

## Chapter 8

# New Material of the Platycheilyd Turtle *Notoemys zapatocaensis* from the Early Cretaceous of Colombia; Implications for Understanding Pleurodira Evolution

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**Abstract** *Notoemys zapatocaensis* is the youngest representative of the Platycheilyidae, a group of Late Jurassic-Early Cretaceous pleurodires. Here we describe two new specimens of this species represented by a partial carapace and a nearly complete articulated shell. *Notoemys zapatocaensis* is different from other platycheilyd turtles in having: (1) two fairly reduced lateral tuberosities on the margin of the anterior plastral lobe, (2) a shallow notch on the posterolateral margin of the epiplastra, giving a convex posterolateral edge to this bone, (3) gular scales that are rectangular in shape and much wider than long, (4) a long intergular scale that has a slight medial contact with the pectorals, resulting in a complete separation of the humeral scales, (5) a central plastral fontanelle that projects posteriorly into the xiphiplastral region, (6) a very small marginal 3, (7) a slightly shorter neural 1 than neural 2, with an exclusive lateral contact with costal 1, resulting in a complete separation of neural 2 and costal 1, (8) narrower vertebral scales, and (9) peripheral 3 lacking a posteromedial contact with costal 2. Phylogenetic analysis indicates

that *N. zapatocaensis* is a sister taxon of *N. oxfordiensis*, and that *Proterochersis robusta* can be resolved in two different positions in the testudines tree: (1) with *Odontochelys semitestacea* based on the fact that both taxa share two mesoplastra meeting at midline, or (2) as the most basal pleurodire, based on a suture articulation of pelvis to shell. Anal notch shape and potentially fontanelle size are indicators of sexual dimorphism in platycheilyds.

**Keywords** Rosablanca Formation • South America • Valanginian • Zapatoca

## Introduction

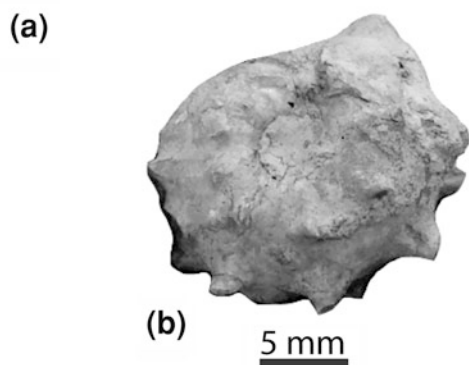
Turtles diverged in two infraorders (Pleurodira and Cryptodira) during the Late Triassic or earlier (Gaffney and Jenkins 2010), around 221 Ma, maximum estimated based on molecular studies (Shaffer 2009). The earliest pleurodire so far known is *Proterochersis robusta* Frass (1913) from the Late Triassic of Germany, however is important to mention here that new material is being studied from the Early to Middle Jurassic that would change the current state of *P. robusta* (Joyce and Sterli, in press). *P. robusta*, as with most other Late Triassic-Early Cretaceous pleurodires, is known only by shells. The only exception to this is *Notoemys laticentralis* Cattoi and Freiberg (1961), which is represented by a partial skull recently re-described by de Lapparent de Broin et al. (2007). Following Gaffney et al. (2006) below *Proterochersis*, all pleurodires are included in the Parvorder Megapleurodira, which is divided into Nanorders Platycheilyra and Eupleurodira (Cheloides and Pelomedusoides). Platycheilyra is represented by the single Family Platycheilyidae, which includes *Platycheilya oberndorferi* from the Late Jurassic (Kimmeridgian) of Germany (Wagner 1853), and the three species of *Notoemys*: *Notoemys laticentralis* from the Late Jurassic (Tithonian) of Argentina (Cattoi and Freiberg 1961; Fernandez and de la

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**Fig. 8.1** **a** Location of the town of Zapatoca, Department of Santander, Colombia:  $6^{\circ} 50' 35''\text{N}$ ,  $73^{\circ} 13' 50''\text{W}$ . **b** *Saynoceras verrucosum*, ammonite indicator of the base of the Late Valanginian, collected at the same layer as *Notoemys zapatoacaensis* holotype and paratype (MG61)

Fuente 1988, 1994; de Lapparent de Broin et al. 2007; de la Fuente 2007), *N. zapatoacaensis* from the Early Cretaceous (Valanginian) of Colombia (Cadena and Gaffney 2005), and *N. oxfordiensis* from the Late Jurassic (Oxfordian) of Cuba, known by a single poorly preserved shell (de la Fuente and Iturralde-Vinent 2001; Cadena and Gaffney 2005). None of the three species of *Notoemys* has a completely preserved anterior plastral lobe, which is unfortunate because that region has morphological features that are key to understanding the evolution of the turtle shell.

Two new specimens of *Notoemys zapatoacaensis* are described here. The first is an almost complete and articulated shell (here designated as the paratype), and the second other is a partial carapace (here designated as a referred specimen). Both specimens were collected by the senior author in 2006 in Zapatoca, Colombia, from the same locality and stratum as the holotype (Fig. 8.1). The excellent preservation of the anterior plastral and carapace elements allows us to amend the diagnosis for this species,

and the specimens allow a revised phylogenetic analysis of pleurodires and the most basal testudines.

Institutional Abbreviations used in this paper are: *IPN-EAC* Museo Geológico José Royo y Gómez–Instituto Colombiano de Geología y Minería–Ingeominas, Bogotá, Colombia; *MACN* Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; *MNHN* Muséum national d'histoire naturelle, Paris, France; *MNHN AC* Anatomie Comparée collections of MNHN; *MNHN Cu* Museo Nacional de Historia Natural, La Habana, Cuba; and *MOZP* Museo “Prof. Dr. Olsacher” Zapala, Argentina.

## Systematic Paleontology

Testudines Batsch 1788

Pleurodira Cope 1864

Platycheilyidae Bräm 1965

*Notoemys* Cattoi and Freiberg 1961

*Notoemys zapatoacaensis* Cadena and Gaffney 2005 (Figs. 8.2, 8.3)

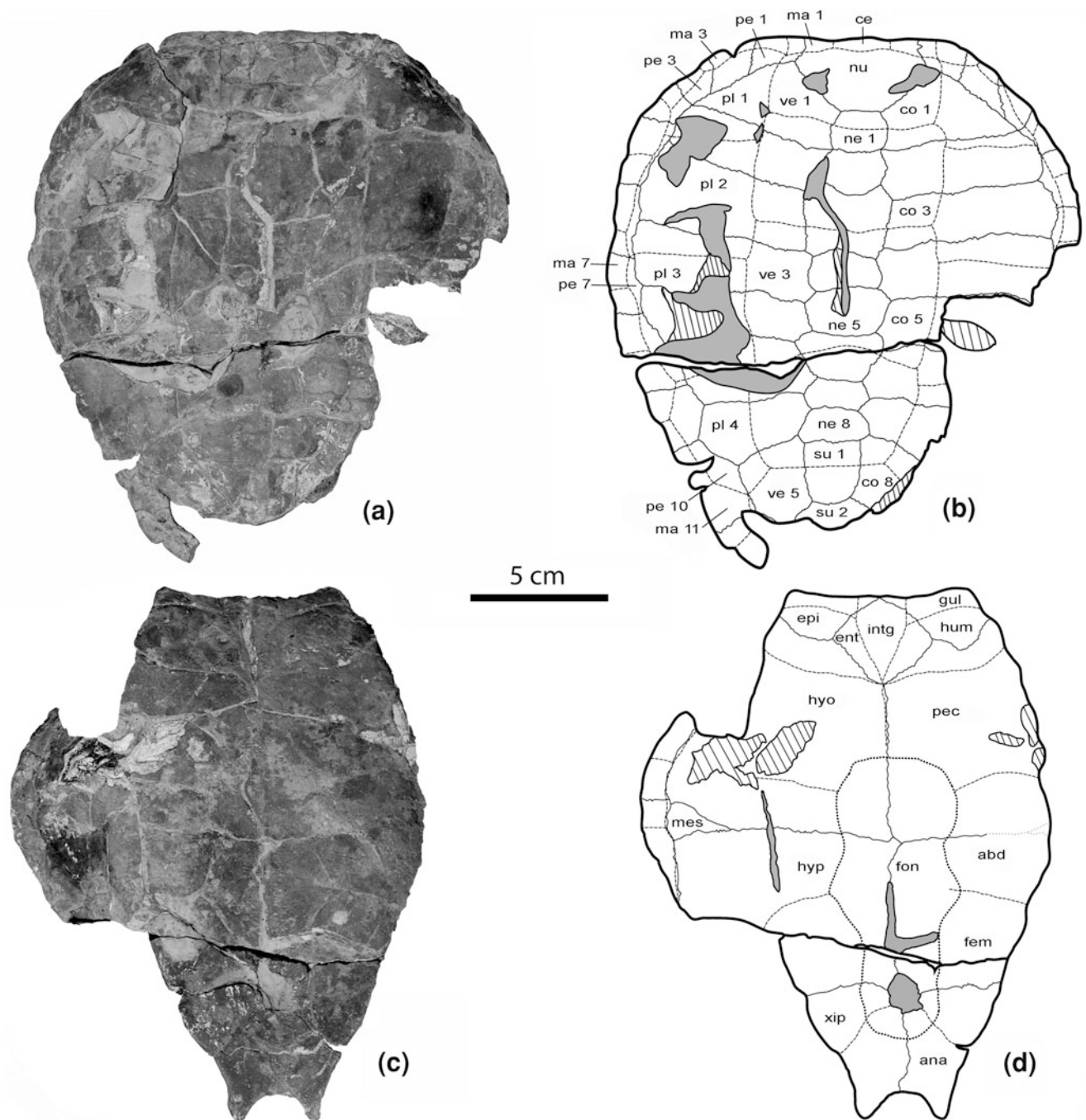
**Holotype:** MGJRG IPN 15-EAC 140120031, nearly complete shell, missing the anteromedial region of the carapace and the anteromedial portion of the plastron; previously described and figured by Cadena and Gaffney (2005).

**Newly designated paratype:** MGJRG IPN 15-EAC 150620061, abbreviated as MG61 (Fig. 8.2a–d), articulated carapace and plastron, missing the right posterolateral portion of the carapace.

**Newly referred specimen:** MGJRG IPN 15-EAC 150620062, abbreviated as MG62, a partial central portion of a carapace including neurals 2–8, the most medial portion of costals 2–7, and an isolated medial portion of the left costal 8 that preserves an iliac scar (Fig. 8.3a, b).

**Locality, horizon, and age:** All three specimens are from the same locality and unit. The El Caucho Farm locality ( $6^{\circ} 50' 35''\text{N}$ ,  $73^{\circ} 13' 50''\text{W}$ ) is northeast of Zapatoca town, Department of Santander, Colombia. The locality is in a limestone layer belonging to the upper segment of the shallow marine Rosablanca Formation (Guzman 1985). The occurrence of the ammonite *Saynoceras verrucosum* (F. Etayo 2008, personal communication) indicates that this part of the Rosablanca Formation corresponds to the base of the late Valanginian stage (Early Cretaceous), approximately 138 Ma according to the biochronostratigraphic framework of Ogg et al. (2008).

**Revised diagnosis:** *Notoemys zapatoacaensis* is recognized as a pleurodire turtle on the basis of the following characteristics: (1) sutural articulation of the pelvis with the shell, (2) well-developed anal notch that is U- or V-shaped. It is a megapleurodire, based on (1) one pair of mesoplastra,



**Fig. 8.2** *Notoemys zapatoacaensis* paratype (MG61), MGJRG IPN 15-EAC 150620061. **a, b** Carapace in dorsal view: **a** photograph; **b** interpretive drawing. **c, d** Plastron in ventral view: **c** photograph; **d** interpretive drawing. Abbreviations: *abd* abdominal; *ce* cervical; *co* costal; *ent* entoplastron; *epi* epiplastron; *fem* femoral; *fon* fontanelle;

*gul* gular; *hum* humeral; *hyo* hyoplastron; *hyp* hypoplastron; *intg* intergular; *intg* intergular; *ma* marginal; *mes* mesoplastron; *ne* neural; *pec* pectoral scale; *pe* peripheral; *pl* pleural; *su* suprapygial; *ve* vertebral; *xip* xiphiplastron

laterally restricted that lack a medial contact, (2) a single intergular scale. *N. zapatoacaensis* is a platychelyid because it has (1) a costovertebral tunnel that is very wide through its entire length, (2) an articulation tubercle on the anterior face of the first thoracic rib, (3) a carapace with posterior sides tapering medially, (4) the second neural smaller than

the remainder of the neural series, (5) the thoracic vertebrae smooth and flat ventrally, hexagonal in shape with a centrolateral notch, and (6) a carapace with dorsal protuberances, located on the posterior region of the pleural and vertebral scales. It is recognized as a member of the genus *Notoemys* and differs from *Platychelys oberndorferi* in

**Table 8.1** Measurements for the platychelyids, including the paratype (MG61) of *Notoemys zapatoensis*

Taxon	CL	CW	PL	PW	CLe	CWe	PLe	PWe
<i>Notoemys zapatoensis</i> MGRG IPN 15 EAC 150620061. This study	20	18	8	15	21	18	18	16
<i>Notoemys zapatoensis</i> MGRG IPN 15 EAC 140120031. Figured in Cadena and Gaffney (2005)	22	20	19	14	24	20	19	16
<i>Notoemys laticentralis</i> MOZP 2487. Figured in Fernandez and de la Fuente (1994)	27	25	24	22	27	25	25	22
<i>Notoemys oxfordiensis</i> MNHNCu-P 3209. Figured in de la Fuente and Iturralde-Vinent (2001)	25	23	20	20	25	23	22	20
<i>Platycheilus oberndorferi</i> . Figured in de Lapparent de Broin (2001)	20	17	17	13	20	17	17	13

Measurements in centimeters. Abbreviations: CL carapace length; CW carapace width; PL plastron length; PW plastron width; CLe total carapace length, estimated; CWe total carapace width, estimated; PLe total plastron length, estimated; PWe total plastron width, estimated

having (1) a wider and shorter cervical scale, (2) no supramarginal scales, (3) a smooth and relatively flatter shell with lower dorsal protuberances lacking radial striation, (4) a larger suprapyg 1, (5) the neural 3 in posterolateral contact with costal 4, (6) an iliac scar oval in shape and restricted to costal 8, and (8) a very reduced medial space between the first and the second thoracic ribs. Autopomorphies of *Notoemys zapatoensis* are (1) an anterior plastral lobe margin with two rather reduced lateral tuberosities, almost straight in outline, (2) a shallow notch on the posterolateral margin of the epiplastra, giving a convex posterolateral edge to this bone, (3) gular scales rectangular in shape, much wider than long, (4) a long intergular scale slightly touching the pectorals medially, and completely separating the humerals, (5) a central plastral fontanelle projecting posteriorly into the xiphiplastral region, (6) a very small marginal 3, (7) a quadrangular neural 1 that is slightly shorter than neural 2 and exclusively in contact with costal 1 laterally, and neural 2 exclusively in contact with costal 2 laterally, (8) vertebral scales that are narrower than in *N. laticentralis*, *N. oxfordiensis* and *Platycheilus oberndorferi*, and (9) peripheral 3 lacking posteromedial contact with costal 2.

## Description

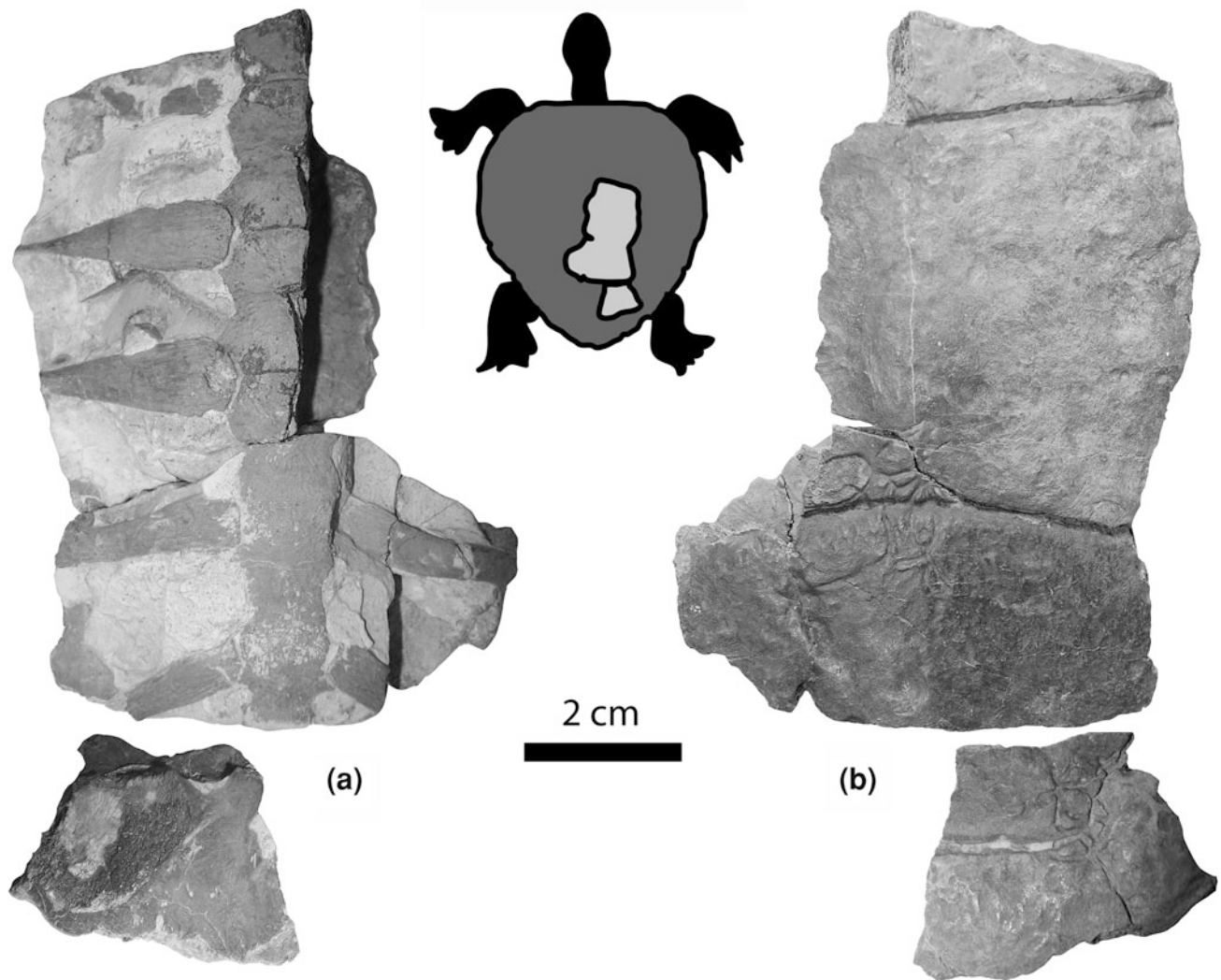
**Carapace:** MG61 has a shell that is cordiform in shape, with an anterior edge that is straight, its widest point at peripheral 7, and posterior lateral sides tapering medially as in the holotype and the other platychelyids. Measurements are given in Table 8.1. Posterior edges are dentate at the contact between marginal scales, as in the holotype, although this is much less pronounced than in *Platycheilus oberndorferi* and slightly more pronounced than in *Notoemys laticentralis* MACN 18403. This morphological feature is unknown for *N. oxfordiensis* due to the poor preservation of its edges. Low protuberances in MG61 are located at the

posterior medial region of each vertebral and pleural scales, as in the holotype and MG62. In *N. laticentralis* the protuberances are slightly lower, and they are not preserved in *N. oxfordiensis* due to the highly eroded surface of the carapace. High and very well developed protuberances are characteristics of *Platycheilus oberndorferi*. The carapace surface of MG61 is smooth, with a light microvermiculation rather than the granulation seen in the holotype, similar to the condition in *N. laticentralis*. In contrast, *Platycheilus oberndorferi* has a carapace surface very sculptured with radial striations originating at the center of the protuberances.

The nuchal bone of MG61 is hexagonal in shape and wider than long as in all other platychelyids and also the cryptodires *Kayentachelys aprix* Gaffney et al. (1987), *Eileanchelys waldami* Anquetin et al. (2009), *Heckerochelys romani* Sukhanov (2006), *Indochelys spatulata* Datta et al. (2000), and *Chengyuchelys baenoides* Young and Chow (1953). In contrast, all pleurodires have a nuchal bone relatively equidimensional or longer than wide.

Eight neurals are present in MG61. Neural 1 is slightly shorter than neural 2, and is the only neural in contact with costal 1, a condition also present in the holotype, although it differs from the holotype in that neural 1 is slightly larger. In contrast, the other two species of *Notoemys* and *Platycheilus oberndorferi* have a neural 1 that is longer than neural 2 and in contact with costal 1 and 2 laterally, preventing an anterolateral contact of neural 2 with costal 1. This is a condition also present in *Kayentachelys aprix*, *Eileanchelys romani*, *Heckerochelys romani*, *Indochelys spatulata*, *Chengyuchelys baenoides*, and retained in the extant chelid *Chelus fimbriata* Schneider (1783). In contrast, *Brasilemys josai* de Lapparent de Broin (2000), *Araipemys barretoii* Price (1973), and one of the specimens of *Cearachelys placidoi* Gaffney et al. (2001) have a slightly more derived condition of neural 1 contacting costal 1 and 2, and neural 2 contacting costal 2 and 3. The most frequent condition for eupleurodires is to have neural 1 only contacting costal 1, and neural 2 contacting costal 1 anterolaterally. Exceptions to this include many of the chelid





**Fig. 8.3** *Notoemys zapatocaensis* MGJRG IPN 15-EAC 150620062 (MG62). Central portion of the carapace, including neurals 2–8, the most medial portion of costals 2–7, and an isolated most? medial

portion of the left costal 8 preserving the iliac scar. See areas shadowed in light grey in the turtle sketch. **a** Ventral view. **b** Dorsal view

genera, the nomen dubium *Eusarkia rotundiformis* Bergounioux (1952), and the podocnemidid *Bairdemys venezuelensis* Wood and de Gamero (1971), which completely lack the neural series. Neural 3 in the paratype (MG61) of *N. zapatocaensis*, as in *N. laticentralis*, is large, almost octagonal in shape, and in contact with costal 4 posterolaterally. In the holotype of *N. zapatocaensis*, neural 3 lacks the right posterolateral contact with costal 4; the same asymmetrical pattern is present in the *Platycheilus oberndorferi* specimen figured in de Lapparent de Broin (2001, Fig. 1). However the holotype of *Platycheilus oberndorferi* lacks a posterolateral contact with costal 4 on both sides, thus exhibiting a more rectangular shape than in the other platychelyids. Neurals 4–8 exhibit the same shape and sutural contacts as the holotype, specimen MG62 (Fig. 8.3a, b), *N. laticentralis*, and *Platycheilus oberndorferi*, although

this latter taxon exhibits neurals slightly more rectangular in shape. The neural series is unrecognizable in *N. oxfordiensis* due to its poor preservation.

Suprapygals 1 is rectangular in shape, slightly longer than wide as in the holotype, similar to *Platycheilus oberndorferi*, *Condorchelys antiqua* Sterli (2008), *Indochelys spatulata*, and *Kayentachelys aprix*. In contrast, the suprapygals 1 in *N. laticentralis* is trapezoidal in shape, wider posteriorly than anteriorly. Suprapygals 1 is absent in most of the eupleurodires. Suprapygals 2 is only preserved in the paratype (MG61) of *N. zapatocaensis*, where it exhibits the same pentagonal shape as the holotype and the other platychelyids. The pygal of *N. zapatocaensis*, missing in the paratype (MG61) but preserved and previously described in the holotype, has a medial notch on its posterior edge. Based on a reexamination of the holotype of *N. laticentralis*

MACN 18403 by the senior author of this paper, such a notch is also present, although shallower, in that specimen. This new interpretation differs from previous studies (de la Fuente and Iturralde-Vinent 2001), which considered the posterior pygal notch to be absent in *N. laticentralis*.

Eight sets of costals are complete in both sides of the carapace of the paratype (MG61) of *Notoemys zapatoacaensis*, with the sets on the right side slightly broken laterally. The shape of the costals is similar to the holotype and the other platychelyids. MG62 preserves the left costal 8 with the iliac scar slightly oval, rounded and restricted to this costal, as in *N. laticentralis*. This seems to be also the condition in *N. oxfordiensis*, although this region is badly preserved in specimens of that taxon. In contrast, *Platychelys oberndorferi* has an elongated iliac scar extending onto costal 8, suprapygal, and the medial margin of the peripherals. Eleven peripheral bones are recognized on the left side of the paratype (MG61). Peripherals 1–3 are in medial contact with costal 1. Peripheral 3 lacks a postero-medial contact with costal 2, differing in this feature from the other platychelyids and other testudines in which peripheral 3 contacts costal 2. The presence of a small peripheral 3 restricted between peripherals 2 and 4 in the holotype was defined as a potential diagnostic characteristic of *N. zapatoacaensis* (Cadena and Gaffney 2005), but this feature is not present in the paratype (MG61) described here, which shows a well-developed peripheral 3 on both sides of the carapace. Thus the condition in the holotype is reinterpreted as a pathology of that specimen, as was initially done by Cadena and Gaffney (2005). Peripherals 5–7 are longer than wide, whereas peripheral 8 and 10 are slightly larger than peripheral 9 and 11, as in the holotype and *N. laticentralis*.

The cervical scale in the paratype (MG61) of *Notoemys zapatoacaensis*, as in the holotype and *N. laticentralis*, is rectangular in shape, much wider than long. The cervical is slightly shorter in many of the specimens of *Platychelys oberndorferi*. This is the primitive condition also present in *Proterochersis robusta*, *Kayentachelys aprix*, *Indochelys spatulata*, *Eileanchelys waldami*, *Heckerochelys romani*, and *Chengyuchelys baenoides* (at least for its middle cervical). In *Dortoka vasconica* de Lapparent de Broin and Murelaga (1996), the cervical is almost equidimensional and in chelids it is slightly longer than wide, except in the extant species *Hydromedusa tectifera* Cope (1870), which has a large cervical enclosed between marginals 1, pleurals 1, and vertebral 1. All pelomedusoids turtles lack a cervical scale. The condition is unknown for euraxemydids.

Five vertebral scales are clearly visible on the dorsal aspect of the carapace in the paratype (MG61) of *Notoemys zapatoacaensis*; vertebrals 1–3 are almost rectangular in shape as in the holotype and *Platychelys oberndorferi*, and much narrower than in *N. laticentralis*, *Proganochelys*

*quenstedti*, *Proterochersis robusta*, *Kayentachelys aprix*, *Heckerochelys romani*, *Indochelys spatulata*, and *Eileanchelys waldami*. The condition is unknown in *N. oxfordiensis*. Vertebral 4 is nearly hexagonal in shape as in *Platychelys oberndorferi*, and much narrower than in *N. laticentralis*, *Proganochelys quenstedti*, *Proterochersis robusta*, *Kayentachelys aprix*, *Heckerochelys romani*, *Indochelys spatulata*, and *Eileanchelys waldami*. The sulcus between vertebrals 3 and 4 is on neural 6 and costal 6, as in *Platychelys oberndorferi* and the other two species of *Notoemys*, as well as in most of the primitive testudines for which five neurals are recognized (Character 74, Joyce 2007; erroneously defined for vertebrals 2 and 3). In eucryptodires and eupleurodires, the sulcus between vertebrals 3 and 4 is on costal 5. This characteristic is related to the narrowing of the vertebral scales. Vertebral 5, although preserved only anterolaterally in the paratype (MG61) of *N. zapatoacaensis*, seems to be heptagonal, as in the holotype and *N. laticentralis*. In contrast it is octagonal in *Platychelys oberndorferi*. The pattern of reduction in the width of vertebral scales described for *N. zapatoacaensis* and *Platychelys oberndorferi* is also shared by eupleurodires and eucryptodires.

Four pleural scales are visible on the left portion of the carapace of MG61, and are the same shape as in the holotype, *Notoemys laticentralis*, and *Platychelys oberndorferi*. Pleural 4 is more nearly rectangular than pentagonal as is the condition in *P. oberndorferi*. *P. oberndorferi* also has straighter medial edges for all pleurals. Twelve marginal scales are visible on the left side of the carapace of MG61. Marginal 1 lacks contact with pleural 1, as is also the condition for the holotype. In contrast, *N. laticentralis* has a marginal 1 contacting pleural 1 posteriorly. Marginal 2 has the same shape and size as the holotype, slightly longer than in *N. laticentralis* and *P. oberndorferi*. In both the paratype (MG61) and the holotype of *N. zapatoacaensis*, marginal 3 is smaller compared to other platychelyids and testudines. Marginals 4–8, marginal 10, and marginal 12 are longer than wide, rectangular in shape. Based on a reinterpretation of the elements that Cadena and Gaffney (2005) erroneously identified as marginals 9 and 11 as marginals 10 and 12, this is also the case in the holotype. Marginals 10–12 of *N. laticentralis*, *Kayentachelys aprix*, and *Condorchelys antiqua* also share the pattern described for *N. zapatoacaensis*. In contrast, in *P. oberndorferi* these marginal scales are slightly more pentagonal in shape. Marginals 9 and 11 are pentagonal in shape for the paratype (MG61) of *N. zapatoacaensis*, the holotype (erroneously identified as marginals 8 and 10 by Cadena and Gaffney 2005), *N. laticentralis*, *Kayentachelys aprix*, *Condorchelys antiqua*, *Heckerochelys romani*, and eupleurodires for which the posterior series of marginals are more equidimensional due to an increase in the size of the peripherals.

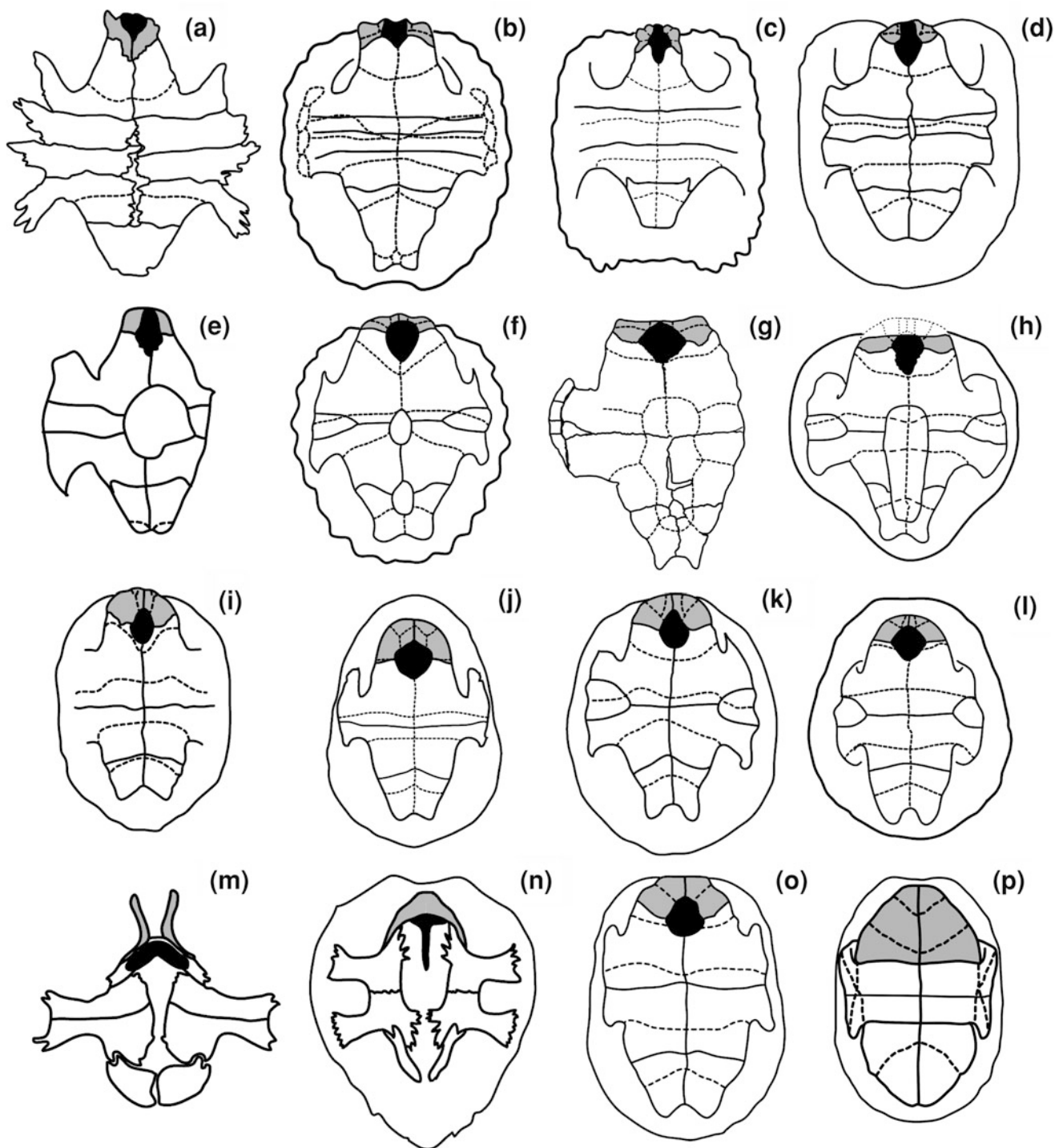
**Plastron:** The anterior plastral lobe of the paratype (MG61) of *Notoemys zapatoacaensis* is shorter than the posterior lobe, and has a straight anterior edge with very reduced tuberosities in both lateral corners and a slight concavity at the medial margin. In *Platycheilus oberndorferi*, the anterior edge exhibits a very short tuberosity at the midline of the plastron, whereas *N. oxfordiensis* lacks tuberosities on the anterior edge. Both *P. oberndorferi* and *N. oxfordiensis* have a slightly more convex anterior plastral edge than *N. zapatoacaensis*. In the case of *N. laticentralis* the arrangement of bones and scales at the margin of the anterior plastral lobe remains unknown because neither the holotype MACN 18403 nor MOZP 2487, figured in de la Fuente (2007), completely preserve this aspect. The primitive condition exhibited by *Odontochelys semitestacea*, *Proganochelys quenstedti*, and *Proterochersis robusta* is the presence of an anterior plastral lobe edge highly decorated with large tuberosities, defining a very dentate anterior margin. Tuberosities persist, although they are much more reduced in number and size, in *Kayentachelys aprix* and *Chengyuchelys baenoides*. They have disappeared completely in *Indochelys spatulata*, which has a very straight anterior edge. *Dortoka vasconica* and most other eupleurodires have a very convex anterior plastral lobe, although some exceptions are present, for example the bothremydids *Taphrosphys* spp., which has a nearly straight anterior plastral edge, or the short projections at the intergular–gular scales region of some pelomedusids.

The entoplastron of *Notoemys zapatoacaensis* is diamond-shaped, slightly touching the edge of the anterior plastral lobe, and completely separating the epiplastra. The most primitive condition, seen ventrally in *Odontochelys semitestacea*, is an entoplastron with an extensive participation in the edge of the anterior plastral lobe, and both epiplastra meeting at midline posteriorly to the entoplastron. *Proganochelys quenstedti*, *Proterochersis robusta*, *Paleochersis talampayensis*, Rougier et al. (1995), *Kayentachelys aprix*, and *Indochelys spatulata* show a more progressive condition in which the entoplastron completely separates the epiplastra. A more advanced condition is present in *N. zapatoacaensis* where the entoplastron does not participate in the edge of the anterior plastral lobe. *Eileanchelys waldami*, *Heckerochelys romani*, *Chengyuchelys baenoides*, *Platycheilus oberndorferi*, *N. oxfordiensis*, and *N. laticentralis* show an entoplastron more withdrawn from the anterior edge of the plastral lobe, with both epiplastra having a short midline contact anterior to the entoplastron. The length of the contact of the epiplastra anterior to the entoplastron is greater in *Dortoka vasconica* and eupleurodires. A graphical reconstruction of the entoplastron and the epiplastra relationships for some testudines is shown in Fig. 8.4.

The epiplastron in the paratype (MG61) of *Notoemys zapatoacaensis* is trapezoidal in shape with a convex posterior edge as in *Chengyuchelys baenoides* and *Heckerochelys romani*. In *N. oxfordiensis*, *N. laticentralis*, *Platycheilus oberndorferi*, *Dortoka vasconica*, and eupleurodires, the posterior edge of the epiplastron is straight to slightly concave, and it is highly concave in *Proganochelys quenstedti* and *Proterochersis robusta*. The hyoplastron and hypoplastron are similar to other platychelyids in shape, but are distinctive in that the central fontanelle extends from the central portion of the hyoplastra to the anteromedial part of the xiphiplastra, and is completely filled by bone that is thinner than the rest of the shell. The outline of the central fontanelle is marked by a sulcus as is also the case in the *N. laticentralis* specimen MOZP 2487, which was figured in de Lapparent de Broin et al. (2007, Fig. 1d). The presence of the central fontanelle in the holotype of *N. zapatoacaensis* remains uncertain, because the margins of the hyoplastra and the xiphiplastra are broken at the midline. However if the central fontanelle existed in the holotype of *N. zapatoacaensis*, it would have been restricted to the central portion of the plastron and would not have extended posteriorly into the xiphiplastral region, since a sulcus is absent and no differences in bone thickness are present that would indicate that the fontanelle has been secondarily filled in. *N. oxfordiensis*, *P. oberndorferi*, the stem testudine *Sichuanachelys* sp. indet., and *Indochelys spatulata* share with the holotype of *N. zapatoacaensis* the presence of a central fontanelle restricted to the area between hyoplastra and hypoplastra and, in the case of *P. oberndorferi* and the stem testudine *Sichuanachelys* sp. indet., a posterior fontanelle restricted to the area between the hypoplastra and xiphiplastra bones. This latter fenestra is unknown for *N. oxfordiensis* and absent in *I. spatulata* and *Heckerochelys romani*. In contrast, *N. laticentralis* and the paratype (MG61) of *N. zapatoacaensis* share the presence of a large central fontanelle posteriorly projected toward the xiphiplastral region. Stem testudines such as *Odontochelys semitestacea*, *Proganochelys quenstedti*, *Proterochersis robusta*, *Paleochersis talampayensis*, and *Kayentachelys aprix*, lack plastral fontanelles. This is also the case in *Dortoka vasconica* and eupleurodires, with the exception of *Araripemys barretoii* which has central and posterior fontanelles. The fontanelles are characteristic of early ontogenetic stages in almost all modern turtles, and filled by bone in later stages; examples of this process are seen in *Podocnemis lewyana* MNHN 1994-286, and *Chelus fimbriata* MNHN AC 5176.

The mesoplastra in the paratype (MG61) of *Notoemys zapatoacaensis* are triangular in shape and wider than long, lack a midline contact, and are smaller than in *N. laticentralis*, *N. oxfordiensis* and *Platycheilus oberndorferi*. The primitive condition seen in *Odontochelys semitestacea* is two pairs of mesoplastra meeting at the midline of the





**Fig. 8.4** Entoplastron and epiplastra relationship in testudines. Sketches of the plastron were redrawn from previous publications, indicated after the species name. Entoplastron shadowed in black, and epiplastra in gray. **a** *Odontochelys semitestacea* Li et al. (2008). **b** *Proterochersis robusta* Joyce (2007). **c** *Proganochelys quenstedtii* Joyce (2007). **d** *Kayentachelys aprix* Gaffney (1990). **e** *Indochelys spatulata* Datta et al. (2000). **f** *Platychelys oberndorferi* de Lapparent

de Broin (2000). **g** *Notoemys zapatoensis* this study. **h** *Notoemys laticentralis* de Lapparent de Broin et al. (2007). **i** *Dortoka vasconica* de Lapparent de Broin et al. (2004). **j** *Chelodina oblonga* Joyce (2007). **k** *Bonapartemys bajobarrealis* de Lapparent de Broin and De la Fuente (2001). **l** *Podocnemis sextuberculata* Joyce (2007). **m** *Apalone ferox* Joyce (2007). **n** *Eretmochelys imbricata* Joyce (2007). **o** *Mauremys leprosa* Claude et al. (2003). **p** *Kinosternon leucostomum* Joyce (2007)



plastron, a condition considered by Li et al. (2008) as a diagnostic characteristic for this genus. However, this characteristic is not exclusive to *Odontochelys semitestacea* since it is also present in *Proterochersis robusta*. In contrast, *Proganochelys quenstedti*, *Kayentachelys aprix*, *Eileanchelys waldami*, *Heckerochelys romani*, and *Chen-gyuchelys baenoides* have only one mesoplastral pair, meeting at midline of the plastron; in the case of *Sichuan-chelys* sp. indet. and *Indochelys spatulata*, the mesoplastra reach the lateral border of the central fontanelle. *Dortoka vasconica*, chelids, and *Araripemys barretoii* lack mesoplastra; all other eupleurodires have one pair of mesoplastra that are laterally restricted, almost equidimensional, and lack a midline contact.

The posterior plastral lobe in the paratype (MG61) of *Notoemys zapatocaensis* is markedly concave, in contrast to the flat surface of the holotype. The lateral edges of the lobe are slightly rounded with two shallow embayments; the anterior embayment is at the lateral aspect of the sutural contact between the hypoplastron and xiphiplastron, and the posterior one at the lateral end of the sulcus between the femoral and the anal scale. This is also the condition for the holotype. *P. oberndorferi* and *N. laticentralis* have a less marked embayment on the lateral edges of the posterior plastral lobe. In *N. oxfordiensis* the condition remains unknown since the most of the posterior plastral lobe is missing.

The xiphiplastron in the paratype (MG61) of *Notoemys zapatocaensis* have a deep U-shaped anal notch with posterior tips, similar to specimen MOZP-2487 of *N. laticentralis*. In contrast the holotype of *N. zapatocaensis* and the specimen of *Platychelys oberndorferi* figured in de Lapparent de Broin (2001, Fig. 1b) have a shallow, wide V-shaped anal notch, lacking well-developed posterior tips. *Odontochelys semitestacea* lacks a xiphiplastral anal notch, exhibiting a narrowly rounded to straight posterior edge. *Proterochersis robusta* has an interanal? scale at the most posterior margin of the plastron, creating a very narrow anal notch. All eupleurodires have a well-developed anal notch but it is variable in size, shape and depth in each family or genus.

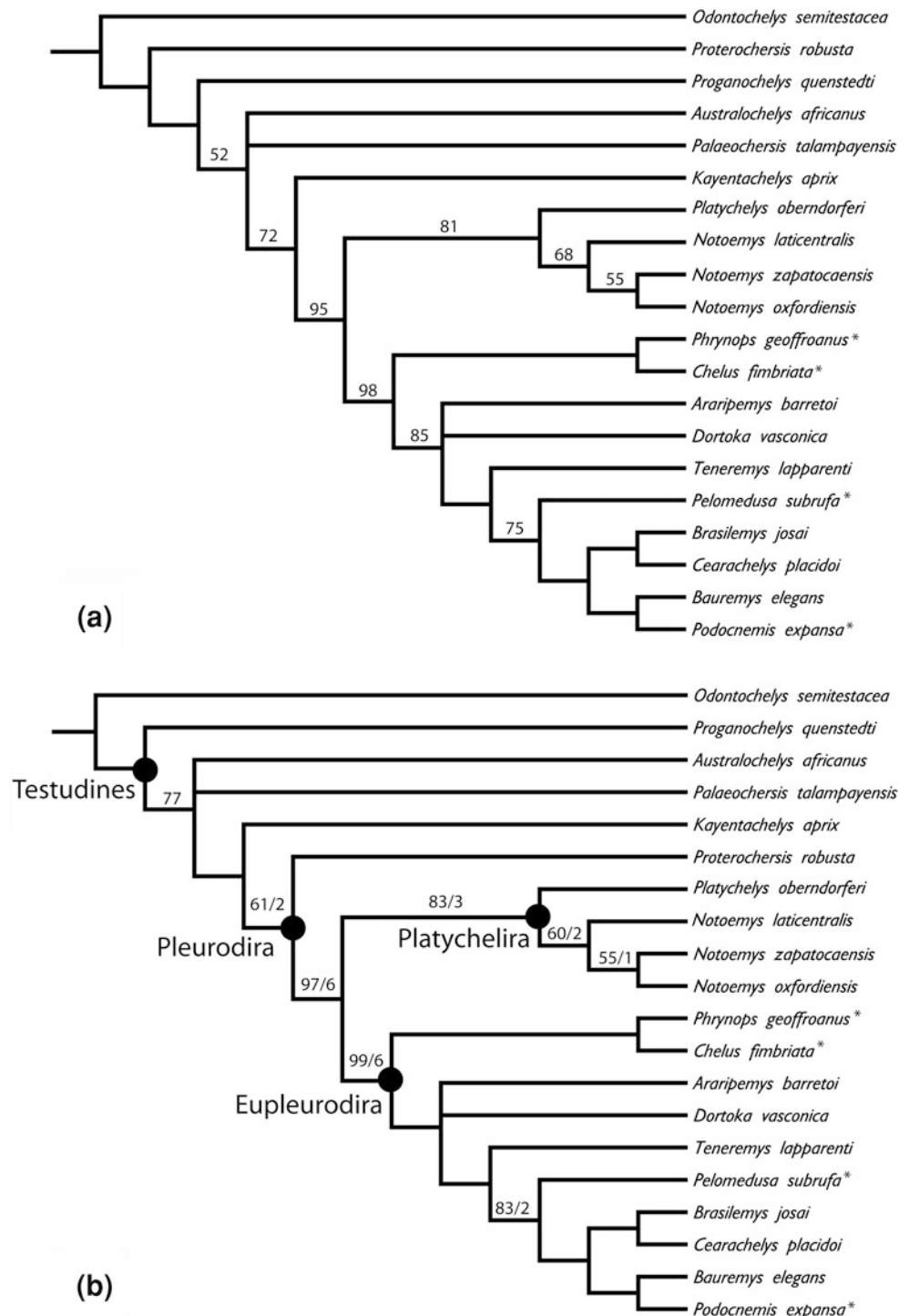
The intergular scale in the paratype (MG61) of *Notoemys zapatocaensis* is pentagonal, elongated in shape, longer than wide, and reaches the posteromedial corner of the entoplastron, as in the bothremydid *Ummulisani rutgersensis* figured in Gaffney et al. (2006, Fig. 269). In contrast, *N. laticentralis*, *N. oxfordiensis*, and *Platychelys oberndorferi* have an intergular scale that extends to the posteromedial margin of the entoplastron, a condition much less advanced than in *Dortoka vasconica* and most of the eupleurodires, where the intergular only covers the most anteromedial corner of the entoplastron; in the case of the podocnemidid *Erymnochelys madagascariensis* the very small intergular is restricted between the gulars. The intergular scale remains unknown for *Odontochelys semitestacea*, and for other

primitive testudines such as *Proganochelys quenstedti*, *Proterochersis robusta*, and *Heckerochelys romani*. *Chen-gyuchelys baenoides* differs in having two small intergulars. The gulars in the paratype (MG61) of *N. zapatocaensis* are almost rectangular in shape, much wider than long, a condition not seen elsewhere within the testudines. This condition is intermediate between the short, square, and more laterally positioned gulars of *Proganochelys quenstedti* and *Proterochersis robusta* and the triangular, more medially positioned gulars of *N. oxfordiensis*, *P. oberndorferi*, *Dortoka vasconica*, and most of the eupleurodires. The humeral scales of MG61 are completely separated medially by the intergular, such as in the bothremydid *Ummulisani rutgersensis*; thus they are smaller than in other platychelyids, *Proganochelys quenstedti*, *Proterochersis robusta*, *Chen-gyuchelys baenoides*, *Heckerochelys romani*, *D. vasconica*, and the eupleurodires. The humeropectoral sulcus in *N. zapatocaensis* is concave, slightly in contact with the posterior corner of the entoplastron as in *N. laticentralis*, while it is more posteriorly positioned in *N. oxfordiensis*, *P. oberndorferi*, *Odontochelys semitestacea*, *Proterochersis robusta*, *Proganochelys quenstedti*, *Ch. baenoides*, *H. romani*, and *D. vasconica* figured in de Lapparent de Broin and Murelaga (1999, Fig. 4). In eupleurodires and *D. vasconica* figured in de Lapparent de Broin et al. (2004, pl. III, 4), the humeropectoral sulcus extends further anteriorly over the posterior region of the entoplastron. The pectoro-abdominal, the abdominofemoral, and the femoroanal sulci in the paratype (MG61) of *N. zapatocaensis*, as well as in *N. laticentralis*, are interrupted at the midline of the plastron by the large central fontanelle.

## Phylogenetic Analysis

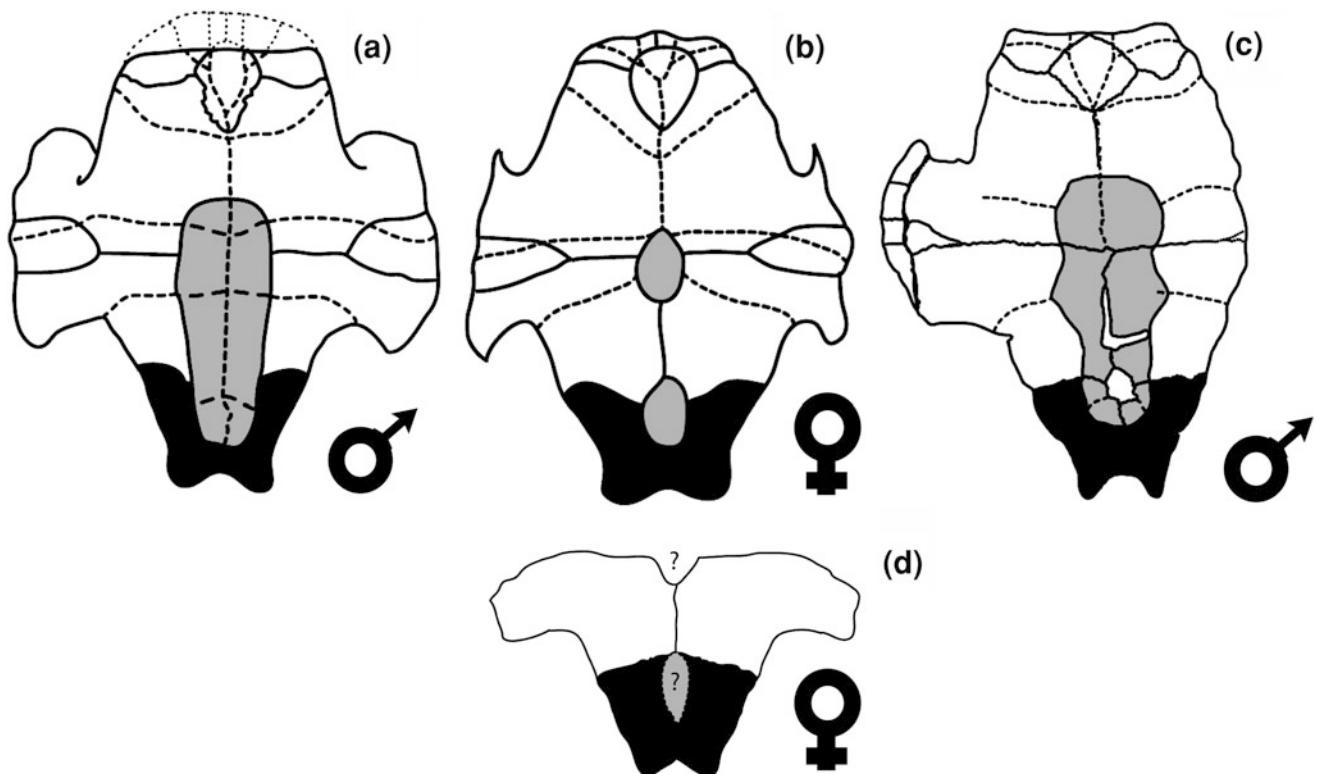
In order to perform a cladistic analysis, we included *Notoemys zapatocaensis* and 19 other taxa (principally pleurodires) in a matrix of 84 characters in total; 61 of them are skull/lower jaw characters (60 taken from Joyce 2007, and one taken from Cadena et al. 2010), 23 are shell characters. There are 19 in-group taxa and 1 out-group taxon (*Odontochelys semitestacea*). See Appendix 1 for the list of characters and Appendix 2 for the character-taxon matrix. The shell characters were taken and in some cases modified from previously published character matrices and detailed systematic studies, including de Lapparent de Broin and de la Fuente (2001), de la Fuente and Iturralde-Vinent (2001), de la Fuente (2003), Cadena and Gaffney (2005), Joyce (2007), and Li et al. (2008). A few of these characters are new to this study and were defined based on direct examination of extant or fossil specimens. We constructed the character-taxon matrix using Mesquite Version 2.72

**Fig. 8.5** Two alternative phylogenetic relationships among pleurodires and basal testudines recovered by this study. **a** Single most parsimonious cladogram, based on analysis in which all characters were unordered and equally weighted, using heuristics search (10,000 replicates) parsimony algorithm. **b** Strict consensus (our preferred phylogenetic hypothesis) of two most parsimonious cladograms, based on analysis in which all characters were unordered, character 81 was weighted four, and rest of characters had a weight of one. Extant taxa are indicated with an *asterisk*. Bootstrap values percentages (upper numbers) were obtained using 1000 replicates. Bremer decay indices (lower numbers) were obtained using TreeRot version 3 (Sorenson and Franzosa 2007)



(Maddison and Maddison 2009). For the phylogenetic analysis we used the parsimony algorithm of PAUP 4.0b10 (Swofford 2002). All characters were equally weighted and unordered in a first run. A second run was performed with all characters remaining unordered, but with weighting character 81 with a value of 4 using the set weight character

option in PAUP; the remaining characters retained an equal weight of 1. The reason to weight character 81 is that it is an undisputably consistent character in the evolution of the pleurodires, with no homoplasy known; see discussion in Gaffney et al. (2006, Character 133, p. 620). Multistate characters were treated as polymorphic. Finally, we



**Fig. 8.6** Differences in the xiphiplastra and fontanelles within platychelyids, potentially related to sexual dimorphism. Males (circle with arrow symbol) are characterized by a concave posterior plastral lobe, long and narrow posterior xiphiplastral tips, a well-developed anal notch in a U shape, and a large central fontanelle. Females (circle with cross down symbol) are characterized by a flat posterior plastral

lobe, short and wide posterior xiphiplastral tips, a V-shaped anal notch, and two interrupted fontanelles. **a** *Notoemys laticentralis* figured in de Lapparent de Broin et al. (2007). **b** *Platycheilus oberndorferi* redrawn from de Lapparent de Broin (2000). **c** *N. zapatoacaensis* this study. **d** *N. zapatoacaensis* figured in Cadena and Gaffney (2005)

performed a heuristics search (10,000 replicates), obtaining bootstrap percentages for 1000 replicates, and Bremer decay support indices using TreeRot Version 3 (Sorenson and Franzosa 2007).

## Discussion

### Phylogenetic Results

The phylogenetic analysis resulted in a single most parsimonious tree (Fig. 8.5a), with a tree length of 104, consistency index (CI) = 0.85, retention index (RI) = 0.90, and homoplasy index (HC) = 0.15. *Proterochersis robusta* is resolved at the base of the cladogram below *Odontochelys semitestacea*, a position mainly influenced by the presence of two pairs of mesoplastra meeting at the midline of the plastron (Character 78), which is a condition lost independently in derived pleurodires and cryptodires. A second run weighting the most unique pleurodire character,

the sutural articulation of pelvis to shell (Character 81), with a minimum value of four resulted in two most parsimonious trees. The consensus tree (Fig. 8.5b) has a consistency index (CI) = 0.84, a retention index (RI) = 0.89, a homoplasy index (HC) = 0.16, and tree length of 109. *P. robusta* is placed in this tree as the most basal pleurodire, the same result as obtained by Gaffney et al. (2006, Fig. 292) it is the hypothesis that we favor here.

The Platycheilidae (*Platycheilus* and *Notoemys* spp.) are a monophyletic clade, the same result obtained by Gaffney et al. (2006, Fig. 292). In contrast, the phylogenetic hypothesis presented by Joyce (2007, Fig. 18) shows that *N. laticentralis* is a sister taxon to the Pleurodira, and not just to the Platycheilidae. *Notoemys zapatoacaensis* and *N. oxfordiensis* are sister taxa based on the fact that both share an intergular scale covering most of the entoplastron posteriorly (Character 76). However this relationship is not strongly supported by Bremer indices values (see Fig. 8.5b), with only one extra step required to collapse the *N. zapatoacaensis*–*N. oxfordiensis* branch, creating a polytomy? between the three species of *Notoemys*. Cadena and Gaffney (2005) hypothesized that *N. zapatoacaensis* is more closely related

to *N. laticentralis* than to *N. oxfordiensis*. This hypothesis is based on the presence of more derived characteristics in common in these two taxa (see description) than in the other two possible combinations of taxa (*N. zapatoensis*–*N. oxfordiensis* or *N. laticentralis*–*N. oxfordiensis*). At this point we favor the result obtained by our phylogenetic analysis (*N. oxfordiensis*–*N. zapatoensis*), pointing out that the phylogenetic relationships among platychelyids will be clearly resolved only with the discovery of skull-shell associated material.

Continuing with the analysis of the phylogenetic hypothesis presented here (Fig. 8.5b), *Araripemys barreto* and *Dortoka vasconica* are resolved as the most basal pelomedusoids, differing from the others in that both lack mesoplastra bones (Character 78). *A. barreto* has been considered to be the sister taxon of Pelomedusidae based on the shared presence of an extreme temporal emargination (Gaffney et al. 2006, Fig. 292; Meylan et al. 2009). In contrast, Joyce (2007) defined the temporal emargination character in terms of squamosal-postorbital contact (Character 18, Appendix 1), a definition that we adopted here. The condition in *A. barreto* and Pelomedusidae is the lack of a squamosal-postorbital contact due to upper temporal emargination. However, our phylogenetic hypothesis shows that even though both *A. barreto* and Pelomedusidae share the same squamosal-postorbital contact condition, this single character is not enough to support a closer relationship. In the case of *D. vasconica*, our phylogenetic hypothesis places this taxon within the Pelomedusoides clade, as was also suggested by de Lapparent de Broin and Murelaga (1999). In contrast, the hypothesis put forward by Gaffney et al. (2006, Fig. 292) placed this taxon below the clade including the Chelidae and Pelomedusoides. The placement of *D. vasconica* and *Teneremys lapparenti* obtained here must wait for the discovery of more complete shells and skulls in order to be strongly supported.

Finally, in our preferred phylogenetic hypothesis *Pelomedusa subrufa* (representing Pelomedusidae) is the sister taxon of the most diverse group of middle Cretaceous–Cenozoic eupleurodires-denominated Panpodocnemidae (following França and Langer 2006). Within Panpodocnemidae, *Brasilemys josai* and *Cearachelys placidoi* (the most basal and better preserved bothremydid) are more closely related, sharing a neural 1 that contacts costals 1 and 2, and a neural 2 that only contacts costal 2. This is in contrast to *Bauremys elegans*, *Podocnemis expansa* and the rest of podocnemidids which have the neural 1 only contacting costal 1 and neural 2 contacting costal 1 anterolaterally (except for *Bardemys venezuelensis* which lacks the complete neural series). Previous phylogenetic hypotheses have placed *Br. josai* with *Hamadachelys escuilliei* and *Portezueloemys patagonica* as the closer relatives to Podocnemidae (Cadena et al. 2010). We attribute the closer

relationship between *Br. josai* and *C. placidoi* advocated here to the way that we built our character-taxon matrix, which uses only single taxon rather than composite taxa or the whole family or genus as previous studies did. In other words, the closer relationship between *Br. josai* and *C. placidoi* does not necessarily imply that *Br. josai* is the closer relative to the Family Bothremydidae.

## Sexual Dimorphism

Sexual dimorphism in turtles is expressed in several ways such as a difference in size between adult males and females, and the presence of a concave plastron in males of terrestrial species (Pritchard 2008). The new specimen of *Notoemys zapatoensis* (MG61) shares with *N. laticentralis* MOZP 2487 the presence of a concave posterior plastral lobe, long and narrow posterior xiphiplastral tips, and an anal notch that has a well-developed U shape. These characters indicate that they represent males for each one of these two species. Thus, the large central fontanelle present in both specimens is a potential morphological character associated with sexual dimorphism, in this case representing males. In contrast, the holotype of *N. zapatoensis* Cadena and Gaffney (2005) and the specimen of *Platychelys oberndorferi* figured in de Lapparent de Broin (2001, Fig. 1b) share a posterior plastral lobe that is flat and has a narrow V-shaped anal notch, as well as smaller central and posterior fontanelles, indicating that they represent females for each one of these two species. This could be also the case for the holotype of *N. oxfordiensis* figured in de la Fuente and Iturralde-Vinent (2001, Fig. 3). A graphic reconstruction of the xiphiplastron for platychelyids, as well as their differences potentially associated to sexual dimorphism, is shown in Fig. 8.6.

The identification of morphological variations associated with sexual dimorphism in fossil turtles has important implications in phylogenetic analysis. For example, de Lapparent de Broin et al. (2007) noted that *Notoemys laticentralis* differs from the rest of platychelyids in the wider and longer central fontanelle, a condition that was interpreted above as representing a potential male morphological condition for *N. laticentralis* and *N. zapatoensis*, and possibly for all males of this clade, making this characteristic useless for phylogenetic or systematic purposes at least at the species or genus taxonomic level.

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## Appendices

### Appendix 1

Description of the characters used in the phylogenetic analysis. Characters 60–83 represent carapace and plastron characters and are described here, whereas characters 1–59 were taken directly from Joyce (2007). Characters were polarized with respect to *Odontochelys semitestacea*, the source of the character, and if the character was modified or new is also indicated at the end of the description. Character 84 represents the only skull character, added from Cadena et al. (2010).

#### (A) Carapace

60. Ossification in the dermal component of the carapace: absent (0); present (1). Modified from Burke (2009).
61. Cervical scale(s): middle cervical wider than long (0); middle cervical as long as wide (1), cervical absent (2). Character modified from de Lapparent de Broin and Murelaga (1999) and Joyce (2007, Character 70).
62. Lateral arrangement between neural 1 and 2, and costals 1 and 2: neural 1 contacts costals 1 and 2, neural 2 only contacts costal 2 (0); neural 1 and costal 1 exclusively in contact with each other, neural 2 only contacts costal 2 (1); neural 1 contacts costals 1 and 2, neural 2 contacts costals 2 and 3 (2); neural 1 only contacts costal 1, neural 2 contacts costal 1 anterolaterally (3); neural series absent (4). New character.
63. Carapace posteriorly notched: present (0); absent (1). Pygal notch character from Cadena and Gaffney (2005).
64. Supramarginal scales: full series of twelve, on both sides of the carapace (0); incomplete series, restricted to the anterior margin on both sides of the carapace (1); absent (2). Character modified from Cadena and Gaffney (2005).
65. Posterior lobe of the carapace: same width as the anterior lobe or slightly wider (0); tapering medially (1). Character modified from Cadena and Gaffney (2005).

66. Articulation tubercle on the anterior face of the first thoracic rib: absent, smooth anterior face (0); present (1). Character modified from Cadena and Gaffney (2005).
67. Thoracic vertebrae: cylindrical, longer than wide, keeled ventrally (0); smooth and flat ventrally, hexagonal in shape with central lateral notch (1). Character modified from Cadena and Gaffney (2005).
68. Axillary process: contacts peripherals only (0); contacts costal 1 or the sutural contact between costals 1 and 2 (1). Character modified from Cadena and Gaffney (2005).
69. Suprapygals 1: parallel-sided (0); tapers anteriorly (1); absent (2). Character modified from Cadena and Gaffney (2005).
70. Vertebral scales 2 and 3: hexagonal in shape, much wider than long (0); rectangular in shape, slightly wider than long (1); hexagonal or rectangular, as long as wide or longer than wide (2). Character modified from Cadena and Gaffney (2005).
71. Medial contact of the posterior costals: absent (0); present (1); present due to complete absence of neural series (2). Character modified from Joyce (2007, Character 68).
72. Lateral position of the sulcus between vertebrae 3 and 4 in taxa with five vertebrae: sulcus positioned on costal 6 (0); sulcus positioned on costal 5 (1). Character modified from Joyce (2007, Character 74).

#### (B) Plastron

73. Posterior epiplastral process: present (0); absent (1). Character from Cadena and Gaffney (2005).
74. Posterior entoplastral process: present (0); absent (1). Character from Cadena and Gaffney (2005).
75. Entoplastron participation in the anterior margin of the plastron in ventral view: wide participation (0); short participation (1); lacking participation (2). Character modified from Cadena and Gaffney (2005).
76. Intergular scale(s): covering slightly the anterior portion of the entoplastron (0); covering most of the entoplastron posteriorly (1); not covering the entoplastron (2). Character modified from Cadena and Gaffney (2005).
77. Anterior plastral lobe margin: defined by tuberosities, dentate margin (0); very reduced tuberosities, straight to slightly dentate margin (1); lacking tuberosities, smooth, highly convex margin (2). New character.
78. Mesoplastra: two pairs meeting at the midline of the plastron (0); one pair of mesoplastra, with midline contact or reaching the central fontanelle margin (1); one pair of mesoplastra, wider than long, without midline contact, (2); one pair of mesoplastra, as long as

- wide, without midline contact, (3); mesoplastra absent (4). Character modified from Cadena and Gaffney (2005).
79. Central plastral fontanelle: absent (0); present (1). Character modified from Cadena and Gaffney (2005).
80. Anal notch: absent, with straight to slightly concave posterior edge of the xiphiplastra (0); present, well-developed in open U- or V-shape (1). Character modified from Joyce (2007, Character 87).
81. Sutural articulation of pelvis to shell: absent (0); present (1). Character modified from Joyce (2007, Character 125).
82. Iliac scar: absent (0); extends from costals onto the peripherals (1); restricted to costal 8 (2); positioned on costal 8 and pygal, sometimes reaching costal 7 (3). Character modified from Joyce (2007, Character 127).
83. Shape of ilium articular site: narrow and pointed posteriorly (0); oval (1). Character from de la Fuente and Iturralde-Vinent (2001).

### (C) Skull

84. Pterygoid, cavum pterygoidei = fossa podocnemidoid of de Lapparent de Broin (2000): absent (0); shallow and slightly hidden anteromedially by the underlapping basisphenoid medially and laterally by the pterygoid (1); deep and partially to totally covered by the pterygoid flange (posterolateral wings of the pterygoid) (2). Character taken from Cadena et al. (2010).

## Appendix 2

Character matrix (20 taxa and 84 characters) used for phylogenetic analysis (Nexus file as Supplementary Data 1). Multistate 0 or 1 is represented by “a”, and ‘not applicable’ by “–”.

*Odontochelys semitestacea*  
000?????0???0?????????????????0?0?00?0?0?0?0?  
?????????0?????????????0000 000–??0

*Proganochelys quenstedti*  
000000000000–000000000000000000000000000000000000  
0000000000000010?000000?0?0010010000?0

*Proterochersis robusta*  
??  
?????????10?010000?0?00100001110?

*Australochelys africanus*  
????????10?0???00?0???0?001001??10000000??  
1?0?100?0?0????????????????????????????

*Palaeochersis talampayensis*  
00000?01000??00000000??00001?0?1001?010000000  
0?1?0?100????1??0?0?????001?1??00??0

*Kayentachelys aprix*  
00001011110??10000001100001010011011?01000000  
000100?10100001001200?000001010110000?0

*Platyechelys oberndorferi*  
??  
?????????100111111010011201211110?

*Notoemys laticentralis*  
?????????????????????????????????2110?11?0?????01?  
0?1010??100121111100011??211121?

*Notoemys zapatoensis*  
??  
?????????101121111010011211211121?

*Notoemys oxfordiensis*  
??  
?????????1001211?1???1?212211121?

*Araripemys barreto*  
1—101011111110003011100002110211123111101000  
1 001001101?0011?2120?0?22011022241a11310

*Dortoka vasconica*  
??  
?????????112120001221111202401131?

*Brasilemys josai*  
1—1010111111100010111?????02111231111010001  
001001 101????1201200012211?????????????

*Cearachelys placidoi*  
1—101011111110101011100002110211123111101000  
100100110100?11201200?12201112023011??0

*Bauremys elegans*  
1—1010111111100010?110000211021?1231111010001  
00?001?0?0001123?200012211112023011?12

*Podocnemis expansa*  
1—10101111111000101110000211021112311110100a  
100100 110100011231200012211112023011312

*Pelomedusa subrufa*  
1—101011111110003011100002110211123111101000  
100100110120011231200012211112023011310

*Phrynops geoffroanus*  
0110011111011101–2011100001010211023111101000  
00110011012010114120 0012221112024011310

*Chelus fimbriata*  
1—00111100111010201110 000101021102311110100  
00001001101?0101101200012211112024011310

*Teneremys lapparenti*  
??  
?????????11212 0??12211112023??1???

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