Two new species of the side necked turtle genus, *Bairdemys* (Pleurodira, Podocnemididae), from the Miocene of Venezuela

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with 9 figures and 3 tables

Abstract: The side-necked turtle genus *Bairdemys* (Podocnemididae, *Shweboemys* Group) from the Miocene of Venezuela and Puerto Rico is revised, and four species are diagnosed on the basis of skull characters; two are described as new. *B. hartsteini* GAFFNEY & WOOD, 2002, from the Cibao Formation of Puerto Rico, is characterized by a higher skull, with a straight labial ridge and a premaxillary notch; *B. venezuelensis* (WOOD & DÍAZ DE GAMERO 1971), from the Urumaco Formation of Venezuela, is characterized by the absence of a premaxillary notch, a high anterior triturating surface convexity, a deep posterior triturating surface concavity, and a short pterygoid midline contact; *B. sanchezi*, new species, from the Urumaco Formation of Venezuela, is characterized by a very low anterior triturating surface convexity and shallow posterior triturating surface concavity, a premaxillary notch, small size, and extensive temporal and cheek emargination; *B. winklerae*, new species, from the Urumaco Formation of Venezuela, is characterized by an elongate, narrow snout, with a concave labial ridge, and no premaxillary notch. Based on osteological and bone histological results, an additional strongly crushed skull and associated carapace fragment of a previously undetermined podocnemidid from the Urumaco Formation of Venezuela can be further referred to *Podocnemis* or a closely related taxon – again underscoring the importance of this formation as one of the major fossil lagerstätten of turtles in South America.

Keywords: Pleurodires • Podocnemididae • *Bairdemys* • Urumaco Fm. • Venezuela • shell bone histology

Zusammenfassung: Die Halswenderschildkröten der Gattung *Bairdemys* (Podocnemididae, *Shweboemys*-Gruppe) aus dem Miozän von Venezuela und Puerto Rico werden revidiert. Aufgrund von diagnostischen Schädelmerkmalen werden vier Arten unterschieden, inklusive zwei hierin neu beschriebener Arten. *B. hartsteini* GAFFNEY & WOOD, 2002, aus der Cibao Formation, Puerto Rico, ist durch einen hohen Schädel, eine gerade Labialkante des Prämaxillare und eine Prämaxillarkerbe gekennzeichnet, *B. venezuelensis* (WOOD & DÍAZ DE GAMERO 1971) aus der Urumaco-Formation Venezuelas durch das Fehlen einer Prämaxillarkerbe, eine hohe anteriore Konvexität und eine tiefe posteriore Konkavität der Kauflächen und einen kurzen Mittellinienkontakt der Pterygoide. Die hier neu beschriebene *B. sanchezi* n. sp. aus der Urumaco-Formation, Venezuela, ist charakterisiert durch eine sehr niedrige anteriore Konvexität und eine flache posteriore Konkavität der Kauflächen, eine geringe Größe und starke Temporal- und Wangeneinbuchtungen, wogegen *B. winklerae* n. sp. aus der Urumaco Formation, Venezuela, durch eine verlängerte schmale Schnauze mit einer konkaven Labialkante charakterisiert ist. Durch osteologische und knochenhistologische Befunde lassen sich ein weiterer stark verdrückter Schädel sowie ein assoziiertes Panzerfragment einer bisher unbestimmten Podocnemidide der Gattung *Podocnemis* oder deren unmittelbarer Verwandtschaft zuordnen. Dies unterstreicht wiederum die Bedeutung der Urumaco-Formation als eine der wichtigsten Lagerstätten fossiler Schildkröten in Südamerika.

Schlüsselwörter: Pleurodira • Podocnemididae • *Bairdemys* • Urumaco-Formation • Knochenhistologie des Schildkrötenpanzers • Venezuela

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Introduction

The genus *Bairdemys* GAFFNEY & WOOD, 2002, is a member of the side-necked turtle family Podocnemididae and belongs to the *Shweboemys* Group of GAFFNEY & WOOD (2002). This group is characterized by a secondary palate separated on the midline by a narrow cleft, unique among pleurodires. The first species referred to the genus, *Podocnemis venezuelensis* WOOD & DÍAZ DE GAMERO, 1971, was based on a shell from the Venezuelan Urumaco Formation, but subsequent material collected by ROGER WOOD and a team from the MCZ included associated shells and skulls, also from the Urumaco Formation. This material was described and referred to *Bairdemys* by GAFFNEY & WOOD (2002), when they erected the genus based on the species *B. hartsteini* from the Cibao Formation of Puerto Rico. SÁNCHEZ-VILLAGRA et al. (2000) and SÁNCHEZ-VILLAGRA et al. (2004) added skull material from the Castillo Formation of Venezuela. SÁNCHEZ-VILLAGRA & WINKLER (2006) added descriptions of four more skulls from the Urumaco Formation of Venezuela and argued that the criteria used by GAFFNEY & WOOD (2002) to diagnose their two species were more widespread in the new Urumaco *Bairdemys* skulls, calling into doubt the validity of the two named *Bairdemys* species.

In this paper we differ with the interpretation of SÁNCHEZ-VILLAGRA & WINKLER (2006). We retain the two original species and describe two more *Bairdemys* species. These new species are based on material described by SÁNCHEZ-VILLAGRA & WINKLER (2006) and a new skull from the Urumaco Fm. This explanation may be an oversplit view of variation in *Bairdemys*, and the senior author hopes that new collections and analyses continue to generate new ideas about diversity within *Bairdemys*. There is also no objective method for dealing with the effects of gender and age in the observed variation, and these effects may be significant. We agree that much of the character analysis presented here is subjective (too much use of "more" and "less" as correctly decried by SÁNCHEZ-VILLAGRA & WINKLER 2006), and that the hoped-for ultimate morphometric analysis might allow a more objective assessment of morphologic variation. Until that is done, however, we can either place all the known *Bairdemys* skulls into the single, relatively variable, widespread, species *venezuelensis*, and hope for future resolution, or we can attempt to recognize specific-level taxa as best we can at present. All systematic work is hypothetical, and the recognition of species at least provides subsequent students with an opportunity for falsification. The taxa recognized here are not clearly defined with numerous unique characters, but they are definable. The characters are not always completely discrete and the specimens are not all well-preserved. However, we have emphasized the use of the best preserved specimens and have taken less seriously character interpretations from poorly-preserved specimens. We would like to explicitly express the need to consult the aforementioned papers, especially GAFFNEY & WOOD (2002) and SÁNCHEZ-VILLAGRA & WINKLER (2006), in terms of additional figures in order to fully reappraise the data presented herein.

The higher taxa classification is from GAFFNEY et al. (2006). Also see this work for an introduction to pleurodire skull morphology and a literature review. The shell of *Bairdemys venezuelensis* is described in WOOD & DÍAZ DE GAMERO (1971), and the plastron is figured in GAFFNEY et al. (2006: fig. 275).

In 1972, the Museum of Comparative Zoology of Harvard University collected a large suite of *Bairdemys venezuelensis* specimens from one locality (see GAFFNEY & WOOD 2002) in the Urumaco Formation of Venezuela. We may at least hypothesize that this material all belongs to one species. Some of this material has since been returned to Venezuela and has acquired two sets of catalogue numbers: MCN Pal-0001 of GAFFNEY & WOOD (2002) equals MCN Pal-21-10708 in SÁNCHEZ-VILLAGRA & WINKLER (2006); and MCN Pal-0002 of GAFFNEY & WOOD (2002) equals MCN Pal-21-10707 in SÁNCHEZ-VILLAGRA & WINKLER (2006).

Material and methods

A persistent problem with current morphologic work on *Bairdemys* is that, since the work of GAFFNEY & WOOD (2002), no author has had all the *Bairdemys* skulls at hand in the same place at the same time. As many of the characters are ones of degree and not just present or absent, figures may be insufficient to resolve the subtleties of character states. As a result, differences of interpretation arise easily among different authors. In the present work, the senior author has had available to him the following specimens: MCZ 9417, MCZ 9418, AMNH 30000, AMNH 27222, UNEFM-CIAPP 1399, and AMU-CURS 186, although he has seen and photographed all the MCZ-collected specimens.

Institutional Abbreviations: AMNH, American Museum of Natural History, New York, USA; AMU-CURS, Alcaldía del Municipio Urumaco, Colección Rodolfo Sánchez, Venezuela; MCN, Museo de Ciencias, Caracas, Venezuela; MCZ, Museum of Comparative Zoology, Harvard University, USA; UNEFM, Universidad Nacional Experimental Francisco de Miranda, Coro, Venezuela.

Anatomical Abbreviations: bo, basioccipital; bs, basisphenoid; co, costal; ent, entoplastron; epi, epiplastron; ex, exoccipital; fr, frontal; gu, gular scale; hu, humeral scale; in, intergular scale; ju, jugal; mx, maxilla; n, neural; nu, nuchal; op, opisthotic; p, peripheral; pa, parietal; pal, palatine; pf, prefrontal; po, postorbital; pt, pterygoid; qj, quadratojugal; qu, quadrate; so, supraoccipital; sq, squamosal; vo, vomer.

Histological Abbreviations: CB, cancellous bone; ECO, external cortex; GM, growth marks; ICO, internal cortex; PC, primary vascular canals; PFB-LB, parallel-fibered bone locally grading into lamellar bone.

Geology

The sampling area (Fig. 1) includes the localities Tío Gregorio, El Mamón, Corralito, El Hatillo, and El Picache, all of them north of the town of Urumaco, Falcón State, northwestern Venezuela. The geological units from which the specimens were obtained are the middle and upper members of the Urumaco Formation.

The middle member of the Urumaco Formation (El Mamón locality) consists mostly of claystone and sand. The gray claystone is rich in microfossils, and the brown claystone contains vertebrate remains such as reptiles, mammals, marine and freshwater fish, as well as coprolites and wood (DÍAZ DE GAMERO & LINARES 1989; AGUILERA 2004). The limestone changes from conchiferous sandstones to consolidated coquina limestone. In the lower half of this middle member, an abundant and diverse marine fish and mollusk fauna exists in a sandy matrix. The paleoenvironments are interpreted as inner sub-littoral and coastal lagoonal with riverine and estuarine influence (DÍAZ DE GAMERO 1996; AGUILERA 2004).

The upper member of the Urumaco Formation (Corralito, El Hatillo, El Picache and Tío Gregorio localities) also comprises gray to brown, often limey, claystones, with intercalated and locally conchiferous thin sandstones. The uppermost layer is referred to as the "capa de tortugas" because of its abundant remains of *Bairdemys* turtles (DÍAZ DE GAMERO & LINARES 1989). Several localities and levels have concentrations of vertebrate fossils. The vertebrate fauna includes marine, estuarine and freshwater fishes, terrestrial, freshwater and marine turtles and crocodilians, and terrestrial and aquatic/semiaquatic mammals (SÁNCHEZ-VILLAGRA et al. 2003; AGUILERA 2004). The paleoenvironments were tropical near shore marine to low coastal savannahs with freshwater rivers.

For additional information about these geological units see MINISTERIO DE ENERGÍA Y MINAS (1997). A complete list of the fossil fauna from the Urumaco Formation has been recently summarized in SÁNCHEZ-VILLAGRA & AGUILERA (2006). A late Miocene age for the Urumaco Formation is indicated by foraminiferans, and the mammals suggest a South American land mammal age between Chasicoan and Huayquerian (DÍAZ DE GAMERO & LINARES 1989).

Systematic paleontology

Infraorder Pleurodira COPE, 1864
Hyperfamily Pelomedusoides COPE, 1868
Epifamily Podocnemidinura COPE, 1868
Family Podocnemididae COPE, 1868

***Bairdemys* GAFFNEY & WOOD, 2002**
Fig. 2, Tabs. 1, 3

Derivatio nominis: For Donald Baird (see GAFFNEY & WOOD 2002).

Type species: *Bairdemys hartsteini* GAFFNEY & WOOD, 2002

Included species: *Bairdemys hartsteini, B. venezuelensis, B. sanchezi* n. sp., *B. winklerae* n. sp. (see Fig. 2 for palatal comparisons). AMNH 30000, an unnamed skull from the Castillo Formation, is probably another species of *Bairdemys* (see below).

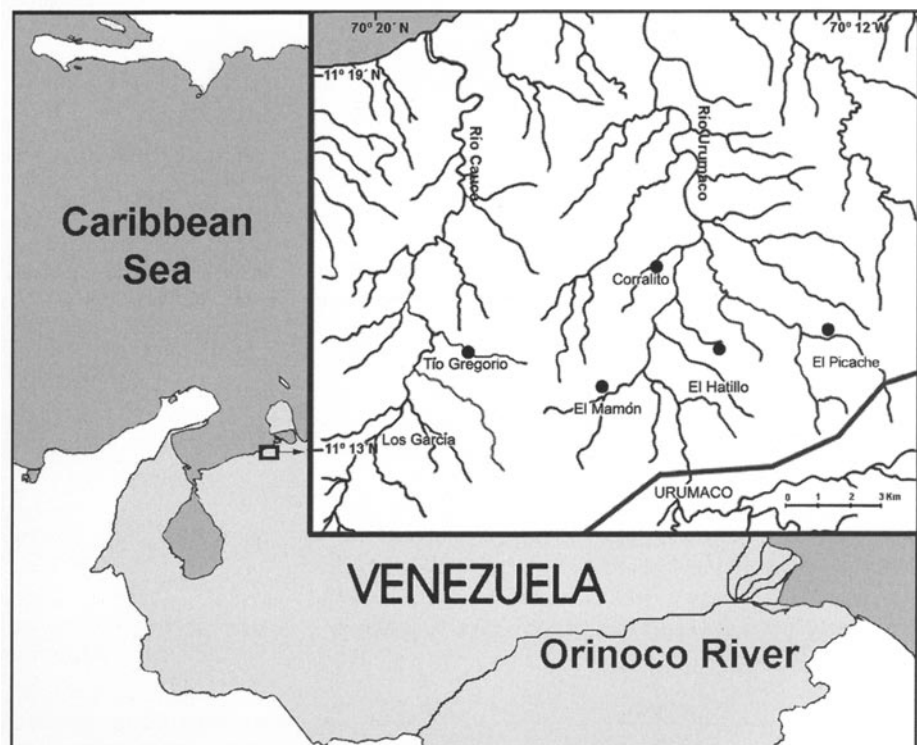**Distribution:** Miocene of Puerto Rico and Venezuela.

Fig. 1. Location of the sampling sites of Tío Gregorio, El Mamón, Corralito, El Picache, and El Hatillo, which lie north of the town of Urumaco, Falcón State, northwestern Venezuela.

Diagnosis: As in WOOD & DÍAZ DE GAMERO (1971). However, the inclusion of *B. sanchezi* n. sp., which has a lower snout profile, makes the "prefrontal and frontal strongly convex on dorsal surface" (GAFFNEY & WOOD 2002: 3) no longer a character for the genus.

Bairdemys hartsteini GAFFNEY & WOOD, 2002
Fig. 2A, Tabs. 1, 3

Derivatio nominis: For Eugene Hartstein (see GAFFNEY & WOOD 2002).

Holotype: AMNH 27222, a skull without associated mandible figured by GAFFNEY & WOOD (2002).

Locus typicus: North side of Highway No. 2, west of Bayamon, Puerto Rico (see GAFFNEY & WOOD 2002: 4).

Stratum typicum: Cibao Formation, middle Miocene (see GAFFNEY & WOOD 2002: 4).

Referred material: None.

Previous work: GAFFNEY & WOOD (2002), SÁNCHEZ-VIL-LAGRA & WINKLER (2006).

Diagnosis: A species of *Bairdemys* differing from all other species in having a higher skull, a straight rather than convex or concave labial ridge in ventral view, and a wider distance between orbits; also differs from *venezuelensis* in having a smaller skull, a premaxillary notch, lower triturating surface convexity, shallower triturating surface concavity and narrower posterior triturating surface width; also differs from *sanchezi* in having a slightly wider skull, a higher triturating surface convexity, a deeper triturating surface concavity, a larger and broader basisphenoid, and a less extensive cheek and temporal emargination; also differs from *winklerae* in having a broader, shorter snout, slightly wider skull, wider triturating surface, a premaxillary notch, and a narrower basisphenoid-quadrate contact.

Discussion: This species is not well-differentiated from *venezuelensis*, and another option for grouping the *Bairdemys* morphs would be to synonymize *hartsteini* with *venezuelensis* but to keep *sanchezi* and *winklerae*, which are more distinct. Although the size range of Urumaco skulls has been expanded, this species continues to differ from *venezuelensis* in its smaller size.

Bairdemys venezuelensis (WOOD & DÍAZ DE GAMERO, 1971)
Fig. 2B, Tabs. 1, 3

Derivatio nominis: For the country of Venezuela.

Holotype: Laboratorio de Paleontología, Universidad Central de Venezuela (Caracas), VF 1176, a complete carapace figured by WOOD & DÍAZ DE GAMERO (1971: pl. 1, 2, 4).

Locus typicus: "... north of Campo El Mamón, state of Falcón, Venezuela" (WOOD & DÍAZ DE GAMERO 1971).

Referred material: See list in GAFFNEY & WOOD (2002).

Previous work: WOOD & DÍAZ DE GAMERO (1971), GAFFNEY & WOOD (2002), SÁNCHEZ-VILLAGRA & WINKLER (2006).

Diagnosis: A species of *Bairdemys* differing from all other species in having a higher anterior triturating surface convexity, a deeper posterior triturating surface

concavity, and a short midline contact of the pterygoids; also differs from *B. hartsteini* in having a larger skull, a convex labial ridge in ventral view, no premaxillary notch, and a wider posterior triturating surface; also differs from *B. sanchezi* in having a wider skull, a wider posterior triturating surface, a larger basisphenoid, no premaxillary notch, and a less extensive cheek and temporal emargination; also differs from *B. winklerae* in having a broad, convex, and short snout, a slightly wider skull, a wider posterior triturating surface, and a narrower basisphenoid-quadrate contact.

Discussion: Although this is the oldest named species in the currently construed *Bairdemys*, the type species of the genus is *hartsteini*, named by GAFFNEY & WOOD (2002), so that the genus had a skull as its type species, in case some or all of the shell features of *venezuelensis* prove to be taxonomically widespread, as is in fact the case according to GAFFNEY et al. (2006). Fortunately, the MCZ-collected specimens consist of skulls and shells from the same quarry (GAFFNEY & WOOD 2002). The large size, broad snout, and straight labial ridge (in anterior view) are characteristic of this species.

Bairdemys winklerae n. sp.
Fig. 2C, Tabs. 1, 3

Derivatio nominis: For Jasmin D. Winkler in recognition of her contributions to *Bairdemys* systematics.

Holotype: AMU-CURS 98 (Fig. 2C).

Locus typicus: North of El Picache, Urumaco Formation, state of Falcón, Venezuela.

Referred material: Possibly AMU-CURS 96, AMU-CURS 97, and AMU-CURS 99, belong to this species, as these specimens have elongate snouts. The specimens come from the same stratigraphic level (quarry level) at the El Picache loca-

Tab. 1. Comparison of triturating surface widths (mm) among *Bairdemys* skulls. A, midline length as preserved; L, anterior width of triturating surface; M, posterior width of triturating surface.

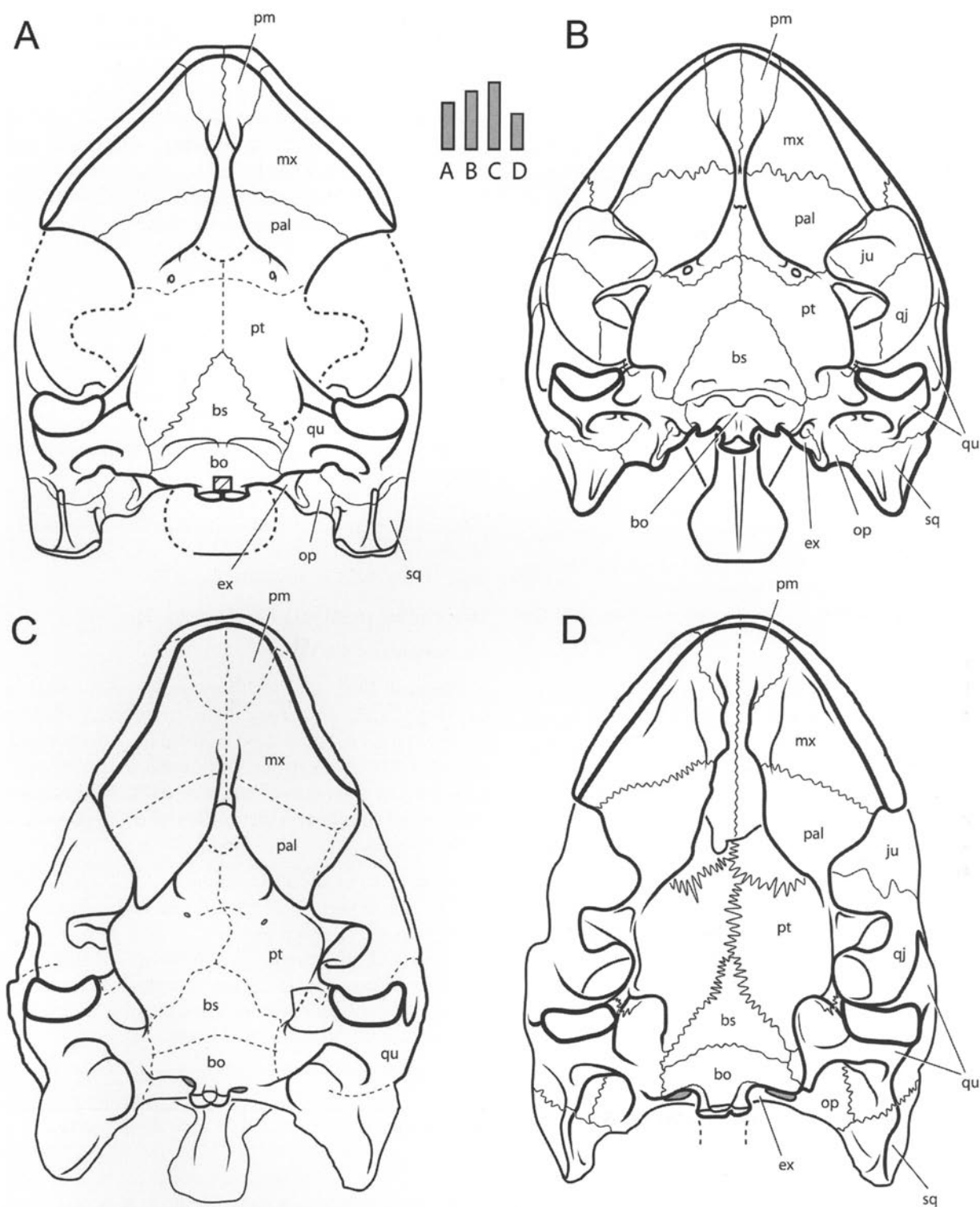|	L/A	M/A
AMU-CURS 96	0.31	0.24
AMU-CURS 97	–	–
AMU-CURS 98	0.26	0.18
AMU-CURS 99	0.27	0.21
MCN Pal 0001	0.20	0.23
MCZ 9417	0.21	0.33
MCZ 9418	0.22	0.36
MCN Pal-0002	–	0.26
AMNH 27222	0.20	0.28
AMNH 30000	0.34	0.29
AMU-CURS 186	0.19	0.27

Fig. 2. Palatal views of *Bairdemys* species. – **A**: *Bairdemys hartsteini* (from GAFFNEY & WOOD, 2002). – **B**: *B. venezuelensis* (from GAFFNEY & WOOD 2002). – **C**: *B. winklerae* n. sp. (drawn from photos in SÁNCHEZ-VILLAGRA & WINKLER 2006). – **D**: *B. sanchezi* n. sp. Bars show relative lengths of skulls (see Tab. 3 for measurements). – Skulls drawn to same length, not to scale.

lity (11°14'40'' N, 70°14'44'' E; top of the upper member in the Urumaco Formation). This locality represents the eastern equivalent of the "capa de Tortuga" located in Corralito (also top of the upper member).

Previous work: SÁNCHEZ-VILLAGRA & WINKLER (2006) as AMU-CURS 98.

Diagnosis: A species of *Bairdemys* differing from all other *Bairdemys* species in having an elongate, narrow snout with the labial ridge concave in ventral view, and

a wide basisphenoid-quadrate contact; also differs from *B. hartsteini* in having a larger skull and no premaxillary notch; also differs from *B. venezuelensis* in having a narrower skull, a wider posterior triturating surface, no premaxillary notch, and a longer midline pterygoid contact; also differs from *B. sanchezi* in having a larger skull, a larger, anteriorly wider, basisphenoid, and a less extensive temporal and cheek emargination.

Discussion: This species is described and figured in SÁNCHEZ-VILLAGRA & WINKLER (2006). Its large size, elongate snout, and concave labial ridges are characteristic. The figure (Fig. 2C) presented here is based only on the figures in SÁNCHEZ-VILLAGRA & WINKLER (2006), not on the original specimen which has not been seen by the senior author. Sutures are based only on the photographs and are shown as dashed in the figure because the senior author has been unable to confirm them.

Bairdemys sp. indet.
Tabs. 1, 3

Specimen: AMNH 30000, a poorly preserved skull (see description below) and partial carapace.
Locality and horizon: Castillo Formation, Venezuela, See SÁNCHEZ-VILLAGRA et al. (2000), SÁNCHEZ-VILLAGRA & WINKLER (2006).

Discussion: This skull has been figured in SÁNCHEZ-VILLAGRA et al. (2000), SÁNCHEZ-VILLAGRA & WINKLER (2006). SÁNCHEZ-VILLAGRA & WINKLER (2006) have most recently argued that it is a distinct species within *Bairdemys*. We agree, but a skull without sutures that is so poorly preserved should not be named. It is in Table 3 and can be differentiated from the other four species recognized here by the posterior position of the condylus articularis, slightly wider anterior portion of the triturating surfaces, and the more horizontal orientation of the orbits.

Bairdemys sanchezi n. sp.
Figs. 2D, 3–6, Tabs. 1, 3

Derivatio nominis: For Marcelo R. Sánchez-Villagra in recognition of his contributions to *Bairdemys* systematics and for his paleontological explorations in Venezuela.
Holotype: Skull, jaws, and anterior plastral fragment (Figs. 2–6). AMU-CURS 186; collector: Orangel Aguilera, Alcaldía del Municipio Urumaco, Colección Rodolfo Sánchez.
Locus typicus: Tío Gregorio, Upper Member of the Urumaco Formation, Falcón State, Venezuela (AGUILERA 2004). Locality coordinates: 11°14'43" N, 70°18'19" W. The Tío Gregorio locality represents the top of the upper member in the Urumaco Formation and may be on the same stratigraphic level as the MCZ quarry in Tío Gregorio.
Referred material: None.
Previous work: None.

Diagnosis: A species of *Bairdemys* differing from all other *Bairdemys* species in having a low triturating surface convexity and shallow triturating surface concav-

ity, a smaller basisphenoid acutely pointed anteriorly, a small skull, and an extensive cheek and temporal emargination; also differs from *B. hartsteini* in having a convex rather than straight labial ridge in ventral view; also differs from *B. venezuelensis* in having a long midline pterygoid contact and a premaxillary notch, and also differs from *B. winklerae* in having a short, broad snout with a convex labial ridge in ventral view, a premaxillary notch, and a triturating surface that is narrower anteriorly and wider posteriorly.

Discussion: This specimen is described and figured here. The nicely preserved skull that is the type specimen of this species allows recognition of a number of characters, but, unfortunately, not very many other *Bairdemys* skulls are well enough preserved to allow comparison. The small size, flatter triturating surface, and extensive temporal and cheek emargination provide ready identification of this species.

The shell fragment (Figs. 5D, E) consists of the entoplastron and most of both epiplastra. The scale pattern is very similar to that of *Bairdemys venezuelensis* figured in GAFFNEY et al. (2006: fig. 275).

Description (AMU-CURS 186, Figs. 2D, 3–6)

Measurements: See Tab. 2.

Prefrontal: Both prefrontals are present and complete in AMU-CURS 186. They differ from MCZ 9417 (*B. venezuelensis*) in being more inclined from the horizontal. MCZ 9417 has a flatter dorsal surface, while AMU-CURS 186 is more curved lateromedially. AMU-CURS 186 is more similar to AMU-CURS 98 (*B. winklerae*) in these features.

Frontal: Both frontals are present in AMU-CURS 186 but the dorsal surface of the left one is damaged. The frontals agree in shape and relative size with those in MCZ 9417 (*B. venezuelensis*). On the ventral surface of the right side of AMU-CURS 186, there is a process that meets the dorsal process of the palatine, as in other members of the *Shweboemys* Group.

Parietal: Both parietals are present in AMU-CURS 186, but the right one is incomplete laterally and both are damaged to some extent on their dorsal surface.

The parietals of AMU-CURS 186 differ from all other *Bairdemys* (and other members of the *Shweboemys* Group) in having a more extensive temporal emargination. The emargination nearly reaches the postorbital so that there is a relatively narrow parietal-quadratojugal contact. This emargination is formed within the parietal as the postorbital and other bones are nearly the same relative size as in the well-roofed *Bairdemys* species. The parietal is emarginated all along its posterior margin so that the flat portion over the supraoccipital is reduced in extent as well.

As in other pleurodires, the parietal in AMU-CURS 186 has a processus inferior parietalis reaching the crista pterygoidea and a more lateral and shorter, de-

Tab. 2. Measurements (mm) of AMU-CURS 186.

A. Midline length as preserved	61.2
B. Maximum width	52.6
C. Width between orbits	13.3
D1. Width of left orbit	16.8
D2. Width of right orbit	16.8
E. Width of external nares	11.7
F. Width of internal nares	12.5
G. Maximum height at quadrate	35.7
H. Width of skull at middle of orbits	38.1
I. Length from anterior margin of prefrontals to posterior margin of parietals	52.1
J1. Height of left orbit	14.1
J2. Height of right orbit	15.2
K. Skull height at occipital condyle	25.4
L. Anterior width of triturating surface	10.3 (L), 13.4 (R)
M. Posterior width of triturating surface	17.3 (L), 16.6 (R)
N. Width of palate across foramina palatinum posterius	24.2
O. Length from front of skull to posterior edge of condylus articularis	54.5
B/A	0.85
M/A	0.27
L/A	0.19
G/A	0.57
C/A	0.34
K/A	0.40
C/H	0.34

scending process reaching the dorsal pterygoid process forming the lateral wall of the septum orbitotemporale, all preserved in AMU-CURS 186. The septum orbitotemporale has an opening in it on each side in AMU-CURS 186, but despite the even margins these openings seem to be artefacts, the result of postmortem breakage and over-zealous preparation. The bone here is very thin and is easily penetrated. The posterior surfaces of the septum on both sides are exposed, and the anterior surfaces are covered with a thin layer of matrix. There is also damage on the ventral part of the septum that prevents determining the exact contacts making up the septum orbitotemporale. However, a jugal contact is unlikely.

Jugal: Both jugals are preserved in AMU-CURS 186, although the external surfaces are slightly eroded, and the medial processes are not complete on either side.

The external part of the jugal in AMU-CURS 186 differs from MCZ 9417 (*B. venezuelensis*) in being relatively thin and much smaller due to the more extensive cheek emargination. In MCZ 9417 the jugal-quadratojugal suture is relatively long, but in AMU-CURS 186 the contact is short. The medial process of the jugal in AMU-CURS 186 forms the ventral part of the septum orbitotemporale, contacting the pterygoid posteromedially, and the postorbital dorsomedially. A parietal contact is unlikely.

Quadratojugal: At least some of both quadratojugals are preserved in AMU-CURS 186, but the right one is largely missing, being represented by a mould of the ventral surface in matrix.

The quadratojugal in AMU-CURS 186 differs from that in MCZ 9417 (*B. venezuelensis*) due to the extent of both temporal and cheek emarginations, which affect the quadratojugal. The cheek emargination results in a shorter quadratojugal-jugal contact and the absence of the quadratojugal-squamosal contact present in MCZ 9417. The right cheek is damaged and the left cheek emargination, while appearing well-preserved, may have been exaggerated in extent from over-preparation. Nonetheless, the extent of the emargination would not have been affected significantly as the bone along the edges is quite thin.

Squamosal: Both squamosals are preserved without significant damage, although there has been some pitting and erosion due to preparation. The squamosal in AMU-CURS 186 is similar to that in MCZ 9417 (*B. venezuelensis*). There is a ventral flange running anteroposteriorly as in MCZ 9417. The posterior projection of the squamosal forms more of a point in dorsal view than in MCZ 9417.

Postorbital: Parts of both postorbitals are preserved in AMU-CURS 186 but they are damaged. The left postorbital is missing its anterior surface, and the right one is represented by only a few fragments on the dorsal surface. Both postorbitals do have some of their medial processes preserved but neither is complete. The dorsal part of the postorbital is similar in size and shape to that in MCZ 9417 (*B. venezuelensis*), as it is not affected by the temporal or cheek emarginations. On the ventral surface, the postorbital has a ventral process that forms the anterior part of the lateral wall of the septum orbitotemporale, along with the parietal. The septum orbitotemporale is formed by the postorbital, jugal, parietal, and pterygoid, although the septum is incomplete on both sides and only visible on its posterior surface.

Premaxilla: Both premaxillae are present but they lack their medial portions, and are preserved only along the maxilla sutures and labial ridge anteriorly.

In MCZ 9417 (*B. venezuelensis*) the premaxilla forms a medially opening groove at the anterior end of the triturating surface cleft (GAFFNEY & WOOD 2002), with a small shelf ventral to the cleft formed by the max-
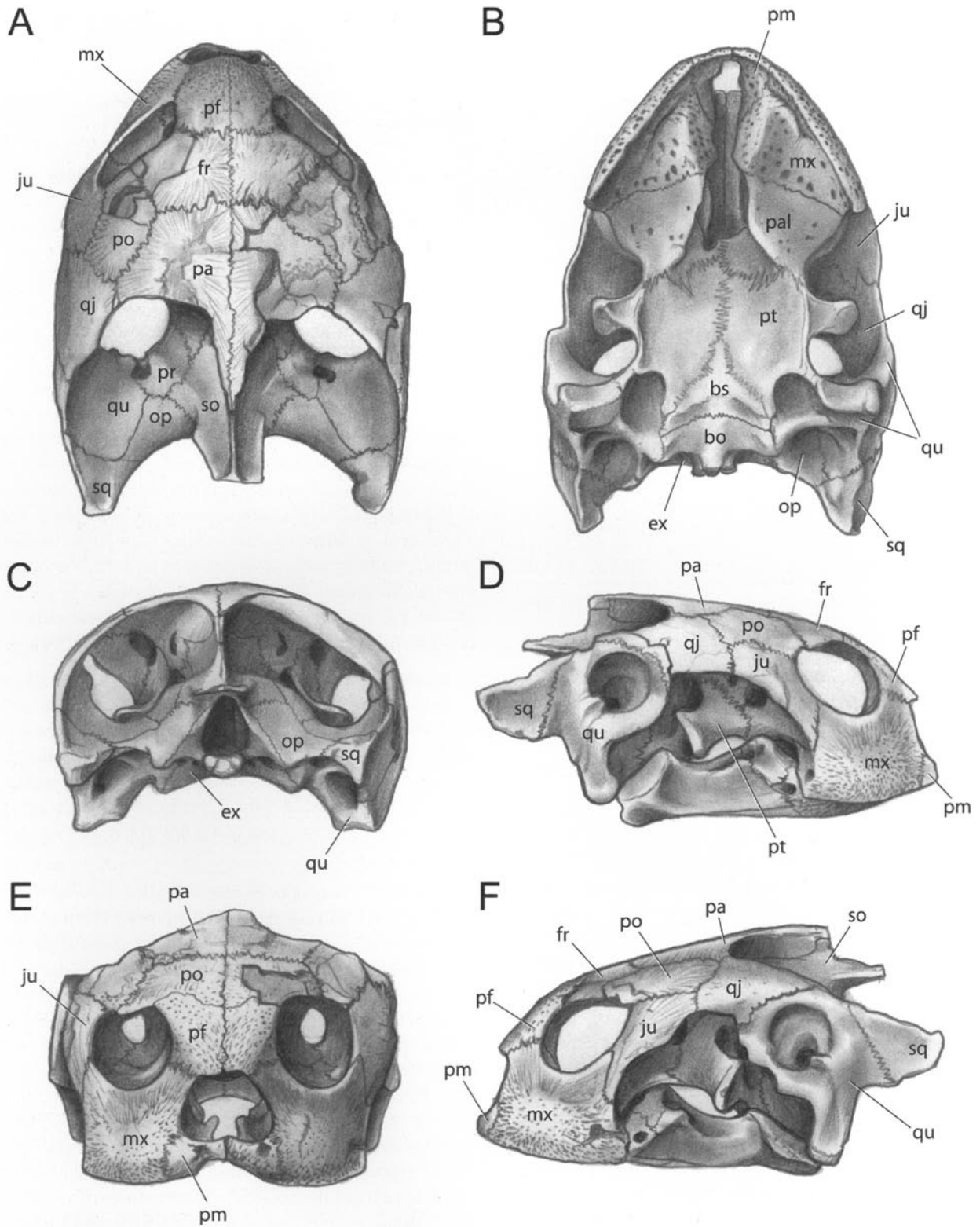
Fig. 3. *Bairdemys sanchezi* n. sp., AMU-CURS 186, holotype. – **A–F**: Six views of skull; A. dorsal; B. ventral; C. occipital; D. right lateral; E. anterior; F. left lateral. – See Fig. 4 for scale.

illae. In AMU-CURS 186 the medial parts of the premaxillae are not preserved, but the lateral part of this groove can be seen. It is likely that, in this area, the premaxilla in AMU-CURS 186 was similar to that in MCZ

9417. On the other hand, the labial ridge in AMU-CURS 186 has a notch as in *Bairdemys hartsteini*, and in contrast to MCZ 9417 and other specimens of *B. venezuelensis*.
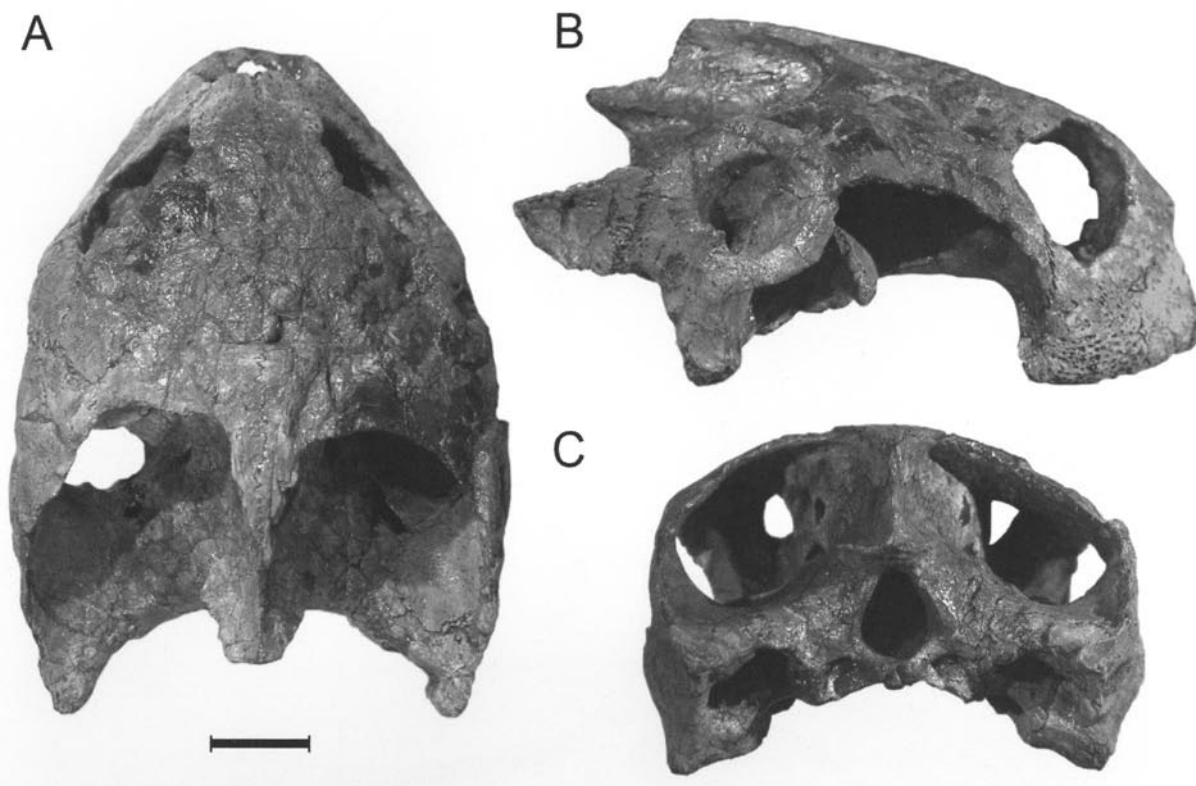
Fig. 4. *Bairdemys sanchezi* n. sp., AMU-CURS 186, holotype. – **A–C**: Three views of skull; **A**. dorsal; **B**. right lateral; **C**. occipital. – Scale bar = 10 mm.

Maxilla: Both maxillae are preserved in AMU-CURS 186. Their medial edges are eroded along the margin of the palatal cleft.

The triturating surface of AMU-CURS 186 is similar to other *Bairdemys* in that the maxilla bears a low convexity and the palatine bears a shallow concavity. The convexity in AMU-CURS 186 is present, but significantly lower than in MCZ 9417 (*B. venezuelensis*) and the other specimens that have it visible and preserved. The whole snout of the skull in AMU-CURS 186 is narrower than in MCZ 9417, and this makes the triturating surface slightly narrower as well. The medial margin is a broken edge, but it could be as in MCZ 9417. The labial ridge in MCZ 9417 is deep and continues anteriorly at a roughly even height. In AMU-CURS 186 the labial ridge is deep posteriorly but becomes shallower anteriorly, similar to that in *hartsteini*.

On the dorsal surface, the maxilla forms a ridge separating the fossa orbitalis from the lateral surface of the maxilla. This ridge is deep in AMU-CURS 186 and shallow in MCZ 9417. The dorsal process of the maxilla separates the orbit from the apertura narium externa. It is similar in shape and relative size in AMU-CURS 186 and MCZ 9417.

Palatine: Both palatines are present in AMU-CURS 186. They are complete on the triturating surface but lack their medial edges above the apertura narium interna. The margins of the apertura narium interna are slightly eroded, but seem to be close to their original shape.

The palatine forms the posterior part of the triturating surface, and, in *Bairdemys*, the more concave portion. In AMU-CURS 186 the concavity is shallower than in MCZ 9417 and other *Bairdemys venezuelensis*. In MCZ 9417 (*B. venezuelensis*) the concavity is so developed that there is a low ridge along its lateral margin. This is a sloping surface in AMU-CURS 186. Medially the palatine forms the apertura narium interna margins and roof. Most of the roofing portion is very thin and is broken in AMU-CURS 186. The apertura margin is represented by broken edges, but looks as if it was slightly wider than in MCZ 9417. Although the area is relatively well preserved, the senior author has been unable to find either foramen palatinum posterius.

The palatine presumably forms much of the anterior surface of the septum orbitotemporale, as in other pleurodires, but in AMU-CURS 186 it is covered on its anterior surface. Its posterior surface shows no contribution of the palatine to this surface, again as in other pleurodires. The palatine does form the posterior part of the fossa orbitalis floor. On the right side of AMU-CURS 186 there is a dorsal process of the palatine that contacts the ventral process of the frontal to form the anterior part of the side wall of the braincase, as in other *Shweboemys* Group members.

Quadrate: Both quadrates are present and relatively well-preserved. Both are slightly eroded along their anterior free edge but little bone seems to be missing.
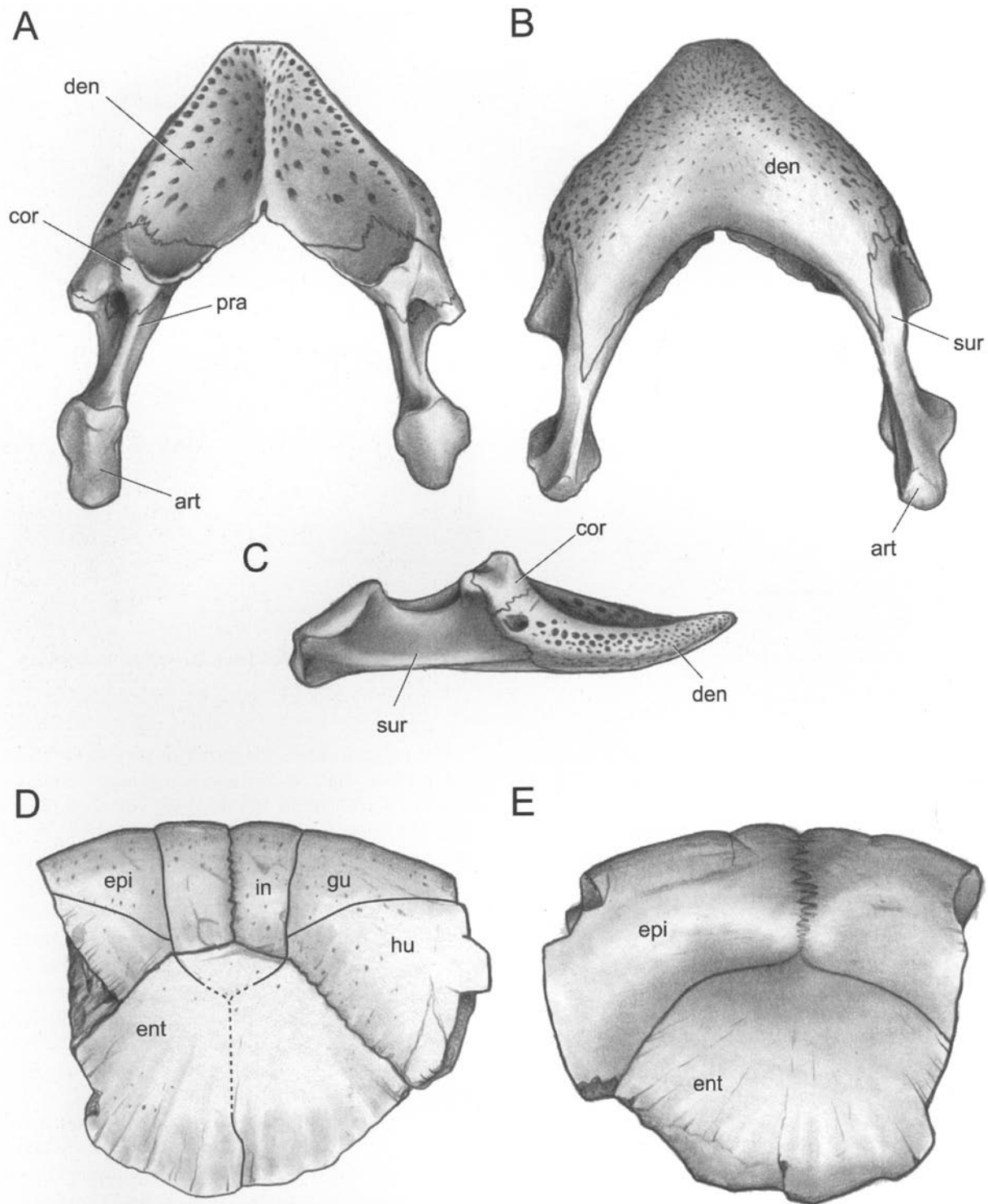
Fig. 5. *Bairdemys sanchezi* n. sp., AMU-CURS 186, holotype. – **A–C**: Lower jaw; A. dorsal, B. ventral, and C. right lateral view. – **D–E**: Plastral fragment consisting of entoplastron and parts of both epiplastra in D. ventral view and E. dorsal view. – See Fig. 6 for scale.

The quadrate of AMU-CURS 186 differs from that in MCZ 9417 (*B. venezuelensis*) primarily in the extent of the cheek emargination, which exposes more of the quadrate in AMU-CURS 186 than in MCZ 9417. The more extensive temporal emargination of AMU-CURS 186 also exposes some of the quadrate along the temporal margin, because the quadratojugal-squa-

mosal contact of MCZ 9417 is absent in AMU-CURS 186.

The antrum postoticum in AMU-CURS 186 agrees with that in MCZ 9417 and other *Bairdemys* in being a small slit, seen on the right quadrate of AMU-CURS 186. As in MCZ 9417, the incisura columellae auris of AMU-CURS 186 is completely enclosed by a thick bar
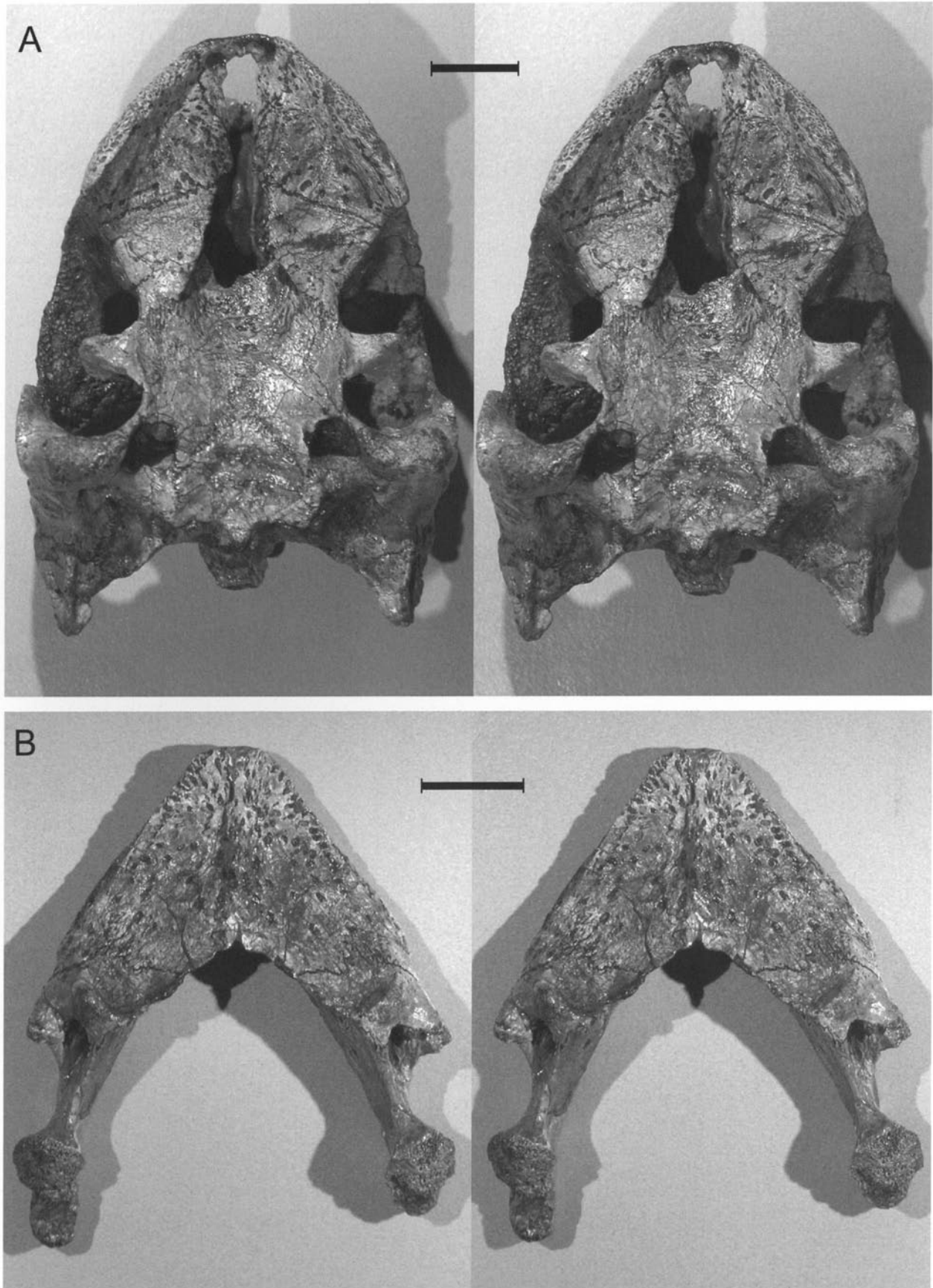
Fig. 6. *Bairdemys sanchezi* n. sp., AMU-CURS 186, holotype. Stereophotos of skull. – **A**: Ventral view of skull. – **B**: Dorsal view of lower jaw. – Scale bar = 10 mm.

Tab. 3. Comparison of the species of *Bairdemys*. All dimensions in mm.

	B. venezuelensis	B. hartsteini	B. sanchezi	B. winklerae	AMNH 30000
Snout shape	broad, convex	broad, straight	broad, convex	narrow, concave	broad, convex
Snout length	short	short	short	long	short
Prefrontal shape in lateral view	flatter, more horizontal		more curved antero-ventrally		
Skull width (B/A)	slightly wider (1.01)	slightly wider (0.92)	slightly narrower (0.85)	slightly narrower (0.87)	slightly wider (0.95)
Premaxillary notch	absent	present	present	absent	indet
Triturating surface convexity	high	low	very low	high	low
Triturating surface concavity	deep	shallow	very shallow	deep	low
Anterior triturating surface width (L/A)	0.20–0.22	0.20	0.19	0.26 (0.26-0.31)	0.34
Posterior triturating surface width (M/A)	0.33–0.36	0.28	0.27	0.18 (0.18-0.24)	0.29
Basisphenoid size	larger	larger	smaller	larger	indet
Basisphenoid shape	broad, curved anteriorly	broad, pointed anteriorly	triangular, acutely pointed anteriorly	broad, curved anteriorly	indet
Midline pterygoid contact	short	indet	long	long	indet
Temporal emargination	less	less	more	less	probably less
Cheek emargination	less	less	more	less	probably less
Basisphenoid-quadrate contact	narrow	narrow	narrow	wide	indet
Skull height	low	high	low	low	low
Position of condylus articularis	anterior	anterior	anterior	anterior	posterior
Orbital orientation	vertical	vertical	vertical	vertical	more horizontal
Skull size (A)	105–20	80	61	115	92
Distance between orbits (C/A)	0.41-0.42	0.47	0.34	0.40	0.41

of bone also enclosing the Eustachian tube. The Eustachian tube has a posterior opening extending from the cavum tympani to the occiput just below the fenestra postotica, also as in MCZ 9417 and other *Bairdemys*.

The foramen stapedio-temporale in AMU-CURS 186 is formed by the quadrate and prootic and faces anterodorsally as in other podocnemidids. The fenestra postotica is formed laterally and ventrally by the quadrate, also as in other podocnemidids. The fenestra postotica is not divided in AMU-CURS 186. The condylus articularis in AMU-CURS 186 is slightly more anteriorly placed than it is in MCZ 9417, nearly the same as in *B. hartsteini*.

Pterygoid: Most of both pterygoids are present in AMU-CURS 186, but the thin ventrolateral flange found in all pleurodires is broken off on both sides. As with most of the bone surface in AMU-CURS 186, there is some damage due to over-preparation and the pterygoid suffers from this along the margins of the cavum pterygoideus

(although long known in podocnemidids, it was first formally named in *Bairdemys* in GAFFNEY & WOOD 2002: 20). These margins and the associated pterygoid flange are not as extensive as they were in life.

The pterygoid in AMU-CURS 186 differs from that in MCZ 9417 (*B. venezuelensis*) primarily in the relative size of the ventral surface. In AMU-CURS 186 the basisphenoid is small, smaller than in *B. venezuelensis* and *B. hartsteini*. It is, apparently, of about the same size as in AMU-CURS 98 (*B. winklerae*), although this is unclear from the published photographs. In AMU-CURS 186 this difference is matched by the larger size of the pterygoid, which occupies the area formed by basisphenoid in *B. venezuelensis*, and *B. hartsteini*. In AMU-CURS 186 the midline contact of the pterygoids is much longer than in MCZ 9417.

The opening of the cavum pterygoideus appears to be unusually large in AMU-CURS 186, but this seems to be due to erosion of the edges so that in life the opening would have been smaller. The processus trochlearis

pterygoidei in AMU-CURS 186 is at a nearly right angle to the midline as in most of the *Shweboemys* Group. At the base of the processus, the pterygoid forms part of the septum orbitotemporale. In AMU-CURS 186 the pterygoid forms the ventral part of the septum meeting the parietal posterodorsally, the postorbital anterodorsally, and the jugal anteriorly.

Supraoccipital: The supraoccipital is present in AMU-CURS 186, but lacks the posterior half of the crista supraoccipitalis and the edges of the horizontal plate formed along the ventral edge of the crista.

The supraoccipital lies beneath the parietal and is not exposed on the skull roof in AMU-CURS 186, although this area is eroded and unlikely to represent the condition in life. It is possible that a small part of supraoccipital was exposed on the skull roof originally. The ventral, horizontally-expanded plate found in *Shweboemys* Group species is present in AMU-CURS 186 but incomplete. Nonetheless, it can be seen that it is attached to the supraoccipital more anteriorly than in the one skull of *B. venezuelensis* in which it is preserved. In *B. venezuelensis* the plate is separated by some of the crista from the main body of the supraoccipital, but in AMU-CURS 186 the plate is directly attached to the main body just above the foramen magnum.

Exoccipital: Both exoccipitals are preserved and nearly complete in AMU-CURS 186. The exoccipital in AMU-CURS 186 is very similar to that bone in MCZ 9417 (*venezuelensis*). Both have the two foramina nervi hypoglossi sunk into a single combined opening formed entirely by the exoccipital, also occurring in other *Shweboemys* Group species. The foramen jugulare posterius is completely enclosed by bone and formed medially by the exoccipital.

Basioccipital: The basioccipital is preserved and nearly complete in AMU-CURS 186, and it is very similar to that bone in *Bairdemys hartsteini* and *B. venezuelensis*. There is a small, paired tuberculum basioccipitale on each posterolateral margin, with the quadrate participating dorsolaterally. The condylus occipitalis is formed equally by each exoccipital and the basioccipital, as in the other Podocnemididae. The basioccipital of AMU-CURS 186 has a shallow, concave ventral surface, as in the other *Bairdemys* species.

Prootic: The prootics are both present in AMU-CURS 186; the right one is damaged, but the left one is nearly complete. The prootic in AMU-CURS 186 is very similar to that in *B. venezuelensis* and other members of the *Shweboemys* Group. The foramen nervi trigemini is formed by the parietal anterodorsally, the pterygoid ventrally, and the prootic posterodorsally, as in other Podocnemididae.

Opisthotic: The opisthotics are both preserved in AMU-CURS 186; they are complete except for some surface erosion, particularly the right one, and being chewed on along their posterior margin.

The opisthotic in AMU-CURS 186 is very similar to that bone in *Bairdemys hartsteini* and *B. venezuelensis*. It forms the medial portion of the fenestra postotica and the lateral margin of the foramen jugulare posterius. The foramen jugulare posterius has a laterally trending trough coming out of the foramen formed mostly by the opisthotic, as in *B. venezuelensis*. This trough is not so pronounced in other *Shweboemys* Group species. On the left side in AMU-CURS 186, below the foramen jugulare posterius, is a small foramen, but this is an artefact due to preparation and not an original structure.

Basisphenoid: The basisphenoid is nearly complete in AMU-CURS 186. Little of its dorsal surface is visible. The basisphenoid in AMU-CURS 186 differs from that in MCZ 9417 (*B. venezuelensis*) in its relatively small size and more triangular shape. In MCZ 9417 the basisphenoid is triangular but broad anteriorly, coming to a blunt curved anterior end rather than to a point. In AMU-CURS 186 the sides of the basisphenoid are slightly concave, rather than being convex, and the bone comes to an acute point. The amount of contact with the quadrate posterolaterally is about the same in both AMU-CURS 186 and MCZ 9417.

Lower jaw: The lower jaw in AMU-CURS 186 is almost complete and well-preserved. It is very similar to the jaw described for *Bairdemys venezuelensis*. The triturating surface depressions on either side of the medial ridge on the dorsal surface are shallower than in MCN Pal-21-10708. The AMU-CURS 186 jaw is also much smaller than MCN Pal-21-10708. The right side ramus length of MCN Pal-21-10708 is 91.1 mm (SÁNCHEZ-VILLAGRA & WINKLER 2006). In AMU-CURS 186 it is 50.1 mm.

Characters discussed in SÁNCHEZ-VILLAGRA & WINKLER (2006): Because the senior author has taken a more "split" interpretation of variation in *Bairdemys*, it is worthwhile examining the analysis of SÁNCHEZ-VILLAGRA & WINKLER (2006), who have shown that much of the variation in skulls of *Bairdemys* is continuous and overlapping. The character headings are from SÁNCHEZ-VILLAGRA & WINKLER (2006). The reader should see Tab. 3 for character distributions.

Snout shape: The snout shape of "pinched" vs. "straight" of GAFFNEY & WOOD (2002) was questioned by SÁNCHEZ-VILLAGRA & WINKLER (2006), when they identified two Urumaco skulls as "pinched", rather than "straight" as was claimed by GAFFNEY & WOOD (2002) for the single Urumaco species, *B. venezuelensis*. This phrasing of "pinched" and "straight" was a poor way to characterize the morphology. We have altered the anatomical wording and the character descriptions here. However, the snout shape of MCN Pal-0001/MCN Pal-21-10708 (*B. venezuelensis*) was not accurately characterized as "pinched" in any case, because the entire skull is damaged. The better preserved area on the right

side is not pinched or the same as in AMNH 27222 (*B. hartsteini*). The second "pinched" specimen is the new skull described by SÁNCHEZ-VILLAGRA & WINKLER (2006), AMU-CURS 98, which we argue is a new species, *B. winklerae*. This skull might be better characterized as having a third state, in which the snout is elongated as well as concave on its sides. It is true that GAFFNEY & WOOD'S (2002) original characterization was unclear, but the snout shape of the well-preserved MCZ 9417, *Bairdemys venezuelensis*, and AMNH 27222, *Bairdemys hartsteini*, do differ. There is no overlapping character distribution in this case. However, they are clearly more similar to each other than either is to the snout of AMU-CURS 98 (*B. winklerae*).

Only dorsal views are available for three other skulls mentioned by SÁNCHEZ-VILLAGRA & WINKLER (2006), AMU-CURS 96, AMU-CURS 97, and AMU-CURS 99, but all three of these seem similar in snout shape to AMU-CURS 98 (*B. winklerae*). They are clearly more elongate than in MCZ 9417 (*B. venezuelensis*) and AMNH 27222 (*B. hartsteini*). Two of the skulls have either a straight margin (AMU-CURS 96) or a convex margin (AMU-CURS 97), whereas AMU-CURS 99 is concave as in AMU-CURS 98 (*B. winklerae*). In any case, the senior author would characterize all four of these snouts as elongate, in contrast to all other *Bairdemys*, and the specimens are presumably best referred to *B. winklerae*.

AMNH 30000 (*Bairdemys* sp. indet.) agrees with MCZ 9417 (*B. venezuelensis*) and AMNH 27222 (*B. hartsteini*) in having a shorter, broader snout in contrast to the four AMU-CURS specimens. However, poor preservation makes close comparison fraught with ambiguity.

Does the snout shape indicate different taxa? The snout shape alone would not separate MCZ 9417 (*B. venezuelensis*) from AMNH 27222 (*B. hartsteini*). However, the elongate snout of AMU-CURS 98 (*B. winklerae*) would be unusual if found in the same species as MCZ 9417 (*B. venezuelensis*). There are certainly triturating surface differences between genders and populations in the same species of living turtles (CANN 1998; DALRYMPLE 1977; LINDEMAN 2000), but these are actually uncommon, and despite reservations, snout shape is a useful distinction among turtle species.

Premaxillary notch: Unfortunately, perhaps due to a lack of clarity in GAFFNEY & WOOD (2002), SÁNCHEZ-VILLAGRA & WINKLER (2006) mistook a different structure for the term "premaxillary notch" in GAFFNEY & WOOD (2002). GAFFNEY & WOOD (2002) meant the ventral profile of the labial ridge formed by the two premaxillae as seen in anterior view as the area of the notch. If the ventral margin is concave ventrally, as in GAFFNEY & WOOD (2002: fig. 15D), then the notch is present. If the labial ridge margin is horizontal or nearly so, as in GAFFNEY & WOOD (2002: fig. 7D), then the notch is absent. This feature can only be seen in anterior view, in contrast to SÁNCHEZ-VILLAGRA & WINKLER

(2006: fig. 7A), which label their interpretation of the notch in lateral view. The structure labelled here is unclear to this author, but seems to be a deviation of the suture.

Basisphenoid shape: This character does provide variation among the specimens and presumably differentiates AMU-CURS 98 (*B. winklerae*) from MCZ 9417 (*B. venezuelensis*). However, ventral view sutures are not explicitly figured for AMU-CURS 98 (*B. winklerae*) and other AMU-CURS skulls, so its distribution is unclear. Nonetheless, we have interpreted the photograph of AMU-CURS 98 (*B. winklerae*) in SÁNCHEZ-VILLAGRA & WINKLER (2006: figs. 2B, C) as having a relatively wide basisphenoid-quadrate contact, a wide basisphenoid anteriorly, and a blunt anterior margin.

Maxillary-jugal suture: This character seeks to identify a more vertical from a more horizontal position of this suture in lateral view. This feature is not figured by line drawing in SÁNCHEZ-VILLAGRA & WINKLER (2006), although its distribution is identified in SÁNCHEZ-VILLAGRA & WINKLER (2006), Table 1. MCZ 9417 (GAFFNEY & WOOD 2002: figs. 7C, E) is identified as having the more vertical condition and MCZ 9418 (GAFFNEY & WOOD 2002: fig. 9) as having the more horizontal condition. In the judgment of the senior author, these figures are hard to differentiate, and this character is not used here for comparisons. The AMU-CURS 186 (*B. sanchezi*) differs from all the others in having a more extreme cheek emargination so the maxilla widely enters the cheek margin and the suture is much more dorsal than in other *Bairdemys*.

Squamosal shape: The posterior squamosal projection in pleurodires usually has very thin edges, making comparisons of its dorsal outline somewhat random due to breakage. SÁNCHEZ-VILLAGRA & WINKLER (2006) used pointed versus flat, as typified by the ventral views seen in GAFFNEY & WOOD (2002: figs. 4–5) of *B. venezuelensis* and *B. hartsteini,* respectively. These features vary within species of pleurodires in the opinion of the senior author, and they even vary from side to side among the specimens used here. This character is not used here for comparisons.

Basisphenoid/cavum pterygoideus: SÁNCHEZ-VILLAGRA & WINKLER (2006) noted that the pterygoid-quadrate contact may entirely prevent the basisphenoid from entering the margin of the cavum pterygoidus in ventral view. The basisphenoid is almost always exposed inside the cavum in podocnemidids, so this is a reflection of the posterior extent of the pterygoid. Ventral sutures are not shown by line drawing for any specimens in SÁNCHEZ-VILLAGRA & WINKLER (2006), but they indicated conditions for specimens figured in GAFFNEY & WOOD (2002). Although coded by SÁNCHEZ-VILLAGRA & WINKLER (2006), MCN Pal-0001 /MCN Pal-21-10708 (*B. venezuelensis*) and MCN Pal-0002/MCN Pal-21-10707 (*B. venezuelensis*) are too

badly damaged in this area to resolve the relative extent of the pterygoid and exactly where the depression for the cavum pterygoidus begins. MCZ 9418 (B. venezuelensis) is also damaged in this area, as the skull is laterally compressed. MCZ 9417 (B. venezuelensis) is supposed to lack the condition, whereas AMNH 27222 (B. hartsteini) and AMU-CURS 98 (B. winklerae) have it. There is a suture or crack in the figure of AMU-CURS 98 (B. winklerae) that shows a short pterygoid and the basisphenoid widely entering the cavum. However, AMNH 27222 (B. hartsteini) has a clear posterior extent of the pterygoid contacting the quadrate and preventing entry of the basisphenoid into the cavum, just as in MCZ 9417 (B. venezuelensis). The length of the basisphenoid-quadrate contact is a variable character in these skulls. We do use the basisphenoid-quadrate contact in this area as a character, but the position of the curved surface leading dorsally into the cavum pterygoideus is ambiguous even when all specimens are at hand and they are not in this case.

Maxilla-palatine contact: This character is illustrated by SÁNCHEZ-VILLAGRA & WINKLER (2006: fig. 7) and describes the position of this suture on the triturating surface. SÁNCHEZ-VILLAGRA & WINKLER (2006: fig. 7B), however, showed a position (black dotted line) for AMU-CURS 98 (B. winklerae), also shown in their fig. 2B. This dotted line agrees with the apparent suture in fig 2B. However, the gray dotted line is supposed to be for AMNH 27222, B. hartsteini, figured in GAFFNEY & WOOD (2002: figs. 5, 12, 15B), but it does not agree with these figures. The position in AMNH 27222 is very close to that in AMU-CURS 98 (B. winklerae) as well as in MCZ 9417, the best preserved skull of B. venezuelensis. The sutures in AMNH 30000 (Bairdemys sp. indet.) are not determinable in this area, in the opinion of the senior author.

Orbital positions: SÁNCHEZ-VILLAGRA & WINKLER (2006) used the figures in GAFFNEY & WOOD (2002: figs. 2A and 3A) to distinguish a more horizontal versus a more vertical orientation. Unfortunately, after examination of these skulls, the senior author cannot confirm the real difference of this distinction. The vagaries of specimen orientation and lighting, while every effort is made to equalize these problems, can still suggest differences that are not great in magnitude. A different comparison of GAFFNEY & WOOD (2002) fig. 6A and fig. 12 (upper) show photographs of the same skulls with almost exactly the same amount of orbital rim exposed.

However, the difference in orbital exposure of AMNH 30000 (Bairdemys sp. indet.) and AMU-CURS 96 (B. winklerae) is distinctly greater than in MCZ 9417 (B. venezuelensis) and AMNH 27222 (B. hartsteini), but AMU-CURS 98 (B. winklerae) also seems to be very similar to MCZ 9417 (B. venezuelensis).

Palatine/pterygoid contact: This feature is only visible in a few of the specimens. However, according to

SÁNCHEZ-VILLAGRA & WINKLER (2006) it is supposed to be narrow in MCZ 9417 (B. venezuelensis; GAFFNEY & WOOD 2002: fig. 4) and wide in AMU-CURS 98 (B. winklerae; SÁNCHEZ-VILLAGRA & WINKLER 2006: figs. 2B, 7B). The senior author's interpretation of these specimens and figures, however, is that the widths are nearly the same, with MCZ 9417 being the wider of the two, not narrower.

Crista supraoccipitalis: The relative length/width of the crista supraoccipitalis was described in SÁNCHEZ-VILLAGRA & WINKLER (2006), but their character refers to the extent of the crista in reference to the posterior limits of the squamosals. Using the GAFFNEY & WOOD (2002: figs. 4, 5) reconstructions, SÁNCHEZ-VILLAGRA & WINKLER (2006) noted that B. venezuelensis has a crista extending well past the squamosals whereas B. hartsteini has one that just reaches the extent of the squamosals. Reexamination of the specimens confirms this observation. However, it is based on a composite figure in B. venezuelensis. AMU-CURS 98 has a crista just barely extending past the squamosals and can be coded as the same as in B. hartsteini. AMU-CURS 96 (B. winklerae), although pretty beat up, seems to have a slightly longer crista but not as long as in B. venezuelensis, and can also be coded as "longer". Table 1 in SÁNCHEZ-VILLAGRA & WINKLER (2006) coded the MCZ-collected specimens all as indeterminate, presumably due to the composite nature of the reconstruction.

Palatal depressions: Bairdemys is unique in having a broad triturating surface with an anterior convexity and a posterior concavity. In the MCZ-collected specimens (B. venezuelensis), the concavity is deeper than in AMNH 27222, B. hartsteini. SÁNCHEZ-VILLAGRA & WINKLER (2006) coded AMU-CURS 98 (B. winklerae) as also having a deeper depression or concavity. Although they stated that AMNH 30000 (Bairdemys sp. indet.) and AMU-CURS 96 (B. winklerae) "have shallower palatal depressions than CURS 98" (SÁNCHEZ-VILLAGRA & WINKLER 2006: p. 247), in Table 1 they code AMNH 30000 as "deeper" and AMU-CURS 98 as "shallower". The new skull, AMU-CURS 186 (B. sanchezi), clearly has the shallower condition, even shallower than in AMNH 27222 (B. hartsteini).

Size of secondary palate and distance between foramen palatinum posterius: SÁNCHEZ-VILLAGRA & WINKLER (2006) stated that the triturating surface in AMNH 30000 (Bairdemys sp. indet.) is larger than in the other specimens. Measurements from SÁNCHEZ-VILLAGRA & WINKLER (2006) and GAFFNEY & WOOD (2002) of the anterior and posterior widths of the triturating surfaces partially support this character (Tab. 1). The ratios based on the posterior widths (M/A) show AMNH 30000 (0.29) falling within the range with some MCZ-collected Bairdemys (0.33, 0.36) exceeding AMNH 30000. The anterior triturating surface width (L/A) of

0.34 for AMNH 30000, however, shows a definite increase in width over the MCZ-collected specimens, which range from 0.20–0.22. However, AMU-CURS 96 (*B. winklerae*; which is damaged) comes close at 0.31, and the other AMU-CURS specimens range from 0.26–0.27, so this distinction may not be significant.

SÁNCHEZ-VILLAGRA & WINKLER (2006) also stated that AMNH 30000 has a smaller width of the internal nares (apertura narium interna) and a narrower distance between each foramen palatinum posterius. The senior author has been unable find either foramen palatinum posterius in AMNH 30000 (*Bairdemys* sp. indet.) due to poor preservation but they may be there. These foramina are very small in *Bairdemys* (GAFFNEY & WOOD 2002) and hard to find at best. GAFFNEY & WOOD (2002) inadvertently caused confusion in the table of measurements for measurement N "width of palate across foramina palatinum posterius" which was interpreted by SÁNCHEZ-VILLAGRA & WINKLER (2006) to mean "width between foraminae palatini posterius". Measurement N of GAFFNEY & WOOD (2002) does not equal measurement 12 in SÁNCHEZ-VILLAGRA & WINKLER (2006). For GAFFNEY & WOOD (2002) this measurement was between the bony edges of the palate from the internal wall of the fossa temporalis in the plane of the foramen palatinum posterius, which is wider than measured between the foramina (this is figured in GAFFNEY et al., 2006, fig. 315, measurement N).

The cleft which separates the triturating surfaces is presumably what SÁNCHEZ-VILLAGRA & WINKLER (2006) meant by narrower internal nares. This cleft and the apertura narium interna posterior to it seem to be relatively narrow in this skull. The poor preservation makes comparisons difficult, but these features seem narrower in AMNH 30000 than in any of the MCZ-collected skulls. However, AMU-CURS 98 also seems to have a relatively narrow apertura narium interna as well.

Relative position of the quadrate: SÁNCHEZ-VILLAGRA & WINKLER (2006) stated that the position of the condylus articularis of the quadrate is farther posterior in AMNH 30000 (*Bairdemys* sp. indet.) in relation to the condylus occipitalis than in other *Bairdemys*, and we agree with this observation. In all the *Bairdemys*, including AMNH 30000, the articular condyles are anterior to the condylus occipitalis, but the exact position of them in AMNH 30000 is compromised, because the condylus occipitalis itself is missing. Comparison with surrounding structures, however, suggests that the condylus articularis in AMNH 30000 lies close to or on the plane of the condylus occipitalis.

Skull width: SÁNCHEZ-VILLAGRA & WINKLER (2006) correctly showed that GAFFNEY & WOOD (2002) mistakenly stated that *B. hartsteini* had a narrower skull than *B. venezuelensis* by actually using measurements, apparently ignored by GAFFNEY & WOOD (2002). SÁNCHEZ-VILLAGRA & WINKLER (2006) presented ratios of skull height and width of the available skulls that

show no particular grouping of specimens. However, we have shown these measurements in Table 3 for the better preserved skulls, because the width does vary and doers distinguish some taxa. The significance of slight differences in width is dubious, however.

Skull height: SÁNCHEZ-VILLAGRA & WINKLER (2006) presented ratios of skull height and width that show *B. hartsteini* as having a relatively higher skull than other *Bairdemys*. However, even the well-preserved MCZ 9417 (*B. venezuelensis*) may have some dorsoventral deformation.

Skull width between orbits: SÁNCHEZ-VILLAGRA & WINKLER (2006) showed that ratios of width between orbits versus width of skull at middle of orbits (GAFFNEY & WOOD 2002: tab. 2) places *B. hartsteini* outside the other *Bairdemys* skulls.

Description of a Podocnemididae specimen (gen. et. sp. indet.) from the Urumaco Formation

Figs. 7–9, Tab. 1

Specimen: Complete, but poorly preserved skull (Fig. 7) and partial shell (Fig. 8), UNEFM-CIAPP 1399; collector: Jean Bocquentin Villanueva.

Locality and Horizon: 1.5 km north of El Hatillo locality, possibly upper member of the Urumaco Formation (upper Miocene), north of the town of Urumaco, Falcón State, Venezuela. Other faunal elements from this site, including remains of the freshwater turtle *Chelus lewisi* (UNEFM-CIAAP 1371, 1379, 1391), small neural plates of a Testudines indet. (UN-EFM-CIAAP 1394), a maxillary of *Mourasuchus* (UNEFM-CIAAP 1378), cranial material of a caiman (UNEFM-CIAAP 1368), and pelvic girdle elements of a dinomyid rodent (UN-EFM-CIAAP 1395), all suggest a continental environment.

Description: Sutures are absent on this skull, so its features are described by region. In dorsal view (Fig. 7A), the skull is relatively long and narrow in contrast to *Shweboemys* Group taxa, but closer in shape to *Podocnemis*, *Peltocephalus* and *Roxochelys*. As preserved, the skull is even narrower than in the living podocnemidids, but this may be due to deformation. The orbits and apertura narium externa are close together at the very anterior end of the skull, also as in *Podocnemis*. There is a narrow interorbital distance on the skull roof, in contrast to *Bairdemys*, but as in *Podocnemis*. The temporal emargination seems to be similar to that in *Peltocephalus* and *Erymnochelys*, that is, less than in *Bairdemys*, but not as extensive as in *Podocnemis*. In lateral view, there seems to be only a slight degree of cheek emargination, similar to that seen in *Bauruemys*, but not as much as in *Podocnemis*.

In ventral view, the lower jaws are articulated in the skull and the labial ridges of the maxillae are partially folded down onto them (Fig. 7B). However, it can be seen that the lower jaws are not thin as in *Podocnemis*, but also are not as wide as in *Bairdemys*. This suggests a moderate expansion to the triturating surfaces on both lower jaws and maxillae. It is possible that a reduced ver-
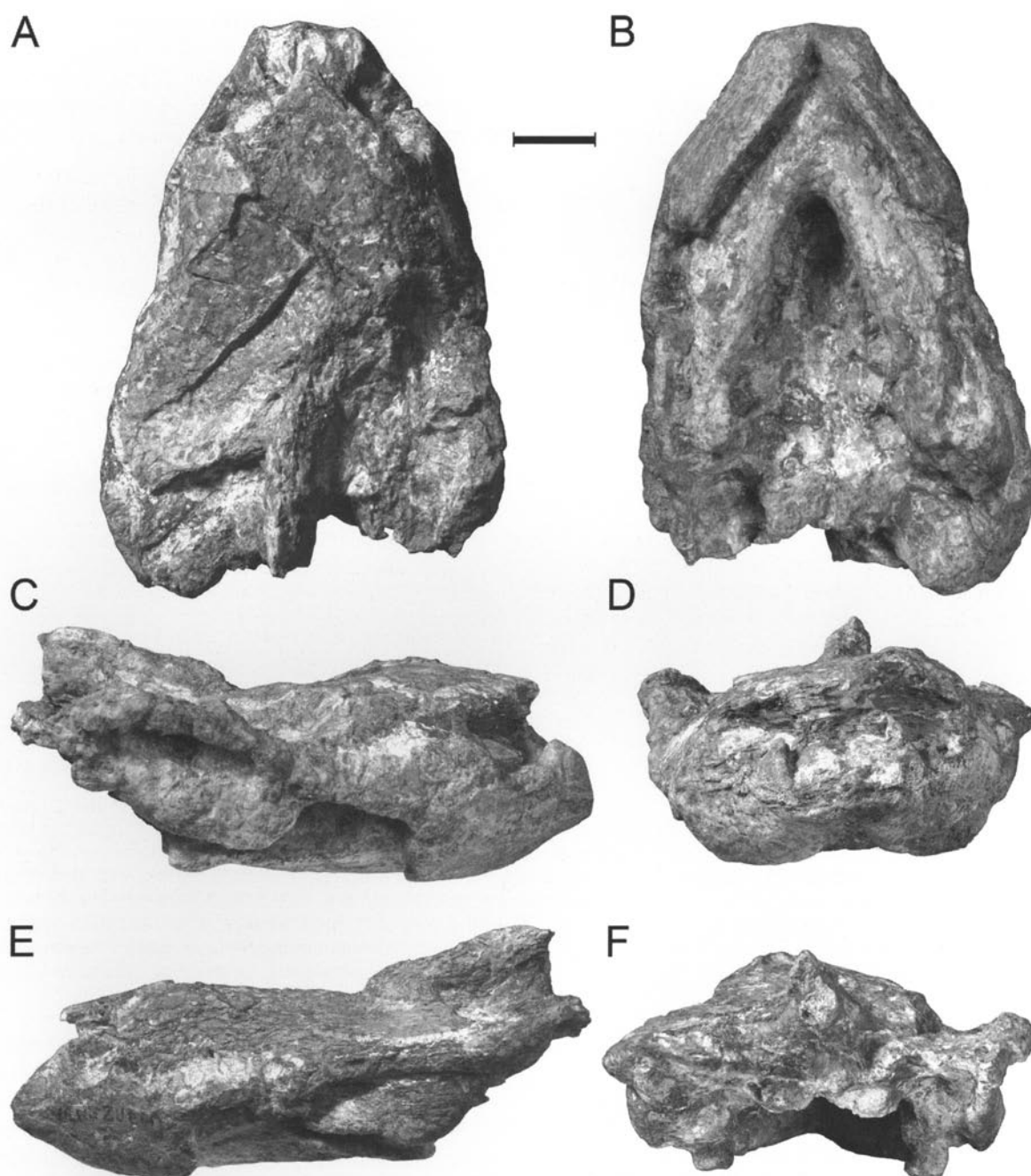
Fig. 7. Skull, UNEFM-CIAPP 1399, indeterminate Podocnemididae. – **A–F**: Six views of skull and jaw; A. dorsal; B. ventral; C. right lateral; D. anterior; E. left lateral; F. occipital. – Scale bar = 20 mm.

sion of the *Shweboemys* Group secondary palate was present, but it is more likely that UNEFM-CIAPP 1399 had a moderately expanded triturating surface, like that in *Dacquemys* and most *Erymnochelys*. There is an acute premaxillary notch, but this could be due to preservation. The presence of a cavum pterygoideus is likely, but not definite, due to poor preservation.

As a guess, this skull could be close to or even within the genus *Podocnemis*. It is unlikely to be a member of the *Shweboemys* Group. The interesting aspect of this specimen is that it demonstrates the presence of another podocnemidid genus in the Urumaco Formation.

Bone histology of the carapace fragment: Two thin-sections of the carapace fragment UNEFM-CIAPP 1399 (Figs. 8A–B) were made, following standard procedures for petrographic thin-sectioning (see SCHEYER & SÁNCHEZ-VILLAGRA 2007). The planes of sectioning (Figs. 8C–D) were chosen to sample the right costals 1 & 2 (section a; extending perpendicular to the rib) and the left peripheral 1 (section b; extending proximodistally through the peripheral). The thin-sections were compared to other pelomedusoides taxa including shell fragments of giant *Stupendemys geographicus* from the Urumaco Formation (SCHEYER & SÁNCHEZ-VILLAGRA
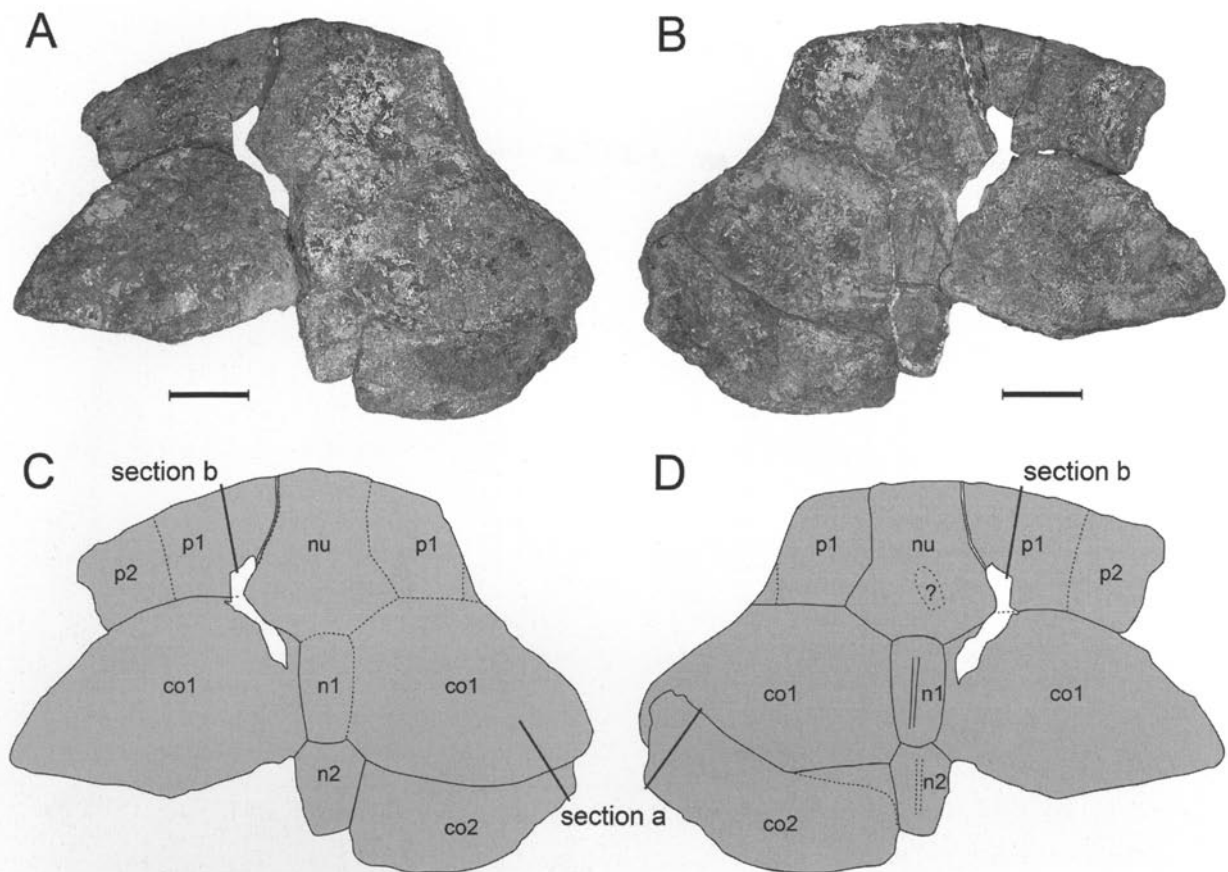
Fig. 8. Carapace fragment UNEFM-CIAPP 1399 of new Podocnemididae (gen. et. sp. indet.) from the Urumaco Formation. – **A–B**: Dorsal (A) and ventral (B) view of the carapace fragment. Note the thick encrusting of the bones that mostly obscure the surface details of the bones as well as the sutures between the bones. Based on the general poor preservation, shield impressions were not observable on the surfaces of the shell bones. – **C–D**: Interpretative sketches of the dorsal (C) and ventral (D) sides of the carapace fragment. The dotted lines reflect sutures that are mostly obscured by the sediment and mineral crust. Note the rest of spongy bone attached to the ventral side of the nuchal bone (dotted area marked with "?"; maybe representing a remnant of the last cervical). The solid black lines labelled "section a" and "section b" mark the position of the planes of sectioning for histological study. – Scale bars = 50 mm.

2007), as well as new shell material of cf. *Bairdemys* sp., also from the Urumaco Formation.

The shell material of UNEFM-CIAPP 1399 is generally poorly preserved. The natural cross-sections in the shell bones and the prepared thin-sections reveal the fossil bone being strongly encrusted, mainly by fibrous gypsum and sediment. The sediment crust was found to obscure almost all details of the bone surfaces, as well as partly altering the internal compact bone composition. Especially in the internal cortical bone, crystallite growth caused delamination in the bone tissue. Still, the bone tissue itself, though crushed and diagenetically altered in many places, is reasonably well preserved to allow comparison with other turtle shell bones.

Both thin-sections of UNEFM-CIAPP 1399 have similar bone microstructures. The samples show a general diploe-structure of the shell, with external and internal cortices framing an area of interior cancellous bone (Fig. 9A). The external and internal cortical bone layers are of similar thickness. The external cortical tissue consists of interwoven structural fiber bundles, vascularized by an extensive reticular pattern of thin

primary vascular canals (Fig. 9B). As was shown in previous studies (SCHEYER & SÁNCHEZ-VILLAGRA 2007; SCHEYER et al. 2007), the presence of interwoven structural fiber bundles in the external cortices is plesiomorphic for Testudines, as it appears both in pleurodiran and cryptodiran taxa. Locally, cyclical growth marks are present throughout the external cortex (Fig. 9C). In the proximal part of section b of peripheral 1 (Fig. 9A), the external and internal cortices consist of different bone tissues, while more distally, the dorsal and ventral compact bone layers share the same composition. Based on this fact, it is hypothesized that, even though a trough or rim is not observable macroscopically, the "visceral seam" extends far to the lateral margin of the shell element.

The interior cancellous bone consists of moderately long and thick bone trabeculae. The trabeculae are lined with secondary lamellar bone. The largest vascular spaces are situated in the central regions of the cancellous bone, while smaller spaces are more common in the transitional zones towards the external and internal compact bone layers (Fig. 9A).
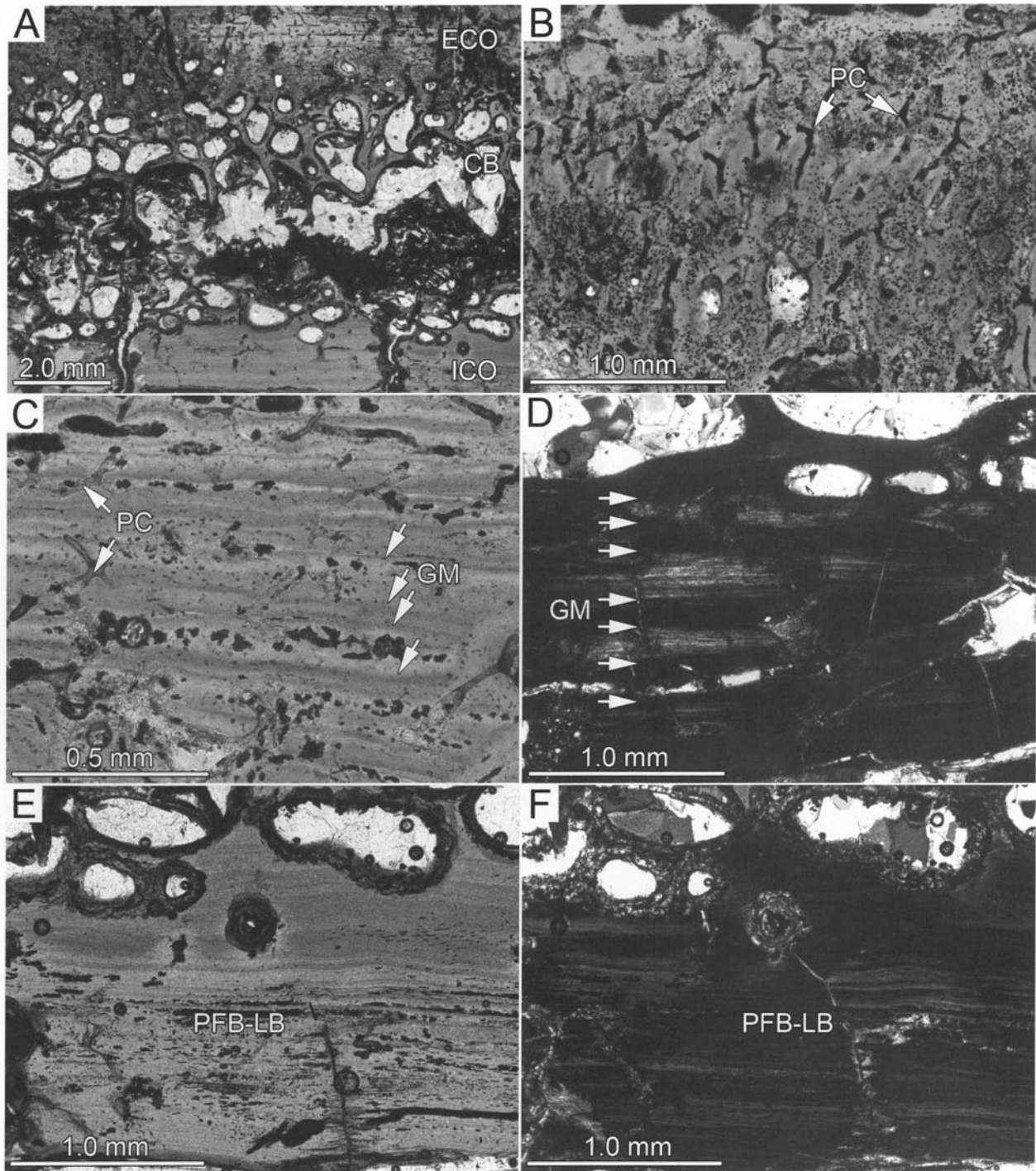
Fig. 9. Bone histology of the carapace fragment UNEFM-CIAPP 1399 of new Podocnemididae (gen. et. sp. indet.) from the Urumaco Formation. – **A**: Overview of thin-section (proximal part of section b of peripheral 1) showing the diploe nature of the shell bone with cortical bone surrounding an area of interior cancellous bone in normal transmitted light. The cortices consist of different bone tissues, indicating that the "visceral seam" extends far proximally towards the lateral margins of the peripheral. Only in the more distal parts of the peripheral, the dorsal and ventral cortical bone tissues share the same composition. Both cortices are well developed. The trabeculae of the cancellous bone have partly collapsed. – **B**: Close-up of the external cortex and adjacent transitional zone towards the cancellous bone (section a) showing the reticular vascularization pattern of the external cortex in normal transmitted light. – **C**: Close-up of the external cortex (section b) in normal transmitted light, focussing on the growth marks in the compact bone. – **D**: Close-up of the internal cortex (section b). Growth marks are visible as thick light and dark colored zones in the compact bone. – **E–F**: Close-up of another portion of the internal cortex (section b) in normal transmitted light (E) and polarized light (F). Locally, the light and dark coloured layers of the bone tissue are fine spaced enough to indicate transition from parallel-fibered bone to lamellar bone. Note the remodelling of the compact bone tissue at the transition zone to the cancellous bone as well as the strong alteration of the bone next to the vascular spaces.

The internal cortical bone (Fig. 9D–F) consists of parallel-fibered bone grading into lamellar bone. The bone tissue is weakly vascularized by scattered secondary osteons and primary vascular canals. Both, larger scale cyclical growth marks (Fig. 9D) and individual bone lamellae (Figs. 9E–F), perceived as light and dark colored layers in the bone tissue, are discernable throughout the internal cortex. In this regard, the shell fragments of UNEFM-CIAPP 1399 closely resemble the shells of Recent *Podocnemis erythrocephala*, but not those of other pelomedusoides taxa, including *Stupendemys geographicus* and cf. *Bairdemys* sp. (SCHEYER & SÁNCHEZ-VILLAGRA 2007). The authors then speculated on the light and dark layering in *P. erythrocephala* as representing a potential apomorphy of that particular taxon. If the light and dark layering pattern of the internal cortex is interpreted as a potential synapomorphy of UNEFM-CIAPP 1399 and *P. erythrocephala*, the shell bone histology would further corroborate the hypothesis that UNEFM-CIAPP 1399 might be near or within the genus *Podocnemis*.

Summary

The Miocene Urumaco Formation in Venezuela comprises a rich turtle fauna, with the side-necked turtle genus *Bairdemys* being the dominant turtle taxon (SÁNCHEZ-VILLAGRA & WINKLER 2006; WINKLER & SÁNCHEZ-VILLAGRA 2006). The Urumaco Formation just starts to rival one of the most important fossil lagerstätten of turtle remains in South America, namely the La Venta fauna (middle Miocene) of Colombia (WOOD 1997), not only in preservation, but also in genus and species level abundance. It is also similar in turtle diversity to the Acre vertebrate fauna of Brazil (COZZUOL 2006).

In the current study, the taxon *Bairdemys* from the Miocene of Venezuela and Puerto Rico is revised, and four separate species are diagnosed on the basis of skull characters (Tab. 3). *Bairdemys* belongs to Podocnemididae, based on its cavum pterygoideus, and to the informally named *Shweboemys* Group, based on its secondary palate with a narrow midline cleft. The species of *Bairdemys* are examined and two are described as new. *B. hartsteini* GAFFNEY & WOOD, 2002, is characterized by a higher skull with a straight labial ridge and a premaxillary notch; *B. venezuelensis* (WOOD & DÍAZ DE GAMERO 1971) is characterized by a larger skull, the absence of a premaxillary notch, a high anterior triturating surface convexity, a deep posterior concavity, and a short pterygoid midline contact; *B. sanchezi* n. sp., is characterized by a very low anterior triturating surface convexity and shallow posterior concavity, a premaxillary notch, a smaller skull, and a more extensive temporal and cheek emargination; *B. winklerae* n. sp., is characterized by a larger skull, an elongate, narrow snout, with a concave labial ridge and no premaxillary notch.

Additionally, a strongly crushed skull and associated carapace fragment reveal the presence of yet another podocnemidid species. Features of both skull morphology and shell bone histology argue for a possible association with or even the inclusion of this specimen in the genus *Podocnemis*. We feel confident that given time, more and better preserved fossils will be recovered that will allow a more detailed analysis of the material. Until then, the assignment of specimen UNEFM-CIAPP 1399 to a genus is elusive.

Acknowledgments

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