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Notoemys zapatocaensis, a New Side-Necked Turtle (Pleurodira: Platychelyidae) from the Early Cretaceous of Colombia

EDWIN ALBERTO CADENA RUEDA[1] AND EUGENE S. GAFFNEY[2]

ABSTRACT

A carapace and posterior plastral lobe from the early Cretaceous Valanginian of northeastern Colombia is a new species of the pleurodire *Notoemys*. It is a pleurodire based on the sutured pelvis and xiphiplastral notch. *Notoemys zapatocaensis*, n.sp., differs from the other two species of *Notoemys*, *N. oxfordiensis* and *N. laticentralis*, in having a slightly serrated posterior margin, a very small third peripheral, no contact of costal 1 and peripheral 3, and protuberances developed on the pleural and vertebral scale areas.

Notoemys zapatocaensis, n.sp., extends the distribution of *Notoemys* from Argentina and Cuba to Colombia geographically, and from the 156 mya Oxfordian late Jurassic to the 135 mya Valanginian early Cretaceous. Reanalysis based on morphology of the new shell suggests that *Notoemys* is the sister taxon to the late Jurassic European *Platychelys* based on the common possession of a very large costovertebral tunnel, tubercle on anterior margin of first thoracic rib, wide, flat thoracic ribs, and a first thoracic centrum that is wider than high.

INTRODUCTION

The Pleurodira, or side-necked turtles, form a significant element of the South American vertebrate fauna. Their record extends back into the Jurassic, although the pre-Aptian part of the record is very sparse. Therefore, a new pleurodire from the early Cretaceous of Colombia (fig. 1) is an important range extension and aids in understanding early pleurodire history. The new specimen belongs to the genus *Notoemys*, first described by Cattoi and Freiburg (1961) on the

[1] Instituto Colombiano del Petroleo (ICP), Micropaleontologia, AA 4185, Bucaramanga, Colombia (geodwins@yahoo.com.mx).
[2] Division of Paleontology, American Museum of Natural History (esg@amnh.org).

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Fig. 1. Northwestern South America, showing Zapatoca, Colombia, where *Notoemys zapatocaensis* was found. Map based on satellite imagery from NASA/JPL/NIMA.

basis of a shell from the late Jurassic of Argentina that was the oldest turtle from South America at that time. Since then, *Palaeochersis*, a primitive turtle from the late Triassic falling outside the Pleurodira and the Casichelydia (Gaffney and Meylan, 1988), has been described by Rougier et al. (1995) as the oldest South American turtle. The original description of *Notoemys laticentralis* has been followed by more detailed descriptions of the type (Wood and Freiburg, 1977) and new specimens (Fuente and Fernandez, 1989; Fernandez and Fuente, 1994). Recently, another Jurassic pleurodire has been described from Cuba, *Caribemys oxfordiensis* (Fuente and Iturralde-Vinent, 2001). The newly discovered Colombian specimen has suggested a reexamination of *Notoemys* and *Caribemys*, as well as the late Jurassic European pleurodire, *Platychelys*.

This study concludes that *Caribemys oxfordiensis* and the new Colombian specimen are best included in a redefined *Notoemys*, which is interpreted as the sister taxon to *Platychelys*. The family Platychelyidae is recognized as consisting of *Notoemys* and *Platychelys*. Comparisons of the Colombian specimen with *Notoemys laticentralis* are based on the above papers plus examination of the described material. We have not seen the specimen of *Caribemys oxfordiensis*. Comparisons of *Platychelys* are based on study of specimens in Solothurn, Basel, and Munich, as well as Wagner (1853), Lang and Rutimeyer (1866), Zittel (1877), Bräm (1965), and Lapparent de Broin (2001).

Anatomical Abbreviations

ab	abdominal scale
an	anal scale
ax	axillary buttress
c	costal rib
ce	cervical scale
co	costal bone
cv	caudal vertebra
ent	entoplastron
epi	epiplastron
fem	femoral scale
gu	gular scale
hu	humeral scale
hyo	hyoplastron
hypo	hypoplastron
in	intergular scale
ing	inguinal buttress
ma	marginal scale
mes	mesoplastron
ne	neural bone
nu	nuchal bone
pe	peripheral bone
pec	pectoral scale
pl	pleural scale
py	pygal
su	suprapygal
t	thoracic centrum
ve	vertebral scale
xip	xiphiplastron

INSTITUTIONAL ABBREVIATIONS

IPN-EAC Museo Geologico Ingeominas, Bogota, Colombia
MOZP Museo ''Prof. Dr. Olsacher'' Zapala, Argentina

SYSTEMATICS

ORDER TESTUDINES LINNAEUS 1758

MEGAORDER PLEURODIRA COPE, 1864 (FIDE GAFFNEY AND MEYLAN, 1988)

FAMILY PLATYCHELYIDAE BRAM, 1965

DIAGNOSIS: Pleurodires with pelvis sutured to carapace and plastron, xiphiplastral notch, and cervical scale; complete series of eight neurals reaching two suprapygals; mesoplastra wider than long and not meeting in midline; differing from all other pleurodires in having very wide costovertebral tunnel (except *Chelus*), articulation tubercle on anterior edge of first thoracic rib, and shell shape with anterior edge wide and straight; posterior sides tapering with straight margin; neurals alternating in size, as in *Dortoka*; hyoplastral-hypoplastral fontanelle present; first thoracic rib nearly as large as second thoracic rib; thoracic vertebral centra flat ventrally, thoracic ribs flat and broad without ventral keel; first thoracic central articulation concave, wider than high; thoracic ribs 9, 10, and 11 forming sacrum and attaching to ilium.

DISTRIBUTION: The family extends from the Oxfordian of Cuba as the oldest to the Valanginian of Colombia as the youngest. The Oxfordian *Notoemys* ''orig. Caribemys'' *oxfordiensis* is about 156 mya, the Kimmeridgian central European *Platychelys oberndorferi* is about 152 mya, the Tithonian Argentinian *Notoemys laticentralis* is about 145 mya, and the youngest is the Valanginian Colombian *Notoemys zapatocaensis*, n.sp., about 135 mya (F. Etayo, personal commun.).

The geographical distribution for the revised family is extensive, but a late Jurassic paleogeography (Smith and Biden, 1977) shows a much closer association of these localities than a modern map (fig. 2). They all occur in marine, micritic limestones that seem to have been deposited in similar environments. Whether or not the shallow sea of Switzerland and Germany was continuous during the late Jurassic and early Cretaceous with the one in Cuba, Colombia, and Argentina is not clear, but seems possible.

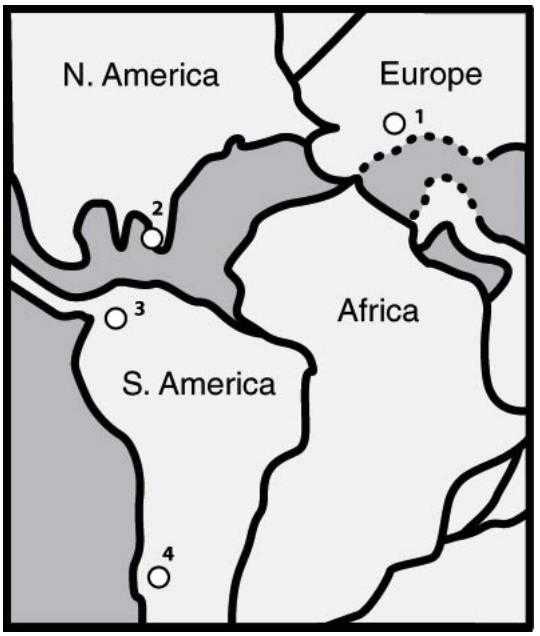

Fig. 2. Map of Tithonian (late Jurassic 140 million years ago) continental reconstruction (Smith and Briden, 1977) showing distribution of Platychelyidae. **1.** *Platychelys oberndorferi*, ca. 152 mya. **2.** *Notoemys oxfordiensis*, ca. 156 mya. **3.** *Notoemys zapatocaensis*, ca. 135 mya. **4.** *Notoemys laticentralis*, ca. 145 mya.

Genus ***Notoemys*** Cattoi and Freiburg, 1961

TYPE SPECIES: *Notoemys laticentralis* Cattoi and Freiburg, 1961.

INCLUDED SPECIES: *laticentralis*, *oxfordiensis*, *zapatocaensis*.

REVISED DIAGNOSIS: Pleurodiran turtle, having the sutured pelvis and xiphiplastral notch characteristic of pleurodires; carapace shape consisting of a wide, straight anterior shell margin, anterior carapace sides roughly parallel, and posterior sides tapering, similar to that in *Platychelys* but distinct from *Proterochersis*, *Dortoka*, Chelidae, and Pelomedusoides; differs from *Proterochersis* in having a low shell, no carapacial anal excavation, and fewer than 14 marginal scales; differs from *Platychelys* in having no supramarginal scales, wide cervical scale, smooth

shell with no high protuberances or strong radiating ridges, relatively flat shell, and large suprapygal one; differs from *Dortoka* in having wide neurals and cordiform rather than oval shell.

Notoemys zapatocaensis, new species

TYPE SPECIMEN: IPN 15-EAC 140120031, a carapace and posterior part of plastron.

TYPE LOCALITY: El Caucho farm (73°15′W–6°49′N), northeast of Ciudad de Zapatoca, Department of Santander, Colombia.

HORIZON: Upper part of Rosablanca Fm (Guzman, 1985), late Valanginian based on ammonoid *Synoceras verrucosum* (F. Etayo, personal commun.).

DIAGNOSIS: A species of *Notoemys* (see table 1) that differs from *N. laticentralis* and *N. oxfordiensis* in having a first costal not contacting peripheral 3, peripheral 3 very small, and marginal scale 3 small and restricted entirely to peripheral 2, marginal 4 reaching peripheral 2; differs from *N. laticentralis* in having a slightly serrated rather than smooth posterior carapace edge, a notched pygal, narrower vertebral scales, and slight rather than no doming along posterior edge of pleural and vertebral scale areas.

MORPHOLOGY

CARAPACE BONES

NUCHAL: The right half of the nuchal bone (figs. 3, 4, 5) is preserved; it is missing its posterior margin, but retains the contact with the first peripheral. Most of its size and shape can be determined by flipping right to left. The nuchal of *Notoemys zapatocaensis* is nearly identical to that in *Notoemys laticentralis* and to what is known of the nuchal in *Notoemys oxfordiensis*.

COSTALS: There are the usual eight costals (figs. 3–6) in IPN 15-EAC 140120031. Costals 5 to 8 are complete on both sides; costals 2 to 4 are best preserved on the left side and are missing only the lateral margins. Costal 1 is preserved laterally on the right side and medially on the left, but it is missing its anteromedial edge. The first costal in *N. zapatocaensis* (figs. 3, 6) is very similar to that bone in *N. laticentralis*. However, *N. zapatocaensis* differs from *N. laticentralis* and from most turtles in having an anterior contact only with peripherals 1 and 2 and not with peripheral 3. This condition is the same on both sides. It is possible that there is a suture in the crack between what we interpret as the two pieces of peripheral 1 (see fig. 3), but this seems unlikely when the pieces are placed using the left side and the ventral surface features as landmarks. Costal 1 has the normal pleurodire shape: anterior margin convex, posterior margin transverse, both meeting laterally in a point.

The first and second costals in *N. zapatocaensis* differ from *N. laticentralis* in the neural contacts. On the right side the second costal of *N. zapatocaensis* does not contact the first neural, and on the left side the contact is very small if present. In *N. laticentralis* the contact is more extensive. The first costal has a very small contact with the second neural in *N. zapatocaensis*, while in *N. laticentralis* there is a wider first neural/second costal contact. Costal 5 in *N. zapatocaensis* has a contact with the sixth neural, absent in one specimen of *N. laticentralis*, MOZP 2487, but present in the type specimen. The contacts of the other costals are the same in *N. zapatocaensis* and *N. laticentralis*.

On the ventral surface (figs. 7, 8), the first costal in *N. zapatocaensis* shows the axillary buttress of the hyoplastron reaching onto the lateral third of the costal, where an elongate pit is present on the adjacent peripherals as well as the first costal, for the buttress articulation. The medial extent of the buttress may be slightly more in *N. zapatocaensis* than in *N. laticentralis*.

The first thoracic rib is preserved in IPN 15-EAC 140120031, but it is damaged laterally on both sides. The rib is large, compared to living pleurodires, but it is not as large as in *Proganochelys*. The first thoracic rib in *N. zapatocaensis* is broad and flat, as are the other thoracic ribs. In *N. laticentralis* the first thoracic rib is smaller than in *N. zapatocaensis*, but it is still larger than in living pleurodires. The remaining ribs in *N. zapatocaensis* (figs. 7, 8) are flat and broad medially, narrowing strongly at the point of costal attachment, as in *N. laticentralis* and *Platychelys*. The costovertebral tunnel formed

between the thoracic neural spine and the costal attachment is very large in *N. zapatocaensis*, *N. laticentralis*, and *Platychelys*, significantly larger than in *Proganochelys* and all other pleurodires except *Chelus*. On the anterior margin of the first thoracic rib in *N. zapatocaensis* is a raised surface that appears to be an articulation facet, possibly for the scapula. This raised tubercle also occurs in *N. laticentralis* and *Platychelys*, but not in *Proganochelys* or living pleurodires. It is indeterminate in *N. oxfordiensis*.

PERIPHERALS: The first peripheral (figs. 4, 6) in *Notoemys zapatocaensis* has a narrow medial edge, where it contacts the nuchal, and a wider lateral contact with the first costal, similar to that in *Notoemys laticentralis*. However, beginning with the second peripheral, *N. zapatocaensis* shows a distinct difference from *N. laticentralis* and *Platychelys*, as well as most other turtles (fig. 5). Peripheral 2 is relatively large, larger than in *N. laticentralis*, and extends laterally to contact costal 2, a condition absent in *N. laticentralis*, *Platychelys*, and other pleurodires. It is unlikely that this is a pathology, as it is the same on both sides. It is probably related to a small triangular ossification, at the anterior end of the suture between peripheral 2 and the peripheral posterolateral to it. It is probable that this small ossification is actually peripheral 3, greatly reduced and squeezed out toward the edge of the shell. This is not certain, but *N. zapatocaensis* has one less pair of peripherals than other specimens of *Notoemys* if this small ossification is not a peripheral. However, the peripherals articulating with costals 2 and 3 are missing, so the number of peripherals cannot be determined by direct count. The remaining peripherals that are present (fig. 6), on costals 4 to the pygal, are in the same positions as peripherals in *N. laticentralis*, so it is likely that the missing peripherals were also consistent with *N. laticentralis*. If this is the case, then *N. zapatocaensis* would only have 10 pairs of peripherals articulating with costals. Another feature supporting the identification of the small ossification as peripheral 3 is that marginal 3, usually extending onto peripheral 3, is a small scale entirely on peripheral 2, just medial to the small ossification.

To make comparison easier, we assume that the above hypothesis concerning peripheral 3 is correct, so that the remaining peripherals in *N. zapatocaensis* are numbered the same as in *N. laticentralis* (fig. 6). A fragment of peripheral 6 is present on the left side along with a complete peripheral 7 (fig. 4). Peripherals 8 to 11 are present on both sides. These peripherals in *N. zapatocaensis* are very similar to those in *N. laticentralis* in size and shape and have the same contacts. The only nearly complete bridge peripheral remaining is 7. It is like *N. laticentralis* in having a relatively small ventromedial plate with the hypoplastron making up most of the ventral plate of the bridge (fig. 8). In both *N. zapatocaensis* and *N. laticentralis*, as well as *N. oxfordiensis*, the hypoplastron contact is not a tight suture but seems to be at least partially ligamentous, with a few pits on peripheral 7 for processes on the hypoplastron. Peripherals 8 to 11 have a low ridge marking the edge of the body wall attachment that parallels the edge of the shell. As in *N. laticentralis*, this ridge in *N. zapatocaensis* lies close to the shell margin, so that there is little overhang of the peripherals.

NEURALS: There are eight neurals in *Notoemys zapatocaensis* (fig. 6), forming a complete series from nuchal to suprapygal, as in *Notoemys laticentralis* and *Platychelys*. Neural 1 has a broken edge anteriorly so its complete extent is not known, but its sides are roughly parallel as in *Platychelys*, differing from the anteriorly tapering sides of *N. laticentralis* and *N. oxfordiensis*. The remaining neurals are complete. They form a series, very similar to that in *N. laticentralis* and *N. oxfordiensis*, and to a lesser extent, in *Platychelys*. The pattern is characterized by roughly alternating large and small neurals, with some asymmetry. The first neural in *N. zapatocaensis* is larger than the second, as in *N. laticentralis*, *N. oxfordiensis*, and *Platychelys*. In *N. zapatocaensis* neural 1 does not contact costal 2 (or the contact is very small, as the sides are asymmetrical), in contrast to these taxa. Neural 2 is four-sided, wider than long, as in *N. laticentralis*, *N. oxfordiensis*, and *Platychelys*. Neural 3 is six-sided, contacting costals 2, 3, and on the left side only, costal 4. This same asymmetry is seen in the specimen of *Platychelys* figured by Lapparent de Broin (2001: fig. 1), and a similar

Fig. 3. *Notoemys zapatocaensis*, n.sp. IPN IS-EAC140120031. Dorsal view of carapace.

asymmetry is in the type specimen of *N. laticentralis* but there is a costal 4 contact on both sides. Neural 4 is smaller than neural 3 in *N. zapatocaensis*, and contacts only costal 4, except at its anterolateral corner, where there is a costal 3 contact. This asymmetry also occurs in the *Platychelys* figured by Lapparent de Broin (2001: fig. 1), but *N. laticentralis* is symmetrical and lacks the costal 3 contact. *N. oxfordiensis* has a costal 3 contact on the left side.

Neural 5 is slightly larger than 4 in *N. zapatocaensis*, and contacts costals 4 and 5 as in *N. oxfordiensis*, *N. laticentralis*, and *Platychelys*. The type of *N. laticentralis* also has a costal 6 contact on the left side. Neural 6 in *N. zapatocaensis* is roughly six-sided, in contrast to the four-sided neurals 4 and 5, and its sides taper posteriorly rather than being parallel in all the anterior neurals. In *N. laticentralis* and *Platychelys*, neural 6 is parallel-sided. Neural 7 in *Notoemys zapatocaensis* is six-sided, almost twice as wide as long, and asymmetric, with its left side lon-

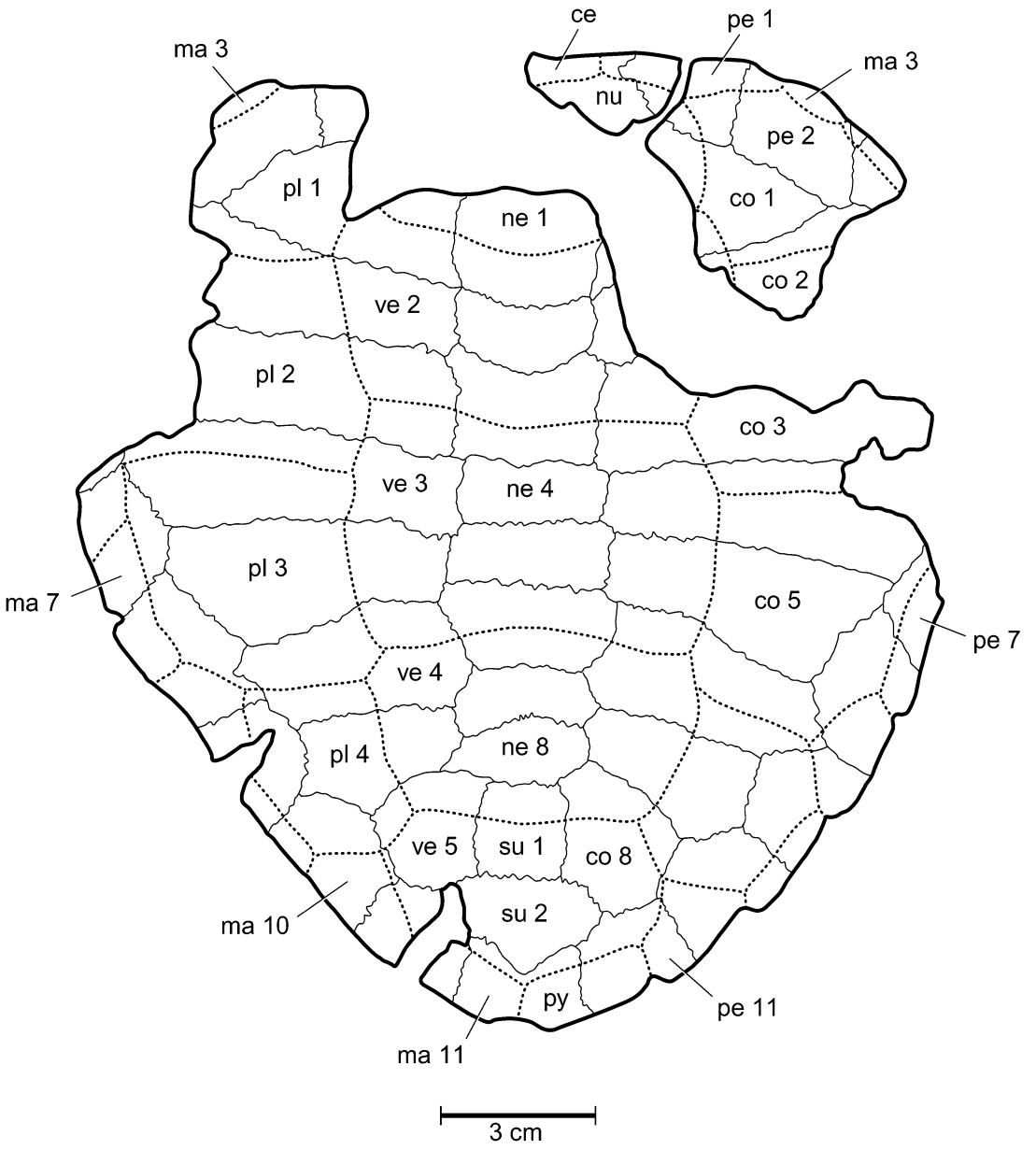

Fig. 4. *Notoemys zapatocaensis*, n.sp. Key to figure 3. Scales labeled on left, bones on right.

ger than the right. In *N. laticentralis* neural 7 is four-sided. Neural 7 in *N. zapatocaensis* has wide contacts with costals 6 and 7, while in *N. laticentralis* most of the neural contacts costal 6 and only a small contact is with costal 7. Neural 8 in *N. zapatocaensis* contacts costals 7 and 8 and suprapygal 1, as in *N. laticentralis*. It would seem that asymmetry in many carapace bones, particularly the neurals, is a consistent feature of *Notoemys*. It also seems to be common in *Platychelys*, and possibly *Dortoka*.

THORACIC VERTEBRAE: Thoracic vertebrae 1 through 11 and the first caudal are preserved and completely visible (figs. 7, 8).

The first thoracic vertebra in *Notoemys za-*

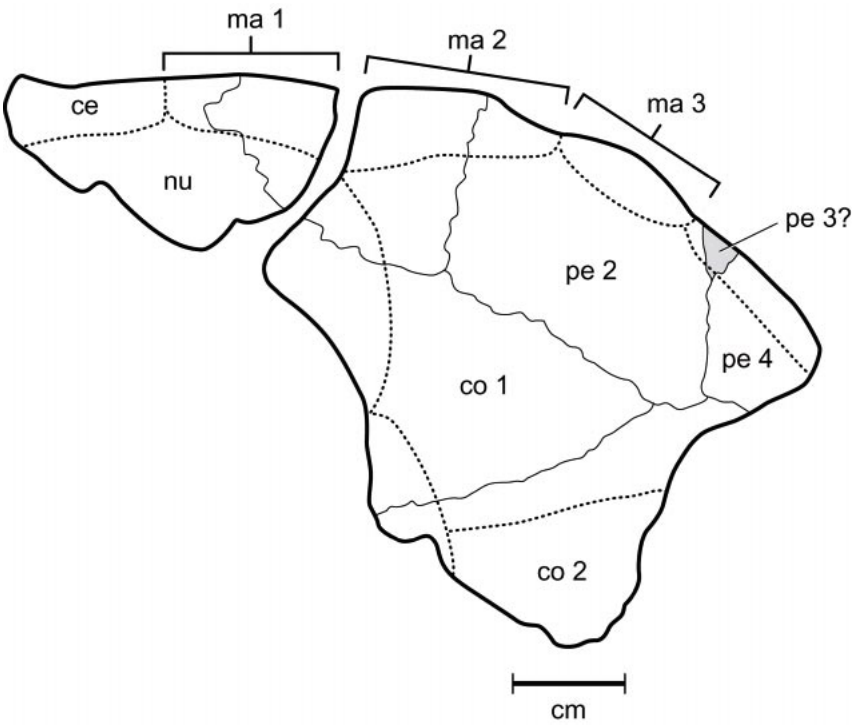

Fig. 5. *Notoemys zapatocaensis*, n.sp. IPN IS-EAC140120031. Anterolateral part of carapace in dorsal view showing very small peripheral 3.

patocaensis has a concave central articulation that is wider than high, as in *Platychelys*. The first thoracic rib has a broad, sutured articulation with the anterior half of the centrum. The second thoracic rib has an angled articulation with the posterior third of the first thoracic centrum and also with the anterior part of the second thoracic centrum, also as in *Platychelys*. The first thoracic rib in *N. zapatocaensis* is nearly as large as the second thoracic rib (equals the first costal rib), with an oval fontanelle between them medially and a sutured contact more laterally. The first thoracic rib seems to end just before reaching the axillary buttress, also as in *Platychelys*. In *N. zapatocaensis* there is an articular protuberance on the anterior edge of the first thoracic, as in *Platychelys*. The second thoracic rib is large and flat on its ventral surface. The costovertebral tunnel is wide here, nearly reaching the axillary buttress. This width is maintained for the length of the shell at least to thoracic rib 8 (costal rib 7). This rib morphology also agrees with *Notoemys laticentralis*, and *Platychelys*.

Thoracic vertebrae 2 through 6 have a similar shape: rib articulation ankylosis anteriorly and posteriorly, with an indented waist between. Thoracic vertebra 7 has only the anterior facet and thoracic vertebra 8 is smaller than the others, with the rib attaching in its middle and no other facets. This differs from *Platychelys*, which has the eighth thoracic rib (equals costal rib 7) articulating on both thoracic centra 7 and 8. Thoracic ribs 9, 10, and 11 attach to the ilium as sacral ribs. Their centra are smaller than the more anterior centra.

The first caudal appears between the ilia in the same position as in *Platychelys* (Bräm, 1965). The anterior central articulation is convex, the posterior one concave. A sutured rib extends directly laterally from the centrum, and reaches the ilial shaft.

SUPRAPYGALS AND PYGAL: *Notoemys zapatocaensis* (figs. 3, 4, 6) has two suprapy-

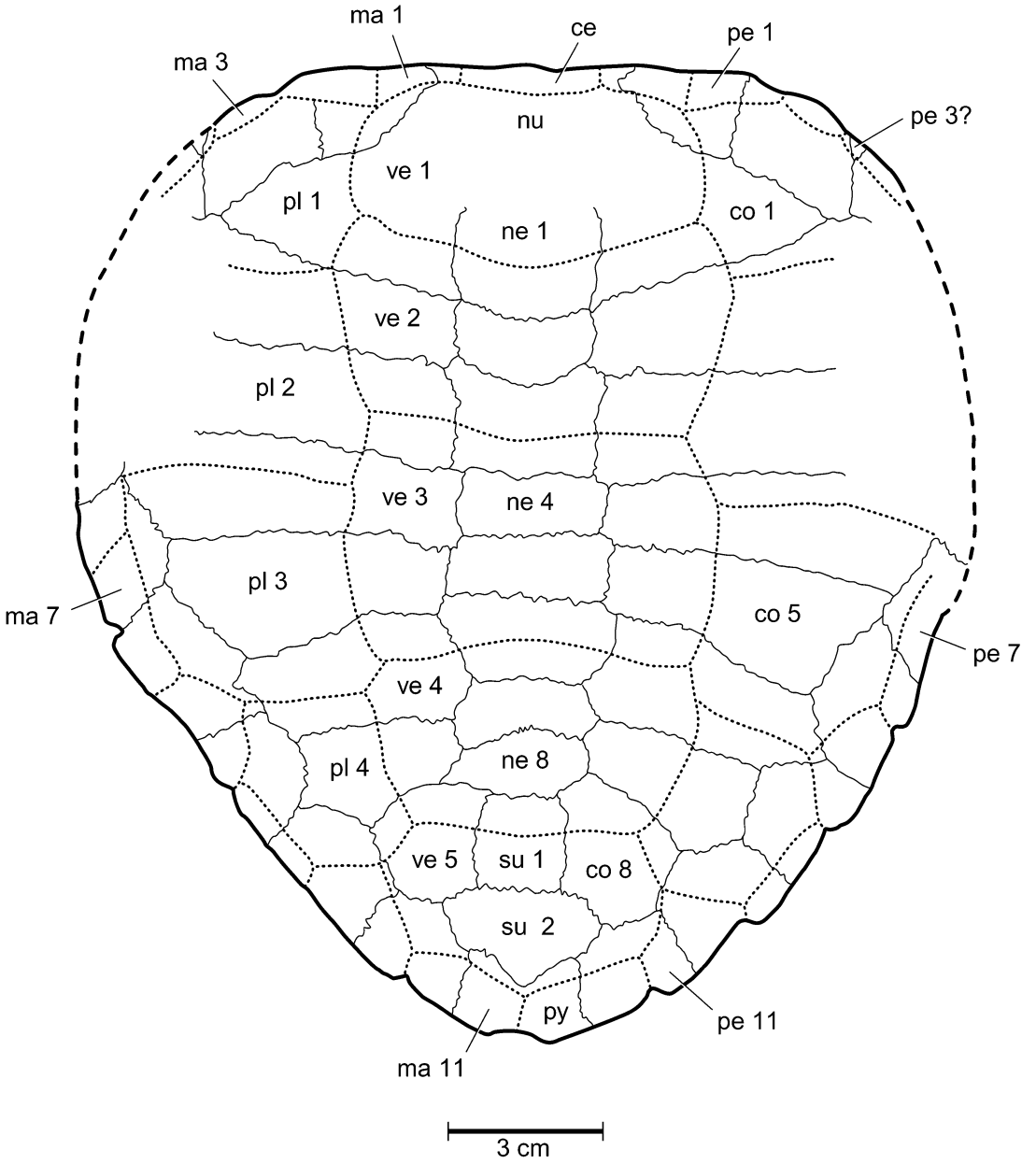

Fig. 6. *Notoemys zapatocaensis*, n.sp. Restoration of carapace in dorsal view. Scales labeled on left, bones on right.

gals and a pygal, as in *Notoemys laticentralis* and *Platychelys*. These are complete in IPN 15-EAC 140120031, except for breakage on the left side of suprapygal 2. The first suprapygal in *N. zapatocaensis* is four-sided, longer than wide, with parallel sides. *N. laticentralis* is also four-sided, but the sides taper anteriorly so the anterior length is about half its posterior length.

Suprapygal 2 in *N. zapatocaensis* is wider anteriorly than posteriorly, as in *N. laticentralis*, both apparently differing from *Notoe-*

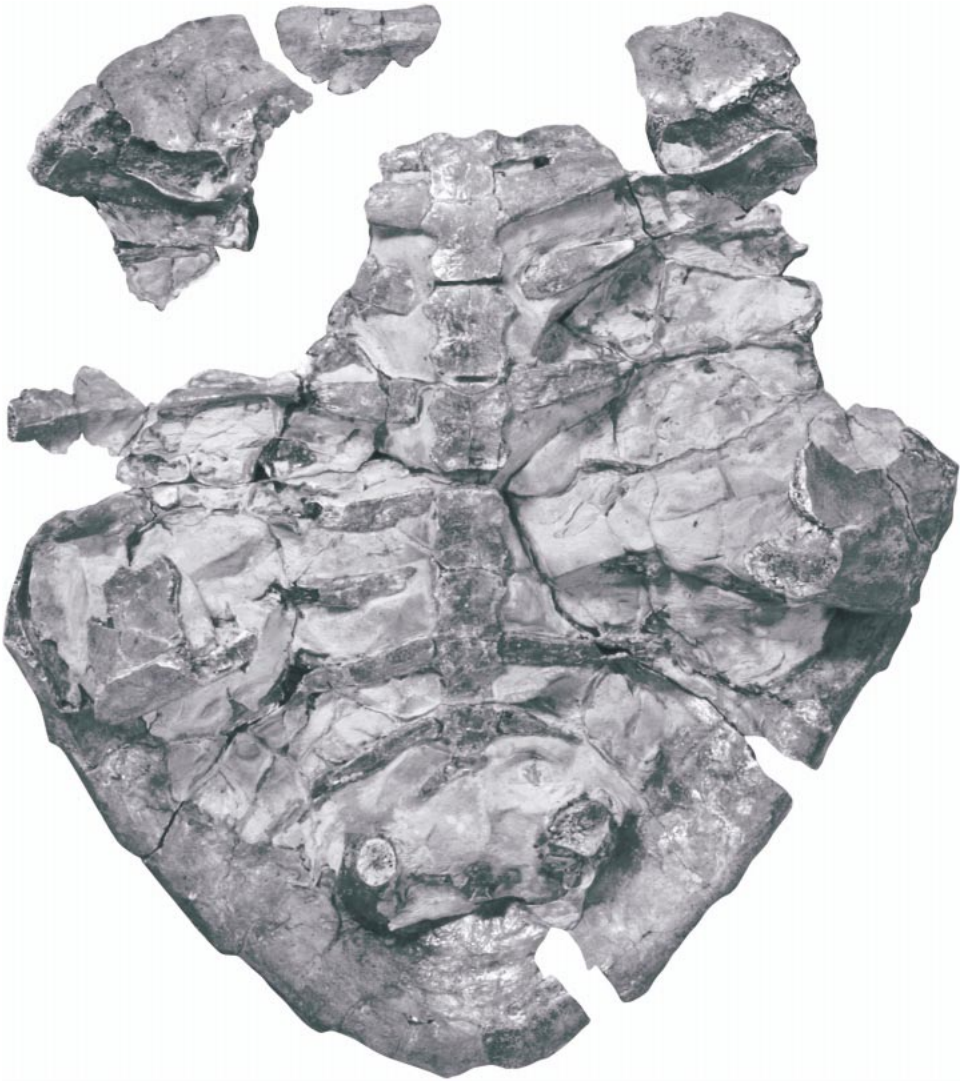

Fig. 7. *Notoemys zapatocaensis*, n.sp. IPN IS-EAC140120031. Ventral view of carapace.

mys oxfordiensis, which is widest in the middle. Suprapygal 2 contacts the first suprapygal anteriorly, costal 8 anterolaterally, peripheral 11 posterolaterally, and the pygal posteriorly. The pygal contact in *N. zapatocaensis* is V-shaped posteriorly, rather than straight or curved as in *N. laticentralis* and *N. oxfordiensis*. In *Platychelys* suprapygal 2 differs from all *Notoemys* in being parallel-sided and much narrower.

The pygal in *Notoemys zapatocaensis* (fig. 6) has a deep indentation for the second suprapygal and is slightly notched on the midline at its posterior edge for the marginal 11 sulcus. *N. laticentralis* has no indented suture for the suprapygal, although a very slight notch seems to be present.

Carapace Scales

Cervical Scales and Vertebrals: *Notoemys zapatocaensis* (fig. 6) has a short, wide cervical scale as in *Notoemys laticentralis*, wider than in *Platychelys*. The vertebral scales are very similar to those in *Platychelys*, differing from those in *N. laticentralis*,

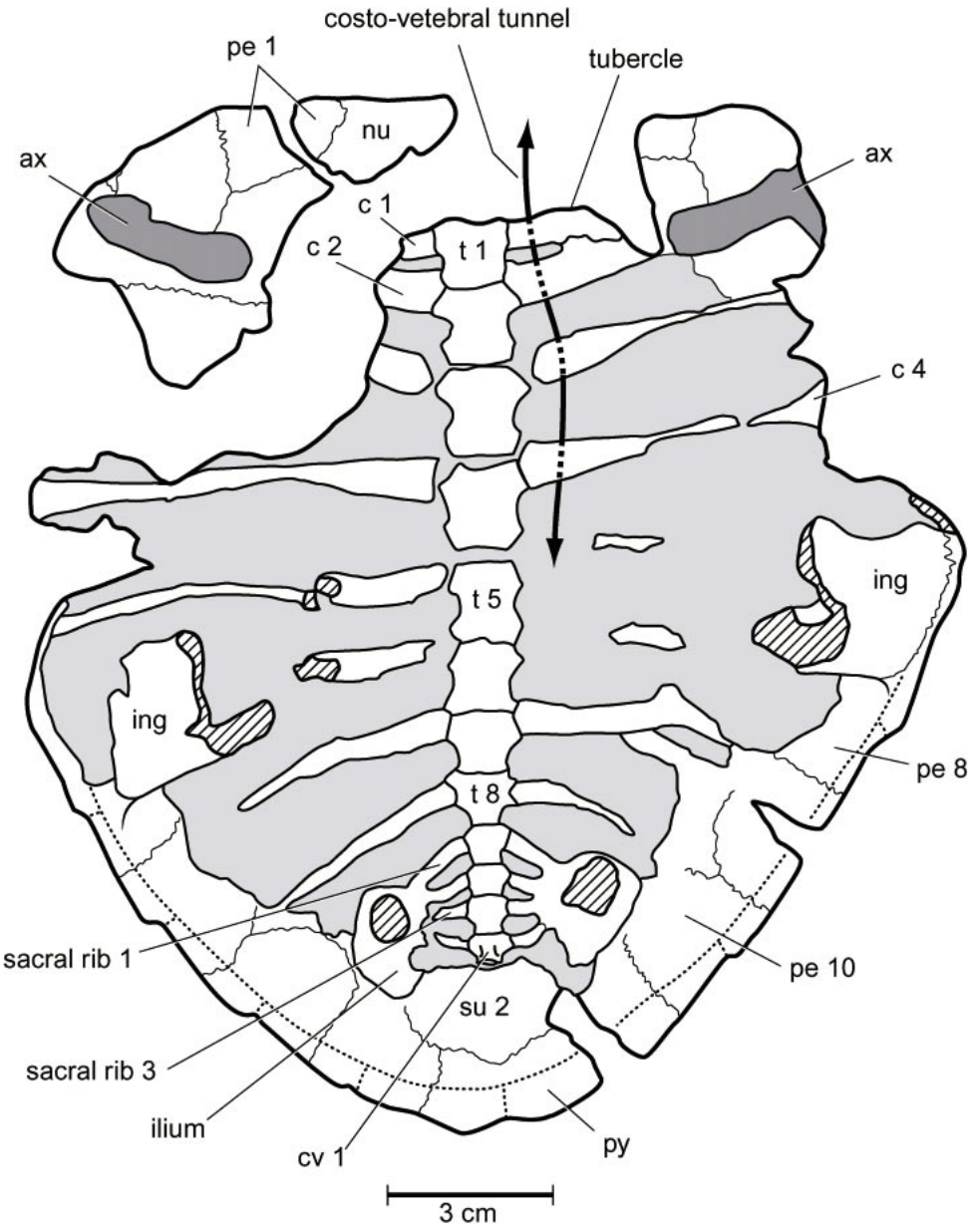

Fig. 8. *Notoemys zapatocaensis*, n.sp. Key to figure 7.

because vertebrals 2 and 3 are distinctly wider in *N. zapatocaensis* than in *N. laticentralis*. In *N. zapatocaensis* the scale sulcus lies about one-third the distance from neural to distal end of the costal; in *N. laticentralis* the sulcus is one-half or more of the distance to the lateral end of the costal. The lateral edges of the vertebrals in *N. zapatocaensis* are straighter than in *N. laticentralis*, in which they jut laterally where the pleurals meet.

PLEURAL SCALES: The four pairs of pleural scales in *Notoemys zapatocaensis* (fig. 6) are very similar to those in *Notoemys laticentralis*, except that they are wider due to the narrower vertebrals.

MARGINAL SCALES: The marginal scales in

TABLE 1
Comparisons of the Family Platychelyidae

	Notoemys zapatocaensis	*Notoemys laticentralis*	*Notoemys oxfordiensis*	*Platychelys oberndorferi*
Cervical scale	Wider	Wider	?	Narrower
First costal contacts peripheral 3	No	Yes	Yes	Yes
First neural contacts second costal	No	Yes	Yes	Yes
Fifth costal contacts sixth neural	Yes	Yes and No	Yes	Yes
First thoracic rib	Slightly larger	Slightly smaller	?	Slightly larger
First peripheral	Wider than long	Wider than long	?	Longer than wide
Tubercle on anterior edge of first thoracic rib	Yes	Yes	?	Yes
Peripheral three reduced or absent	Yes	No	?	No
Marginal three small and limited to peripheral three	Yes	No	?	No
Peripheral 2 large	Yes	No	No	No
All neurals wider than long	Yes	Yes	Yes	No
Neural 1 parallel sided	Yes	No	No	Yes
Neural 1 contacts	4-sided	6-sided	6-sided	6-sided
Neural 6 tapers posteriorly	Yes	No	?	No
Suprapygal 1	Parallel sided	Tapers anteriorly	?	Parallel sided
Suprapygal 2	Wider	Wider	Wider	Narrower
Vertebral scales 2 and 3	Narrower	Wider	?	Narrower
Posterior marginals	Slightly serrated	Smooth	?	Deeply serrated
Protuberances on posterior margins of vertebrals and pleurals	Yes, weak	No	?	Yes, strong
Low ridge down midline of carapace	Yes	Yes	?	No (high ridge)
Shell height	Lower	Lower	Lower	Higher
Supramarginal scales	Absent	Absent	Absent	Present
Anterior shell margin wide and straight	Yes	Yes	Yes	Yes
Anterior sides roughly parallel	Yes	Yes	Yes	No, oval
Posterior sides of carapace tapering	Yes	Yes	Yes	Yes
Pygal	Notched	Smooth	?	Notched
Midline scale on pygal	No	No	?	Yes
Hypoplastral-hyoplastral fontanelle	Present	Present	Present	Present
Xiphiplastral-hypoplastral fonanelle	Possibly	Possibly	Possibly	Yes
Anterior plastral lobe	?	Slight taper	Slight taper	Strong taper
Intergular scale covers most of entoplastron	?	Yes	Yes	No
First thoracic vertebra	Wider than high, flat ventrally	Same as *zapatocaensis*	?	Same as *zapatocaensis*
First thoracic centrum	Wider than high	?	?	Wider than high
Thoracic centra broad & flat, without ventral keel	Yes	Yes	?	Yes
Nuchal without neural spine articulation on ventral surface	Yes	?	Yes	Yes
Pelvis with acetabular surface wider than high	Yes	?	?	Yes
Ilium scar	Costal 8 only	Costal 8 only	?	Costal 8, peripheral 11, suprapygal 2
Bridge peripheral 7 ventral process	Short	Short	?	Long
Marginal scales 8 & 10 five-sided	Yes	Yes	Yes	No, four-sided
Locality	Columbia	Argentina	Cuba	Central Europe
Age	Valanginian 135 mya	Tithonian 145 mya	Oxfordian 156 mya	Kimmeridgian 152 mya

TABLE 2
Character List for *Notoemys* Data Set

1. Nuchal bone: (0) width much greater than length, (1) width slightly more or equal to length.
2. Supramarginals: (0) full series present, (1) incomplete series present, (2) absent.
3. Neural series: (0) regular, (1) irregular.
4. Pygal notch: (0) present, (1) absent.
5. Anterior shell margin wide and straight: (0) no, rounded, (1) yes.
6. Posterior sides of carapace tapering: (0) no, rounded, (1) yes, straighter and tapering posteriorly.
7. Marginal scales 8 and 10 five-sided: (0) no, four contacts, (1) yes.
8. Suprapygal one: (0) narrower than long, (1) wider than long.
9. All neurals wider than long: (0) no, (1) yes.
10. First thoracic ribs: (0) close to second thoracic rib in size, (1) smaller than second thoracic rib.
11. First thoracic central articulation: (0) higher than wide, equidimensional, (1) wider than high.
12. Articulation tubercle on thoracic rib: (0) anterior face of rib smooth, (1) tubercle on first thoracic rib.
13. Costovertebral tunnel: (0) wide anteriorly and posteriorly, (1) very wide entire length, (2) small entire length.
14. Thoracic centra: (0) keeled ventrally, (1) flat ventral surface.
15. Axillary process contacts costal 1: (0) absent, (1) present.
16. Inguinal process contacts costal 5: (0) absent, (1) present.
17. Epiplastron: (0) long posterior process present, (1) posterior process absent.
18. Posterior entoplastral process: (0) present, (1) absent.
19. Entoplastral participation in anterior border: (0) present, (1) absent.
20. Intergular scales: (0) two, (1) one.
21. Mesoplastra: (0) midline contact, (1) no midline contact, wider than long, (2) no midline contact, equidimensional, (3) absent.
22. Thyroid fenestra: (0) two small and separated openings, (1) united into one larger opening.
23. Iliac scar extent: (0) scar absent, (1) on costal 8 only, (2) extends beyond costal 8.
24. Iliac scar shape: (0) scar absent, (1) elongate shape, (2) oval shape.
25. Sacral ribs: (0) large, (1) smaller, closely attached to ilia.
26. Plastral fontanelles: (0) absent, (1) present.

Notoemys zapatocaensis (fig. 6) show differences with those in *Notoemys laticentralis*. The first marginal lies on the nuchal and peripheral 1, as in *N. laticentralis*, and marginal 2 extends from peripheral 1 onto peripheral 2, as in *N. laticentralis*. Marginal 3, however, is a small, oval scale, lying on the edge of peripheral 2, and not extending onto peripheral 3. This may be related to the apparent reduction of peripheral 3, which seems to be a small ossification in the peripheral 2–peripheral 4 suture (see above). Marginal 4 barely extends onto peripheral 2, a condition not found in *N. laticentralis*, *Platychelys*, or other pleurodires, which have marginal 4 lying on peripherals 3 and 4. As in *N. laticentralis* and *Platychelys*, the anterior marginals are short and restricted to the edges of the peripherals and do not extend onto the costals.

TABLE 3
***Notoemys* Data Set**

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
1 *Proganochelys*	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2 *Proterochersis*	?	0	?	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
3 *Platychelys*	0	1	1	1	1	1	0	0	0	0	1	1	1	1	1	1	1	0	1	1	1	1	2	1	1	1
4 *Notoemys oxfordiensis*	0	2	1	?	1	1	1	1	1	?	1	1	?	1	1	0	1	?	1	1	1	?	1	1	?	1
5 *Notoemys laticentralis*	0	2	1	1	1	1	1	1	1	0	1	1	1	1	1	0	1	1	?	1	1	?	1	2	1	1
6 *Notoemys zapatocaensis*	0	2	1	1	1	1	1	1	1	0	1	1	1	1	1	0	?	?	?	?	1	2	1	2	1	?
7 Pelomedusoides	1	2	0	1	0	0	0	0	0	1	0	0	2	0	1	1	1	1	1	1	2	2	2	2	1	0&1
8 Chelidae	1	2	0	1	0	0	0	0	0	1	0	0	2	0	1	1	1	1	1	1	3	2	2	2	1	0

Marginal 5 is not preserved; marginals 6 to 11 are very similar to those in *N. laticentralis*. The 8th and 10th marginals are five-sided rather than four-sided, as they extend medially along the sulci between pleurals. This is in both *N. zapatocaensis* and *N. laticentralis* (and seems to be in *N. oxfordiensis*), but not *Platychelys*. There are no supramarginals or anal/pygal scales in *Notoemys*, as occur in *Platychelys*.

Shell Shape and Surface Texture

Notoemys and *Platychelys* are characterized by a shell that has a wide, straight, anterior edge, rounded anterolateral margins followed by the widest part of the shell around costals 4 and 5, with a distinctive posterior taper and nearly straight margins. *Notoemys* differs from *Platychelys* in having the lateral edges more parallel rather than more rounded. *Notoemys zapatocaensis* fits this pattern closely. It differs from other *Notoemys* only in having a more pronounced degree of serration on marginals 7 to 11, but it is not serrated to the degree seen in *Platychelys*. The anterior half of the shell in *N. zapatocaensis* is not well enough preserved to see if these marginal sulci are also more deeply incised.

The carapace surface (fig. 3) has a large number of circular pits, particularly in the area of the vertebral scales. The shell surface is well preserved and shows a smooth surface with a slight, irregular granulation. There is distinct doming along the midline, rising to a protuberance just anterior to the posterior sulcus of each vertebral, in the same position as the much higher projections seen in *Platychelys*. *Notoemys laticentralis* has a low, midline ridge that is not divided by the vertebrals. In a few places on the pleurals and vertebrals of IPN 15-EAC 140120031, the surface shows a very slight radiating pattern of ridges, similar to that in *Platychelys*. *N. laticentralis* has a smooth surface, particularly well preserved in the type, that shows no ridges and no pleural doming.

Plastron Bones

Hypoplastron: Most of the right and left hypoplastra are preserved (figs. 9, 10). The anterior margin shows the contact with the mesoplastron. Dorsomedially, the margin is broken, and the bone is thin, but there is no sign of a fontanelle. Medially, both hypoplastra meet on the midline. Posteromedially, both hypoplastra show a thin, natural edge, indicating a possible narrow fontanelle, just anterior to the xiphiplastron contact. The femoral–abdominal sulcus is not visible, although the area where it is usually located is present on both sides.

Xiphiplastron: Most of both xiphiplastra are present (figs. 9, 10, 11), but broken along their medial edges, so there is no midline contact. There is no indication of a fontanelle on the xiphiplastron; the medial margins are all broken edges. On the ventral surface, there is a clear anal–femoral sulcus, with an indentation on the lateral xiphiplastron margin. The xiphiplastron narrows posteriorly and comes to a rounded margin, as in *Platychelys*. There is an anal notch, also as in *Platychelys*. Although *Notoemys laticentralis* is not well preserved in this area, what is known is entirely consistent with the Colombian xiphiplastron.

The pubic scar (fig. 11) is covered by the pubis on both sides, but it is clearly wide and relatively large, and reaches the lateral margin of the xiphiplastron, in contrast to podocnemidids and bothremydids. The ischiac scar is visible on the left side; the ischium is in contact on the right side. The ischiac scar is relatively large, reaching the lateral edge of the xiphiplastron. The scar is roughly triangular, but widens medially to reach the midline, in contrast to bothremydids and podocnemidids.

Pelvis

Ilium: The ilium (fig. 8) is preserved on both sides, with thoracic ribs 9, 10, and 11 reaching it. These are very similar in position to those in *Platychelys*. The iliac articulation is on costals 7 and 8 in *Notoemys zapatocaensis*. It seems that the medial edge of peripherals 10 and 11 lie just against the ilium, so that the sutural scar does not quite reach the peripherals. The suprapygal is less clear, but it also does not seem to have the iliac scar on it, although this is not clear anteriorly. The ilium blade is elongate, without a lateral pro-

cess seen in pelomedusids and podocnemidids. The ilium neck is shorter than it is in Pelomedusoides. The acetabulum shows the usual tripartite formation; it is best preserved on the right side. The articulation surface is wider and oval as in *Platychelys*, rather than more circular as in Pelomedusoides.

PUBIS: The right pubis is in articulation and nearly complete, although much is obscured by matrix. The anterior process is damaged on both sides and the shape of the pubic scar (fig. 11) can only be seen in a few places, but it is relatively wide, as in *Platychelys*, rather than narrow as in Pelomedusoides. The thyroid fenestra is poorly preserved, but enough can be seen to show that it was confluent and large as in *Platychelys*, not small as in *Proganochelys*. The pubis contact goes right to the edge of the xiphiplastron, as in *Platychelys*. It is not retracted from the edge as in Pelomedusoides.

ISCHIUM: Most of the right ischium is present, but its medial margin is missing. The ischium scar (fig. 11) is preserved on the left xiphiplastron and some of the left ischium can be articulated on it. The right ischium is disarticulated from the acetabulum and moved posterodorsally. The ischium of *Notoemys* has a wider shaft than in Pelomedusoides and its posterior process is more like a sheet of bone than a column.

RELATIONSHIPS

Fuente and Iturralde-Vinent (2001) published a cladogram, including *oxfordiensis*, *laticentralis*, and *Platychelys*. Of their 30 characters, 11 are parsimony uninformative, but most of the rest have been incorporated in our analysis. We also add characters from an as yet unpublished pleurodire data set (Gaffney et al., in prep.). The Fuente and Iturralde-Vinent (2001) cladogram is: (*Proganochelys* (*Proterochersis* (*Platychelys* (*oxfordiensis* (*laticentralis* (Pelomedusoides, chelidae)))))). Our analysis (fig. 12; tables 2, 3) using PAUP 4.0 has a different resolution of *Platychelys*, *oxfordiensis*, and *laticentralis*. We use 26 characters, all postcranial and all parsimony informative, resulting in a single tree of 36 steps. The grouping of *zapatocaensis* and *laticentralis* is only one step from a trichotomy with *oxfordiensis*, but the other nodes have a Bremer support index of 3 or higher. Most of the newly added characters are from the thoracic vertebrae and ribs, features not clearly seen in *oxfordiensis*.

The reinterpretation of *Notoemys* and *Platychelys* as sister taxa is based on the shared characters of wide, flat thoracic ribs forming a very wide costovertebral tunnel, articulation tubercle (probably for the scapula) on the anterior edge of a broad, flat thoracic rib one, and the shell shape combining an anterior transverse margin with straight edged, posteriorly tapering sides. The contradictory characters are the three supramarginal and one intermarginal scales in *Platychelys* but absent in *Notoemys*, that usually put *Platychelys* as the sister group to *Notoemys* plus all remaining Eupleurodires, as analyzed by Fuente and Iturralde-Vinent (2001) and Lapparent de Broin and Murelaga (1999). When skulls and more postcranial material is found, it may reassert the earlier idea that *Platychelys* is the sister group of *Notoemys* plus Pelomedusoides and Chelidae. However, the available postcranial characters lean in favor of *Notoemys* plus *Platychelys*.

The conclusion that ''*Caribemys*'' *oxfordiensis* should be placed within *Notoemys* is based on a reevaluation of the diagnostic criteria provided by the new Colombian specimen. As long as they are monophyletic, recognition of genera is nonetheless, a matter of opinion and taste, and some may choose to retain *Caribemys* and a paraphyletic *Notoemys*. We do not dispute the identification of *oxfordiensis* as a distinct taxon. Fuente and Iturralde-Vinent (2001) have the following features differentiating *oxfordiensis* from *laticentralis*:

1. Carapace shape ''subquadrangular'' (*oxfordiensis*) versus ''cordiform'' (*laticentralis*). In the published figures the type and only known specimen of *oxfordiensis* is badly damaged dorsally and has a broken edge as the shell margin for much of the shell. As restored, and in the available figures, the specimen does not seem to differ from *laticentralis* (see Fuente and Iturralde-Vinent, 2001: figs. 6–1, 6–2).

2. Plastral fontanelle ''small pentagonal'' (*oxfordiensis*) versus ''large and slightly narrow and elongated in antero-posterior way'' (*laticentralis*). The hyoplastral–hypoplastral

Fig. 9. *Notoemys zapatocaensis*, n.sp. IPN IS-EAC140120031. Ventral view of shell with plastron elements.

fontanelle in *oxfordiensis* looks undamaged and intact, although we have not examined this specimen. The single plastron available for *laticentralis*, however, is asymmetrical and clearly damaged, as noted in the description (Fernandez and Fuente, 1994), so the fact that the fontanelle is larger and longer may be due to damage and should not be used as a diagnostic feature.

3. Anterior plastral lobe ''rounded'' (*oxfordiensis*) versus ''subquadrangular'' (*laticentralis*). Despite the nearly identical restoration of both (Fernandez and Fuente, 1994: figs. 6–4, 6–5) and the damage to *laticentralis*, there is a difference in the anterior lobe shape.

The lack of overlapping preserved areas in the carapace of the two taxa makes comparisons there difficult, but the second suprapygal and pygal shapes also seem different in both taxa. Nonetheless, these shells are very similar and could easily be placed in the same species, considering the degree of variation seen within the shell of many living

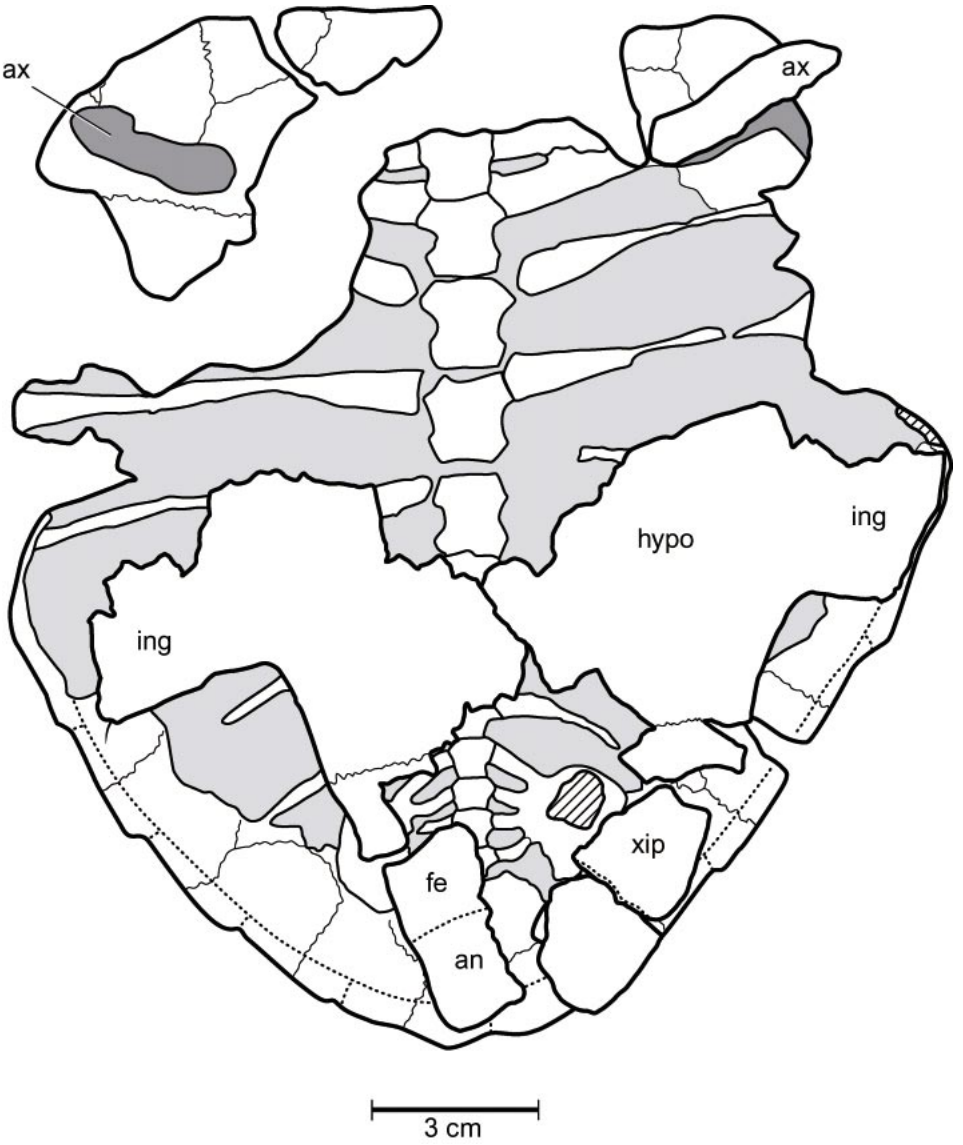

Fig. 10. *Notoemys zapatocaensis*, n.sp. Key to figure 9.

species of pleurodires. However, to do this would imply a geographical and temporal distribution of one species that is probably misleading.

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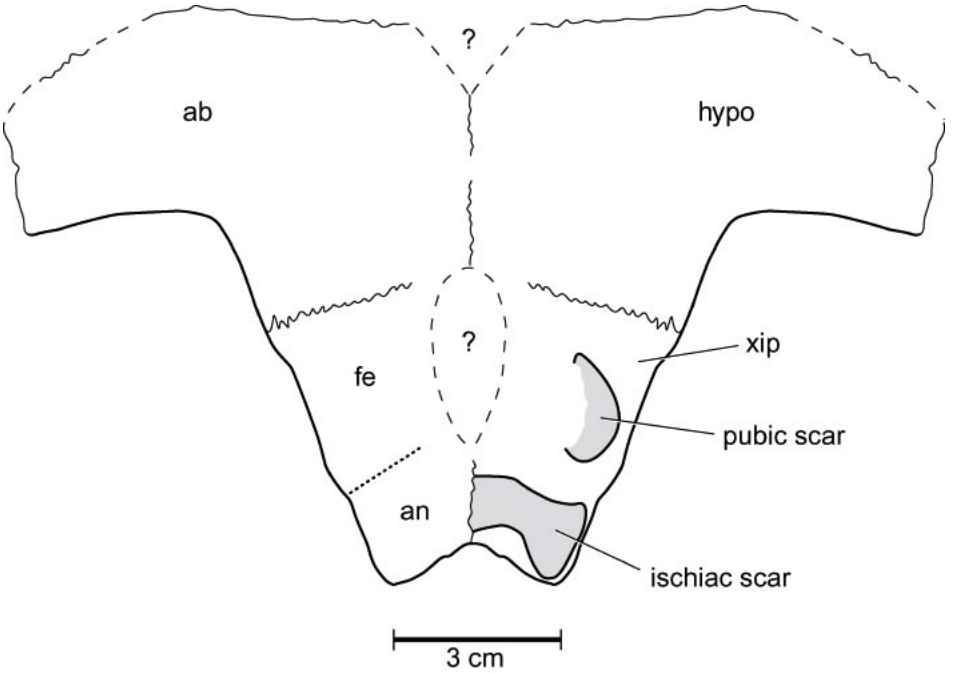

Fig. 11. *Notoemys zapatocaensis*, n.sp. Restoration of known plastron elements. Scales labeled on left, bones on right.

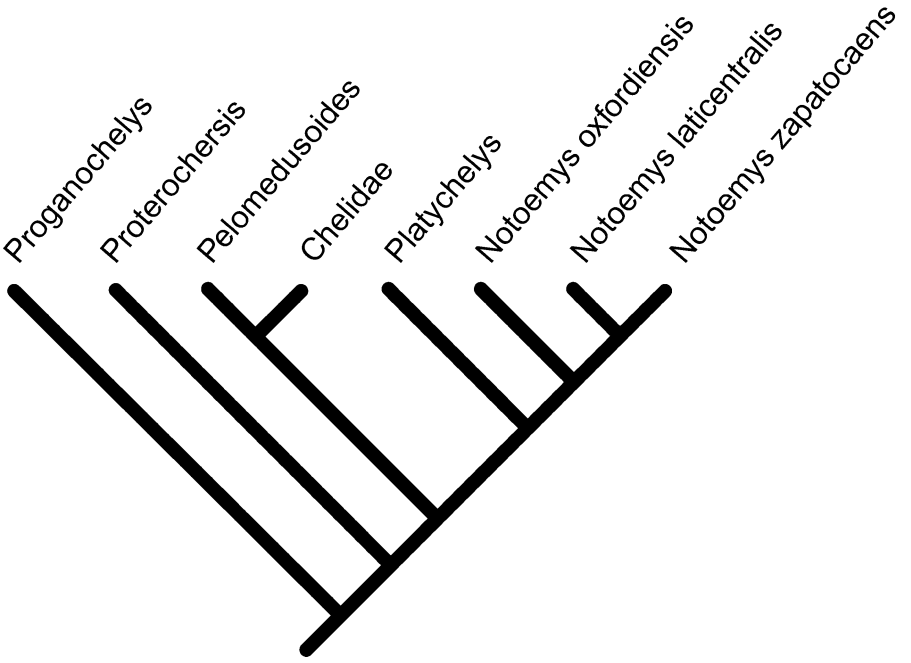

Fig. 12. Cladogram of *Notoemys* and close relatives.

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