen MCNC-Pal-21-10708 (their fig. 11) referred to *B. venezuelensis* is pinched. In CURS 98 the snout is also pinched. Four specimens referred to *B. venezuelensis* were studied by Gaffney & Wood (2002: *Bairdemys venezuelensis* MCZ 9417 (Gaffney & Wood 2002: fig. 7) shows a straight snout shape, as does CURS 97 (Fig. 3) and AMNH 30000 (Fig. 4). As described by Gaffney & Wood (2002: fig. 15), *B. hartsteini* (AMNH 27222) has a pinched snout shape.

Character 2. Premaxillary notch. Following Gaffney & Wood (2002) a premaxillary notch (Fig. 7A) is present in *B. hartsteini* (AMNH 27222) (Gaffney & Wood 2002: table 1, fig. 14) and absent in *B. venezuelensis* (Gaffney & Wood 2002: table 1, fig. 6). However, a premaxillary notch is present in MCZ 9418, referred by Gaffney & Wood (2002: fig. 9) to *B. venezuelensis*. CURS 98 (Fig. 2) and AMNH 30000 (Fig. 4) also have a premaxillary notch, whereas MCZ 9417 does not (Gaffney & Wood 2002: fig. 7).

Character 3. Basisphenoid shape. Three different shapes of the basisphenoid have been recorded in the skulls examined: triangular (anteriorly pointed and posteriorly more or less straight), oval (anteriorly rounded) and rectangular (basisphenoid is not pointed posteriorly but rather is parallel to its basioccipital contact). The basisphenoid in MCZ 9417 is oval, in MCNC-Pal-21-10707 it is triangular (Gaffney & Wood 2002: figs 6 & 8) and in CURS 98 (Fig. 2) it is rectangular. AMNH 27222 shows either a triangular or rectangular shaped basisphenoid (the anterior top of the basisphenoid is not preserved), whereas the shape of an oval basisphenoid is most unlikely (Gaffney & Wood 2002: fig. 12).

Character 4. Maxillary–jugal suture. The maxillary–jugal suture extends from the ventral border of the orbita with two different orientations: (1) it runs vertically towards the ventral border of the maxilla in MCZ 9417 (Gaffney & Wood 2002: fig. 6) and CURS 98 (Fig. 2), or (2) it runs more or less horizontally, ending not on the ventral border of the maxilla but rather more dorsally (Gaffney & Wood 2002: fig. 14), as in AMNH 27222,

Table 2 Comparison of skull characters in specimens of *Bairdemys* spp.

Characters	CURS 96	CURS 97	CURS 98	MCNC-Pal-21-10707	MCNC-Pal-21-10708	MCZ 9417	MCZ 9418	AMNH 27222	AMNH 30000
1. Snout shape [†]	-	Straight	Pinched	-	Pinched	Straight	-	Pinched	Pinched
2. Premaxillary notch [†]	-	-	Present	-	Present	Absent	Present	Present	Present
3. Basisphenoid shape	-	-	Rectangular	Triangular	-	Oval	-	Triangular/rectangular	-
4. Maxillary/jugal contact	-	Vertical	Vertical	-	Horizontal	Vertical	Horizontal	Horizontal	-
5. Squamosal shape	-	-	Pointed	-	Pointed	Pointed	-	Flat	-
6. Basisphenoid/cavum pterygoideus/cp. contact	-	-	Present	Present	Absent	Absent	-	Present	Present
7. Maxillary/palatine contact	-	-	Ends lateral	Ends lateral	-	Ends lateral	-	Ends Medial	Ends medial
8. Orbital position	Horizontal	-	Vertical	-	Horizontal	Horizontal	-	Vertical	Horizontal
9. Palatine/pterygoid contact	Wide	-	Wide	-	-	Narrow	-	-	Narrow
10. Crista supraoccipitalis	Longer	-	Longer	-	-	-	-	Shorter	-
11. Palatal depressions [†]	(Shallower)	-	Deeper	-	-	(Deeper)	-	Shallower	Deeper

See the text for details.

[†]Characters taken from Gaffney & Wood (2002).

AMNH 30000, MCZ 9418 and MCNC-Pal-21-10708 (Gaffney & Wood 2002: figs 9 & 10).

Character 5. *Squamosal shape*. Two different shapes of the squamosal in ventral view have been recorded: either posteriorly pointed and triangular, or posteriorly flat. The latter condition is seen in AMNH 27222 (Gaffney & Wood 2002: fig. 12), which clearly shows a different squamosal shape to the other specimens. MCZ 9417, MCNC-Pal-21-10708 (Gaffney & Wood 2002: figs 6 & 10) and CURS 98 (Fig. 2) show a posteriorly pointed squamosal.

Character 6. *Basisphenoid/cavum pterygoideus*. In some specimens the basisphenoid meets the cavum pterygoideus laterally. This is the case in AMNH 27222, AMNH 30000 (Fig. 4), MCNC-Pal-21-10707 (Gaffney & Wood 2002: fig. 8) and CURS 98 (Fig. 2). In MCZ 9417 and MCNC-Pal-21-10708 (Gaffney & Wood 2002: figs 6 & 10) the basisphenoid has no contact with the cavum pterygoideum.

Character 7. *Maxillary palatine contact*. The maxillary-palatine suture ends on the ventral side of the skull laterally, either close to the lateral-most point of the maxilla or further down (Fig. 7B). The latter is the case only in AMNH 27222 (Gaffney & Wood 2002: fig. 12). However, CURS 98, MCZ 9417 and MCNC-Pal-21-10707 (Gaffney & Wood 2002: figs 6 & 8) clearly show a suture ending laterally close to the lateral-most point of the maxilla.

Character 8. *Orbital position*. Following figs 2A & 3A in Gaffney & Wood (2002) the position of the orbits in relation to the skull differs between *B. venezuelensis* and *B. hartsteini*. The orbits of *B. hartsteini* are figured as being more vertically positioned, so that only their dorsal rims are seen in dorsal view (e.g. AMNH 27222, Gaffney & Wood 2002: fig. 12). The orbits of *B. venezuelensis* are figured as a complete circle in dorsal view and their position within the skull is more lateral than in *B. hartsteini* (e.g. MCNC-Pal-21-10708, Gaffney & Wood 2002: fig. 10). Comparable variation is present in the new sample from Urumaco. Whereas the orbits of CURS 98 (Fig. 2) and CURS 97 are 'vertical' and therefore look like the ones of *B. hartsteini*, those of CURS 96, MCZ 9417 and AMNH 30000 (Fig. 4) are 'horizontal' like the ones of *B. venezuelensis* reconstructed by Gaffney & Wood (2002).

Character 9. *Palatine/pterygoid contact*. As illustrated in fig. 6 in Gaffney & Wood (2002) the region of the ventral contact area of the palatine and pterygoid medial to the processus pterygoideus externus is relatively narrow in MCZ 9417. CURS 97 and CURS 98 show a much wider contact area (Fig. 7B).

Character 10. *Crista supraoccipitalis*. The horizontal and vertical sheets of the crista supraoccipitalis have not been described in *Bairdemys* due to their poor preservation in specimens previously available (Gaffney & Wood 2002: 23, figs 6, 9, 10 & 12). These features are preserved in CURS 98 (Fig. 2). According to Gaffney & Wood (2002) in most Podocnemididae, excluding the

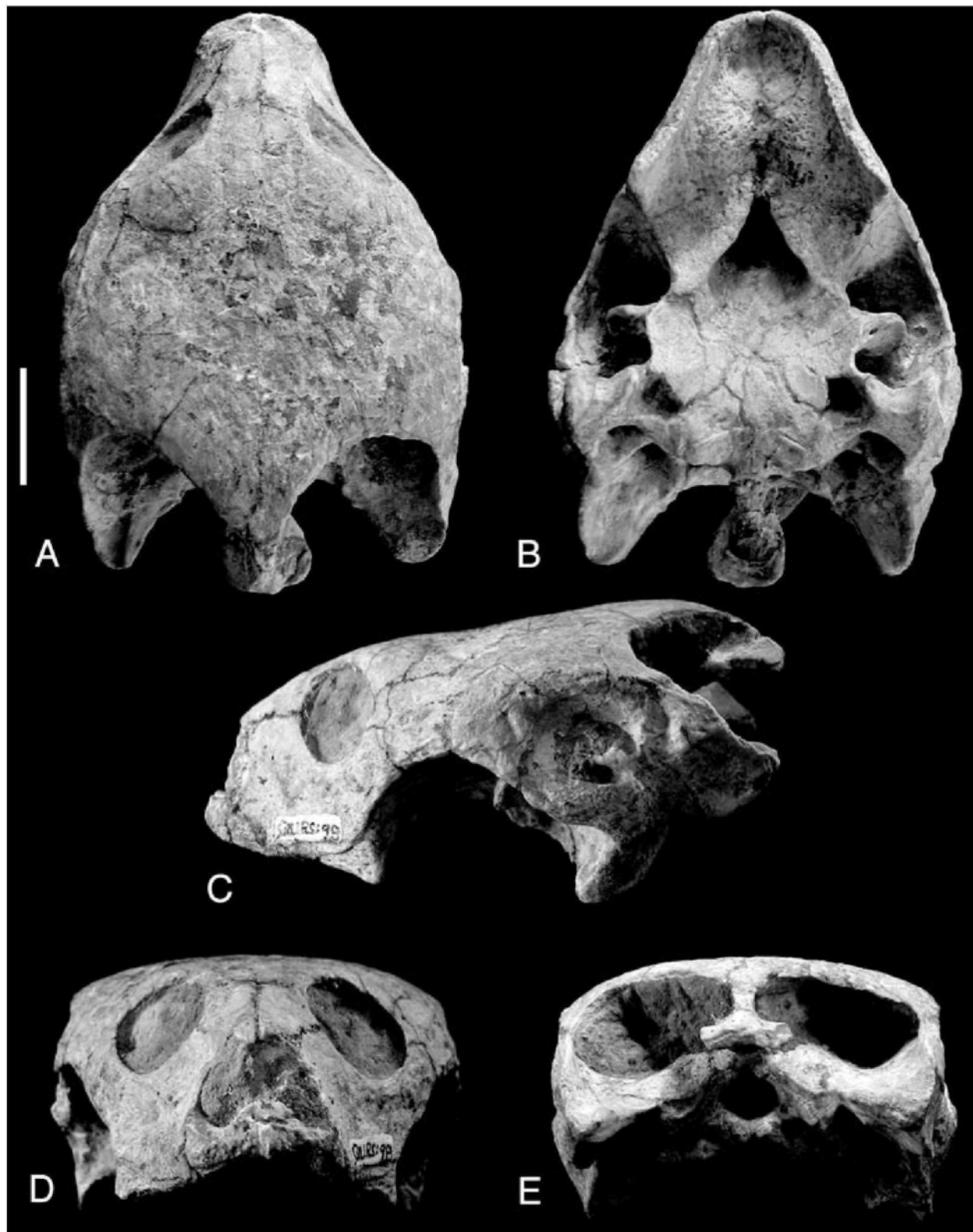


Figure 2 A, Dorsal, B, ventral, C, left lateral, D, anterior and E, posterior views of CURS 98 (*Bairdemys* sp.) from the Urumaco Formation. Scale bar = 30 mm.

Shweboemys Group, the crista is variably thickened and extended only vertically and some *Podocnemis* have a small horizontal extension on the crista's ventral side. In *Bairdemys* this horizontal extension of the supraoccipital

is much larger, elongated to the same extent as the vertical sheet, as in '*Shweboemys*' *antiqua* (Gaffney 1979: fig. 136). In CURS 98 the crista supraoccipitalis is as wide (20.2 mm) as the ventral sheet of the supraoccipital

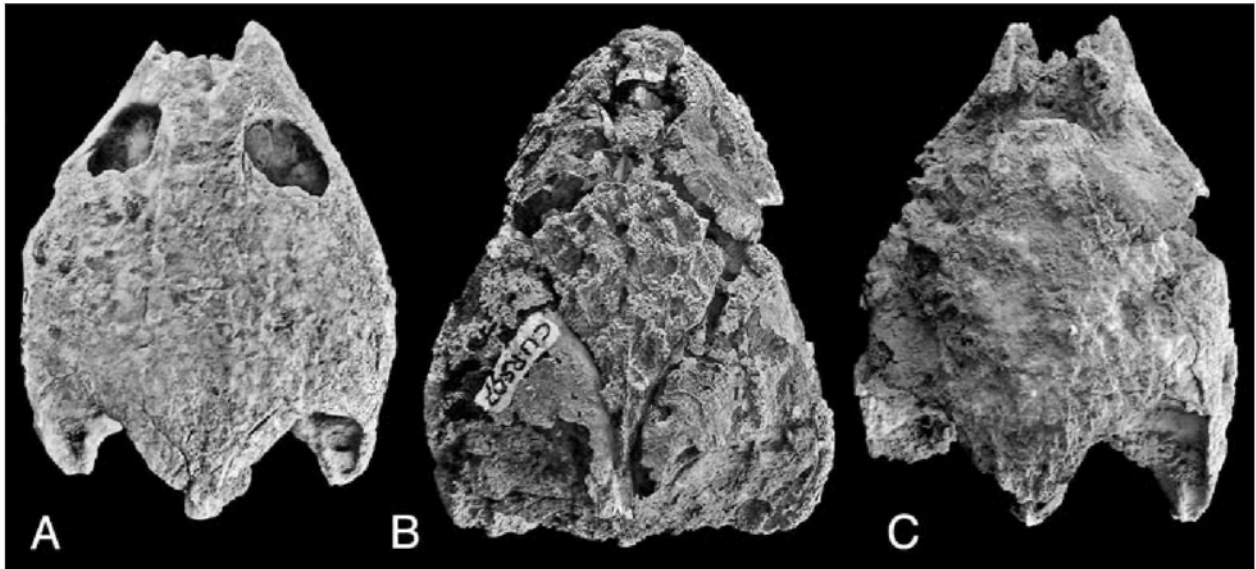


Figure 3 Dorsal views of **A**, CURS 96, **B**, CURS 97 and **C**, CURS 99 (*Bairdemys* sp.) from the Urumaco Formation. Approximately to scale. Maximum width of CURS 96 = 88 mm.

is high (19.9 mm). The length of the horizontal sheet is 19.4 mm. The maximum length of the supraoccipital is 25.7 mm (dorsal), which implies that four-fifths of this bone consists of the horizontal and ventral sheet. At its minimum the supraoccipital is 7.2 mm (ventral) and 4.9 mm (dorsal) and is positioned anterior to the posterior extension of the supraoccipital. Following reconstructions figured in Gaffney & Wood (2002: figs 2A–B; 3A–B) the crista supraoccipitalis is shorter in *B. hartsteini* than it is in *B. venezuelensis* (where it ends, in comparison with the squamosal position, more posteriorly). CURS 98 and 96, both with a preserved squamosal and posterior extension of the supraoccipital, have a longer crista than *B. hartsteini*.

Character 11. Palatal depressions. Gaffney & Wood (2002: table 1) characterised *B. hartsteini* as having shallower palatal depressions than *B. venezuelensis*. In the only new Urumaco specimen in which this feature can be clearly recorded (CURS 98, Fig. 2) the palatal depression appears to be deep, although not having well defined boundaries between alternative states makes this characterisation rather subjective. Specimens AMNH 30000 (Fig. 4) and CURS 96 have shallower palatal depressions than CURS 98.

Features unique to *Bairdemys* from the Castillo Formation

Two features distinguish AMNH 30000 (Fig. 4) and MBLUZ-P-5045 from the Castillo Formation (Sánchez-Villagra *et al.* 2000, 2004) in comparison to all other *Bairdemys* specimens described to date.

Character 12. Size of the secondary palate and distance between foramina palatinae. The ventral surface of the secondary palate is proportionally larger and is correlated

with a smaller width of the internal nares and the distance between the foramina palatinae, which is relatively shorter (not preserved in MBLUZ-P-5045). In addition, the internal nares apparently project further anteriorly in the Castillo specimen (Fig. 7C) and in *B. hartsteini* (Gaffney & Wood 2002: fig. 12) than in *B. venezuelensis* (Gaffney & Wood 2002: fig. 6).

Character 13. Relative position of the quadrate. The ventral position of the quadrate in relation to the basisphenoid is far more posterior in AMNH 30000 (Fig. 4) and MBLUZ-P-5045 than in any other *Bairdemys* specimen. In *Bairdemys* from Urumaco and in *B. hartsteini*, the articular surface of the quadrate, and therefore the jaw joint, is in one line with the posterior end of the basisphenoid (Fig. 2).

Skull proportions of *Bairdemys* spp. (Table 1, Fig. 1)

Bairdemys hartsteini was diagnosed by Gaffney & Wood (2002: 5, table 1) as having a narrower skull than *B. venezuelensis*. However, ratios of overall width to length of the skull in our sample contradict this assessment. The highest ratio of skull width to skull length is detected for MCZ 9417 (1.01), followed by AMNH 27222 (0.93). MCNC-Pal-21-10708 (0.88) and CURS 98 (0.87) are in the same range, whereas CURS 97, with the lowest ratio (0.74), differs significantly. The relation of skull width to skull length in *B. hartsteini* AMNH 27222 follows within the range of variation of the Urumaco specimen.

Two other skull proportions show *B. hartsteini* AMNH 27222 as an outlier: AMNH 27222 has the highest ratio of skull height at occipital condyle to midline length of skull (0.44), followed by MCZ 9417 and CURS 98 with values of 0.39 and 0.38, respectively. The lowest ratio is detected in MCNC-Pal-21-10708 (0.37). AMNH 27222 shows a ratio 11–16% higher than any other specimens measured.

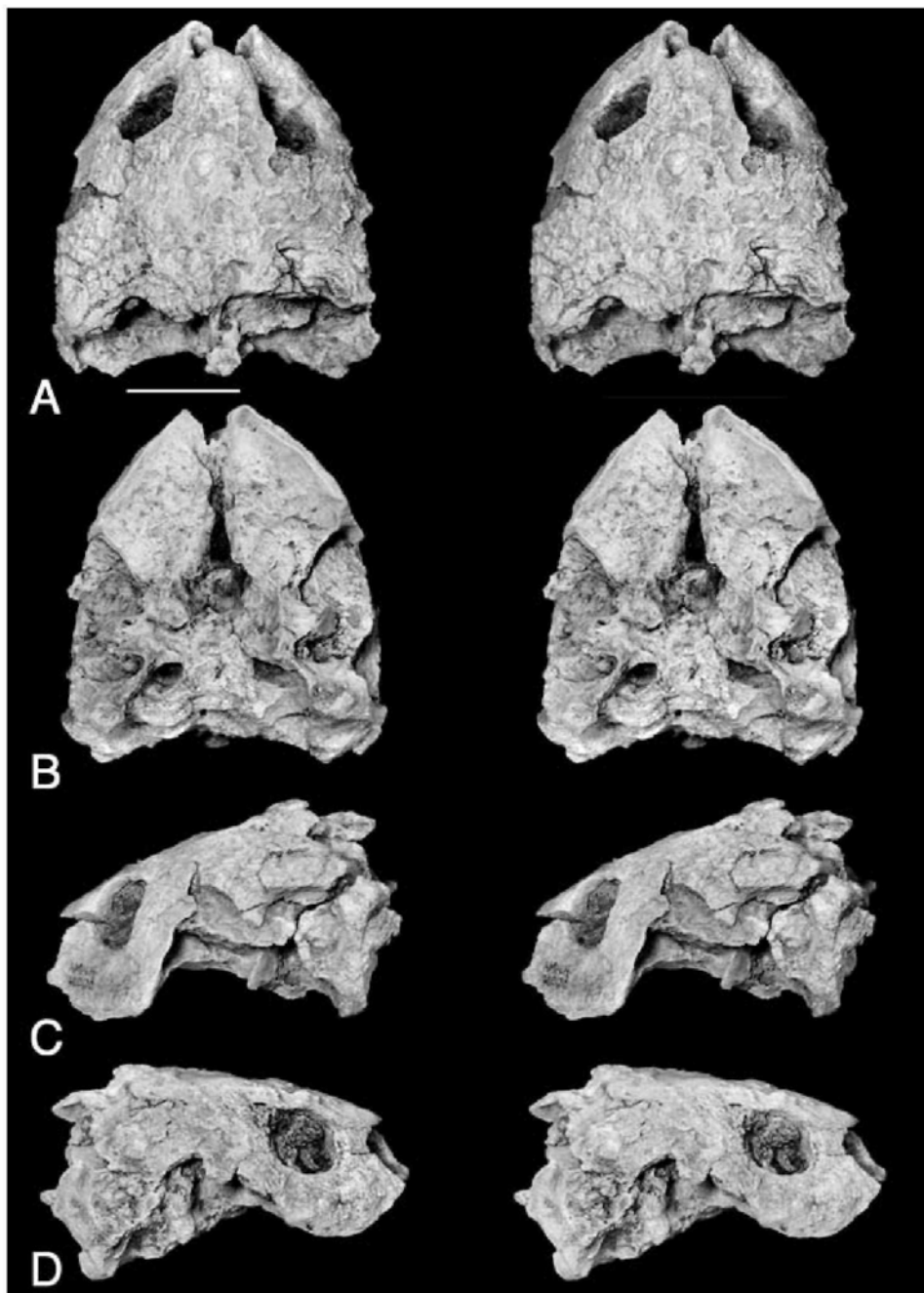


Figure 4 Stereopairs of **A**, dorsal, **B**, ventral, **C**, left lateral and **D**, right lateral views of the skull of *Bairdemys* sp. AMNH 30000, from the Castillo Formation. Scale bar = 30 mm.

The ratio 'width between orbits/width of skull in the middle of orbits' ranges between 0.47 (AMNH 27222) and 0.35 (CURS 96). Both MCNC-Pal-21-10708 and CURS 98 have a ratio of 0.41. A ratio of 0.39 was detected in CURS 97. The ratio of AMNH 27222 is 13–26% higher than the ratios of other specimens observed.

The lower jaw of *Bairdemys*

Comparisons with other Pelomedusoides and measurements are summarised in Tables 3 and 4. Both lower jaw rami of MCNC-Pal-21-10708 are preserved and length is 91.1 mm (right side). Compared to those of *Stereogenys*, the rami are

slender in shape, tapering in width posteriorly (Fig. 8). The processus retroarticularis and the whole anterior and posterior part of the triturating surface of the left ramus are missing. The left ramus is laterally depressed and, therefore, most anatomical features described here are taken from the right ramus.

Triturating surface

Compared to *Stereogenys* the triturating surface of MCNC-Pal-21-10708 is relatively small, but its size stands out compared to other Pelomedusoides which do not belong to the *Shweboemys* Group, including *Erymnochelys* and *Roxochelys*. The ratio of the width of the triturating

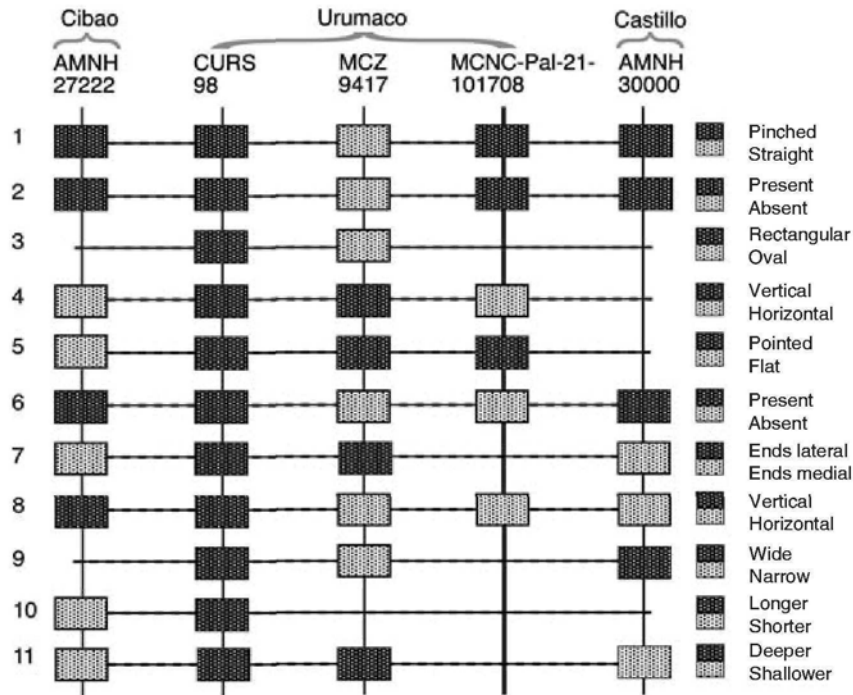


Figure 5 Distribution of character states (see Table 2) summarised graphically. Different states of preservation prevent comparison of all characters. Note the variation within the Urumaco sample.

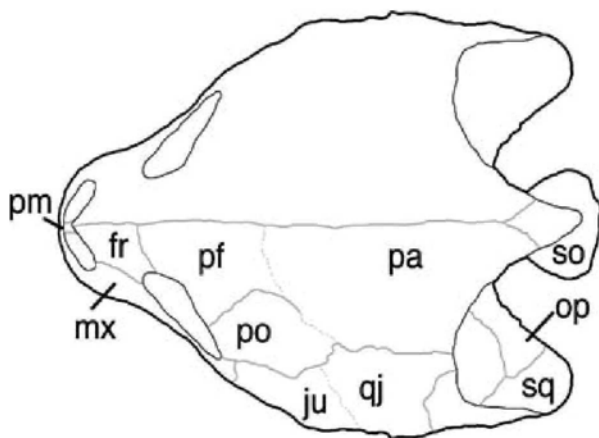


Figure 6 Sketch of the dorsal view of CURS 98, showing reconstructed sutures (fine lines) and presumed sutures (dotted fine lines) in one half of the skull. Abbreviations: fr, frontal; ju, jugal; mx, maxilla; op, opisthotic; pa, palatine; pf, prefrontal; pm, premaxilla; po, postorbital; qj, quadratojugal; so, supraoccipital; sq, squamosal.

surface/width of the rami at the processus coronoideus in MCNC-Pal-21-10708 (0.51) is 21.5% ($\pm 4.5\%$) higher than in other Podocnemididae observed by us e.g. *Podocnemis unifilis* (0.43). The triturating surface mainly consists of well-developed oval grooves posterolateral to the symphysis. Although these grooves are more concave in other pleurodire species, the grooves of MCNC-Pal-21-10708 are still conspicuous structures. No obvious accessory ridges

comparable to ridges in other Podocnemididae are present, as is the case in *Stereogenys*; the tomial ridge is curved and slopes dorsally to a prominent and wide bulge, which continues anteriorly parallel to the symphysis and disappears rostrally. *Stereogenys* lacks this tuberosity. In *Bairdemys* and *Stereogenys* the labial ridge is curved but less acute than in *Podocnemis* and *Erymnochelys* (Gaffney & Forster 2003: fig. 1D). The symphysis is fused.

Processus retroarticularis

The processus retroarticularis is well developed, being elongated, narrow and posteriorly directed; in *Stereogenys* this structure is broader and shorter. The anterior slope of the dentary is in lateral view less dominant and less pointed than in *Podocnemis* or *Pelusios*. In *Erymnochelys* the processus retroarticularis projects posteriorly and is wide and robust (Gaffney & Forster 2003: figs 1A & B), comparable to that of *Stereogenys*, although not as long and slender as in *Bairdemys*. In *Roxochelys* it projects posteriorly but it is relatively shorter than in *Bairdemys*, *Stereogenys* or *Erymnochelys* (Broin 1991: plate 2, fig. 6).

Processus coronoideus

In members of the *Shweboemys* Group the processus coronoideus is more prominent than in other Podocnemididae. It is in lateral view the highest point of the lower jaw, as in *Pelusios sinuatus* amongst the Recent and *Erymnochelys* amongst the fossil species studied (Gaffney & Forster 2003: figs 1E & F). In *Stereogenys* the processus is relatively higher than in *Bairdemys*, projecting dorsally approximately twice as much

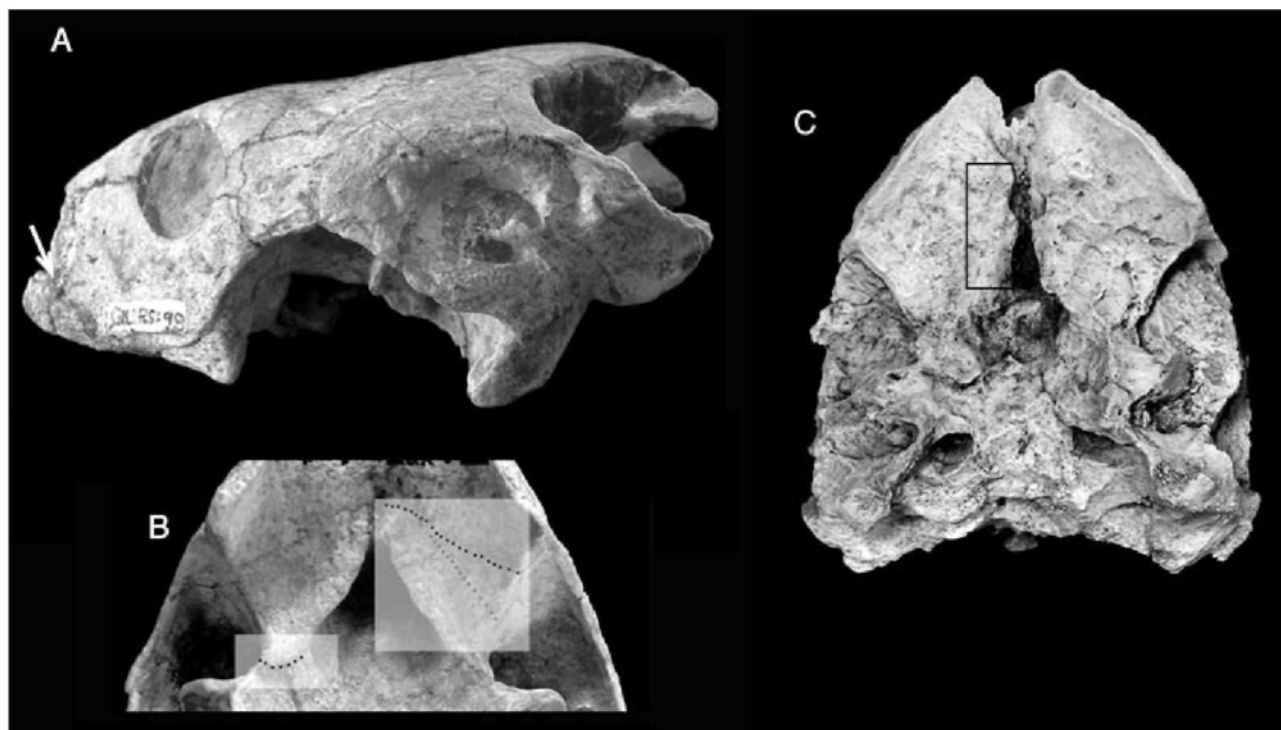


Figure 7 **A**, Lateral view of CURS 98, showing the premaxillary notch (arrow). **B**, Ventral view of CURS 98, showing the maxillary–palatine contact (character 7) in CURS 98 (black dotted line) and in AMNH 27222 (grey dotted line) and the palatine–pterygoid contact (character 9) in CURS 98 (black dotted line). **C**, Ventral view of AMNH 30000, showing out the anterior projection of the internal nares (character 12).

as in the latter. Following Andrews (1906) this is correlated with muscle attachment associated with the development of a massive triturating surface.

Foramen dentofacialis

This is located anterior to the processus coronoideus, further anterior to other structures and larger than in the *Podocnemis* and *Pelusios* specimens studied. In *Erymnochelys* the relatively smaller foramen is located slightly anterior to the

processus coronoideus (Gaffney & Forster 2003: fig. 1D). No information concerning this character can be obtained from the figure of *Stereogenys* in Andrews (1906) or that of *Roxochelys* in Broin (1991).

Fossa meckelii

The dorsal opening of the fossa meckelii of MCNC-Pal-10708 is broader than in *Podocnemis* or *Pelusios*, particularly anteriorly. In Recent Pelomedusoides the opening of

Table 3 Comparison of jaw characters in *Bairdemys* MCNC-Pal-21-10708 and several specimens of Recent and fossil Pelomedusoides.

	<i>Bairdemys</i> MCNC-Pal-21-10708	<i>Podocnemis</i> NHM 60.4.16.10, 72.4.29.9, 60.4.16.9, 72.4.29.8.	<i>Peltocephalus</i> [†]	<i>Erymnochelys</i> [†]	<i>Pelusios</i> NHM 87.3.11.10, 1974.3.01, 1974.2.47.8, 70.5.5.4.	<i>Pelomedusa</i> NHM 87.3.11.10	<i>Stereogenys</i> [‡]
<i>Processus articularis</i> well developed	Yes	Yes	Yes	Yes	No	No	Yes
<i>Processus retroarticularis</i> directed ventrally	No	Yes	No	No	No	No	No
Accessory ridge	Absent	Present	Absent	Absent	Absent	Absent	Absent
<i>Symphysis</i>	Fused	Fused	Fused	Fused	Fused	Sutured	Fused

Characters are from Gaffney *et al.* (1998).

[†]Data from Gaffney *et al.* (1998).

[‡]Data from Andrews (1906).

Table 4 Jaw measurements (in mm) from *Bairdemys venezuelensis* MCNC-Pal-21-10708 and from other Pelomedusoides.

Measurement no. in Fig. 1	Skull measurements	MCNC-Pal-21-10708	<i>Pelomedusa subrufa</i>	<i>Pelusios gabonensis</i>	<i>Pelusios niger</i>	<i>Pelusios subniger</i>	<i>Podocnemis expansa</i>	<i>Podocnemis unifilis</i>
13	Total length along long axis of jaw	91.1	21.4	30	45	31.2	58.9	45.9
14	Height of jaw at processus coronoideus	18.4	5.4	8.6	14.4	8	14.7	12.2
-	Width of triturating surface just anterior to processus coronoideus	14.8	-	-	-	-	-	-
15	Length of triturating surface at symphysis	32.1	5.6	9.3	12.2	8.4	17.8	14.6
16	Width of jaw at processus coronoideus	11.0	2.4	4	6.6	4.5	8.9	8
17	Width of area articularis mandibularis	14.7	2.9	4.5	7	4.7	9.9	7.5
-	Length along long axis of jaw from anterior to posterior end of area articularis mandibularis	84.5	-	-	-	-	-	-
-	Height at posterior end of symphysis	15.8	-	-	-	-	-	-
18	Maximum height at area articularis	18.0	3.5	5.5	8.1	5.5	11.4	8.9
19	Length of area articularis mandibularis	11.6	2.5	3.8	5.4	3.9	9.2	7.7
20	Width of rami at processus coronoideus	62.4	19.3	27.4	37.2	26.6	41.9	33.8

See the text and Fig. 1 for explanations.

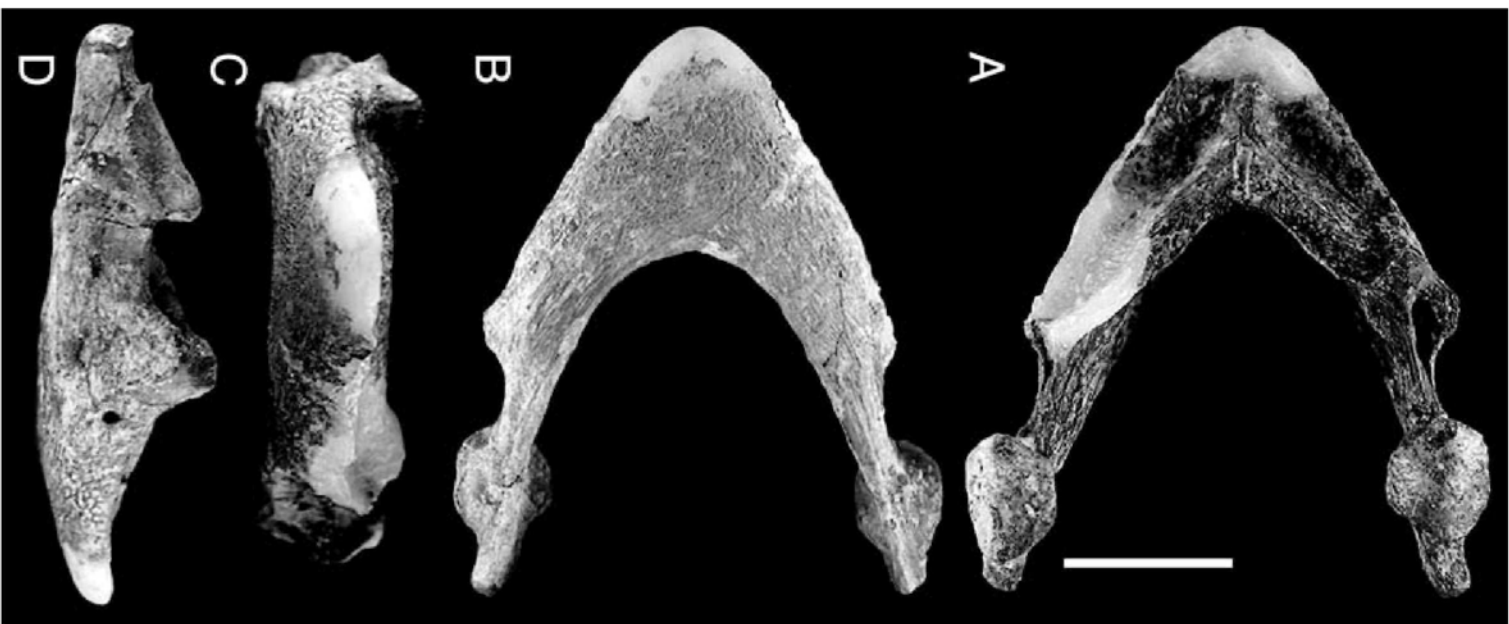


Figure 8 A, Dorsal, B, ventral, C, anterior and D right posterolateral views of MCNC-Pal-21-10708, lower jaw of *Bairdemys venezuelensis* from the Urumaco Formation. Scale bar = 30 mm.

the fossa meckelii appears to be slit-like; this can also be observed in fossil forms such as *Roxochelys* (Broin 1991: fig. 6, plate II). An unnamed podocnemidid turtle, LACM 141498, from Brazil is reported to have a huge opening of the fossa meckelii, which is actually of the size of the entire fossa (Gaffney *et al.* 1998), extending posterolaterally

to the mandibularis articularis area. Following Gaffney *et al.* (1998) this might be correlated with a large main adductor tendon and musculature. The dorsal opening of the fossa meckelii in MCNC-Pal-10708 is particularly larger and wider than in living Pelomedusoides, although it does not continue posteriorly to the area mandibularis articularis as it does in LACM 141498 (Gaffney *et al.* 1998). The figures depicting *Erymnochelys* (Gaffney & Forster 2003: fig. 1) and *Stereogenys* do not contain sufficient information on this feature.

Area mandibularis articularis

The area mandibularis articularis shows a diagnostic anatomical feature for Pleurodires: it lacks the median longitudinal ridge as seen in Cryptodires and consists of a smooth, relatively flat surface. The area mandibularis articularis is relatively narrower than in *Podocnemis*, being more elongated posteriorly on both sides (not an artifact of preservation). *Stereogenys*, *Erymnochelys* and *Roxochelys* do not possess this elongation.

DISCUSSION

Our work has shown the considerable morphological variation within *Bairdemys* skulls from Urumaco. The features that Gaffney & Wood (2002) deemed diagnostic for differentiating the two species of the genus do not show a clearly dichotomous distribution. One could therefore suggest lumping both species into one or, alternatively, reflect the different combination of features in the skulls treated here into more than two species. We have chosen a more conservative approach and prefer not to suggest an alteration to the current taxonomy. *Bairdemys hartsteini* is known only from a single skull, posing limitations to our knowledge of this species. A complete assessment of the taxonomy of *Bairdemys* from Urumaco would require examination of shell morphology and variation across the stratigraphic sequence (encompassing approximately 2000 m of sequence and very likely a time span of at least a few million years: Aguilera 2004). The carapace and plastral anatomy of *B. venezuelensis* is well known; in fact, the original description of this species by Wood & Díaz de Gamero (1971) was based on shells only. Perhaps the most remarkable feature of this species is the lack of neural bones, a condition not found among other Pelomedusoides.

A relatively higher skull and a relatively wider distance between orbits, as measured by ratios reported in this work, distinguish the single known skull of *B. hartsteini* from all *Bairdemys* specimens from Urumaco. Future sampling could show that indeed these two proportions reflect skull shape differences that distinguish *Bairdemys* specimens.

How ontogenetic variation and sexual dimorphism are correlated with the cranial features discussed by Gaffney & Wood (2002) and in this work remain to be studied, since they are potential sources of variation for many of the characters listed by us in Table 1 (F. de Lapparent de Broin, pers. comm.).

Bairdemys and *Stereogenys* possess several shared characters in their lower jaw, namely a well-developed triturating surface and a distinct coronoid process. Some features, presumably correlated with the presence of a secondary palate, separate these two genera from other Podocnemidae and

might help assign single jaw finds, which are frequent for Oligocene and Eocene localities in Fayum, Egypt (M. R. Sánchez-Villagra, pers. obs.).

We have tried to be consistent in our characterisations and comparisons, avoiding dealing with features that, in some taxa, appear to be 'more or less' developed, as often times is described in the literature. Future revisions of several skull features of pleurodires would benefit from the use of morphometric approaches to character definition (*sensu* MacLeod 2002), as exemplified by Jamiczky & Russell (2004).

Taxonomic affinities of *Bairdemys* from the Castillo Formation

Examination of skull variation in *Bairdemys* from Urumaco and comparison with *B. hartsteini* clearly show that the two specimens of this genus described from the Castillo Formation (early Miocene of Lara, Venezuela) belong to a new species, as already suggested by Sánchez-Villagra *et al.* (2000) and Gaffney & Wood (2002). These authors had already noted that AMNH-30000 differs from *B. venezuelensis* and *B. hartsteini* in being 'flatter in profile and in having a less arched snout region' (Sánchez-Villagra *et al.* 2000: 961–962). However, they suggested that these differences may be the result of preservation. In this work, we found two features that undoubtedly distinguish the Castillo skulls from the other *Bairdemys* and which are clearly not the result of preservational biases: (1) a relatively larger size of the ventral surface of the secondary palate, correlated with a smaller width of the internal nares, which project further anteriorly and little distance between the foramina palatina and (2) a more posterior position of the quadrate in relation to the basisphenoid instead of the articular surface of the quadrate being in one line with the posterior end of the basisphenoid. These features do not reflect allometric differences, since the Castillo specimen is within the size range of the Urumaco *Bairdemys* treated in this work.

We do not formally recognise a new *Bairdemys* species from the Castillo Formation in the hope that discoveries in the near future, based on current fieldwork being conducted by M.R.S.V. and colleagues, will result in discovery of better material on which to base the new taxon. The poor condition of AMNH 30000 and MBLUZ-P-5045 precludes determination of other possibly significant characters. The bone surface of the skull has been eroded off and only a few sutures are visible.

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