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A NESTING SITE AND EGG MORPHOLOGY OF A MIOCENE TURTLE FROM URUMACO, VENEZUELA: EVIDENCE OF MARINE ADAPTATIONS IN PELOMEDUSOIDES

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Abstract: Fossil eggshells from the Late Miocene Urumaco Formation of north-western Venezuela are reported. Stereomicroscopy and scanning electron microscopy were used to examine shell gross morphology and ultrastructure, respectively. Diagnostic turtle features in the eggshells include a distinct pattern of crystal aggregations within the shell units. The eggs had an elliptical shape with a maximum diameter of *c.* 56·5 mm and width of *c.* 43·5 mm, as measured in a specimen preserving the egg's outline. Scattered clutches of broken eggshells were found embedded in one horizon of a coarse, sandy sediment, with grains not well sorted containing foraminifera and fragments of bivalve shells. The sediments are rich in ichnofossils and the reddish colour of the sandstone indicates an oxidizing environment. These facts suggest that the eggs were deposited in a beach directly facing the sea or brackish waters, perhaps near a river delta or lagoon, as is typical of the Urumaco sequence. In the same stratigraphical layer and next to one of the egg clusters, a carapace assignable to the pelomedusoid *Bairdemys venezuelensis* was found, suggesting that this species was a colonial nester that laid its eggs in beaches and lived in a marine or nearshore marine environment.

Key words: Neogene, Caribbean, palaeobiology, reproduction, Pleurodira.

TURTLES from the Late Miocene Urumaco Formation in Venezuela are represented by at least four pleurodire species and a trionychid (Aguilera 2004). The most common species in the succession is *Bairdemys venezuelensis*, known from numerous shells and skulls (Wood and Díaz de Gamero 1971; Gaffney and Wood 2002). *Bairdemys* is part of a clade of extinct podocnemidids known from the Tertiary of Africa, Asia and the circum-Caribbean, diagnosed among other things by the presence of a specialized secondary palate (Gaffney *et al.* 1996). Very little is known about the palaeobiology of this group, with all studies to date having been concerned with taxonomic and systematic issues. Here we report a nesting site with eggshells assignable to *Bairdemys venezuelensis*.

Studies of egg ultrastructure and nesting strategies of extant species can reveal a diversity of information relevant to palaeobiology (Horner 2000). Fossil and Recent turtle eggs remain poorly studied, in spite of some notable contributions that describe several species (e.g. Hirsch 1983; Schleich and Kästle 1988; Mikhaïlov 1997; Kohring 1999). These and other studies of individual species reveal structural variation of potential functional and systematic significance.

The material described in this paper is deposited in the Palaeontological Collection of the Universidad Experimental Francisco de Miranda, Coro, Venezuela (UNEFM) and in the Zoological Collection of The Natural History Museum, London, UK (NHM).

MATERIAL AND METHODS

Eggshell surface anatomy and ultrastructure were documented using stereomicroscopy (SM) with a digital camera and scanning electron microscopy. Relatively small fragments were coated with gold and scanned in different planes under a scanning electron microscope (SEM). Several eggshell elements cannot be characterized in detail due to preservational biases, as is the case for the shell membrane. Terminology is based on Hirsch (1983). For comparison, data from the literature were used as well as our own observations and documentation of egg

ultrastructure in *Podocnemis unifilis* NHM 1961.360. *Podocnemis* is a close living relative of *Bairdemys* (Broin 1988; Gaffney *et al.* 1996; Meylan 1996).

CONTEXT

Locality

Domo de Agua Blanca, Urumaco, Estado Falcón, Venezuela (11° 13′ 19·6″N; 70° 15′ 0·5″W). Sediments are from the middle member of the Late Miocene Urumaco Formation (Díaz de Gamero and Linares 1989). The eggshell fragments were found in an area of approximately 600 m^2 (Text-fig. 1A). The egg clusters were distributed in no apparent pattern.

Depositional environment

Scattered clutches of broken eggshells were found embedded in one horizon of a coarse, sandy sediment, with grains not well sorted containing foraminifera and fragments (mostly small) of unidentifiable bivalve shells of possible marine origin (Text-fig. 1B–C). The sediments are rich in ichnofossils (*Thalassinoides* isp.); this, and the red colour of the sandstone, indicates an oxidizing environment. These facts suggest that the eggs were deposited in a beach directly facing the sea or brackish waters, perhaps near a river delta or lagoon as is typical of the Urumaco sequence (Sánchez-Villagra *et al.* 2003).

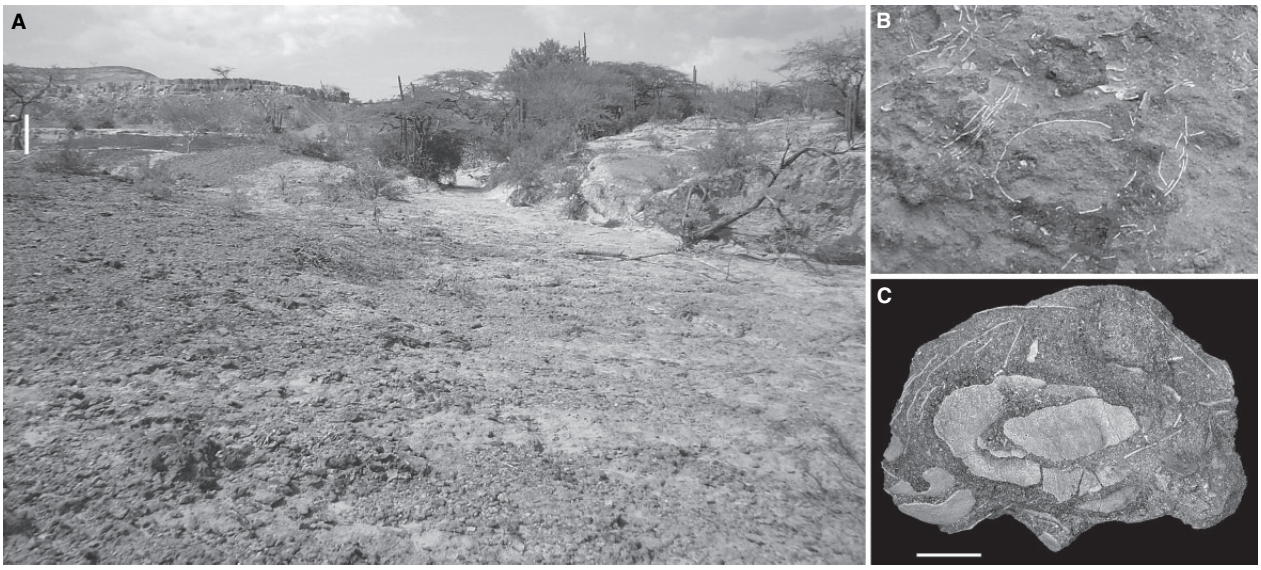
Association

In the same stratigraphical layer where the egg clusters were found, in the middle of the whole area (Text-fig. 1A) and a few centimeters away from an egg cluster, a large carapace in a poor state of preservation was found. Its size, shape and the preserved peripheral bones are consistent with its identification as *Bairdemys venezuelensis*. Assignation to *B. venezuelensis* was confirmed by colleagues familiar with this species (O. Aguilera, pers. comm. 2004) who visited the site before the specimen was weathered to the extent it was by the time of our later visit in June 2004. However, this assignment is tentative since no eggs containing embryos were found.

DESCRIPTION OF EGG MORPHOLOGY AND ULTRASTRUCTURE

The complete outline of an egg fragment preserved *in situ* (Text-fig. 1B) is elliptical, with maximum length and width of 56·5 mm and 43·5 mm, respectively.

The radial calcareous (probably aragonite) ultrastructure, well preserved in our sample, is of considerable taxonomic importance. The eggshells can be identified as hard chelonian eggshells of 'testudoid morphotype' following Mikhaïlov (1991) or 'testudoid basic type' *sensu* Hirsch (1996). Eggs of Recent marine turtles, such as those of *Caretta caretta*, are different as they are globular leathery eggs (Schleich and Kästle 1988). There is a smooth outer surface with a distinct pattern of shell



TEXT-FIG. 1. A, view of nesting locality at Domo de Agua Blanca, Urumaco, Estado Falcon, Venezuela; bar on the upper left side indicates a person for scale. B, complete outline of an egg fragment preserved *in situ*; maximum length 56·5 mm; maximum width 43·5 mm. C, UNEFM-VF60, containing numerous eggshell fragments. Scale bar represents 10 mm.

columns and pores (10 columns per mm^2) (Text-fig. 2A–B). In comparison with Recent reptiles, a similar pattern occurs in several morphologically diverse turtle genera, including *Mauremys*, *Chelus* and *Geochelone* (Schleich and Kästle 1988) and in no other Recent reptile described in the literature (Schleich and Kästle 1988; Packard and Hirsch 1989; Mikhaïlov 1991, 1997; Hirsch 1996; Mikhaïlov *et al.* 1996; Kohring 1999). In contrast to the situation described in *Bairdemys*, *Podocnemis unifilis* (NHM 1961.360) lacks distinct shell patterns; furthermore, the eggshell's smooth outer surface has very sparsely distributed pores (*c.* 1 pore per mm^2) (Text-fig. 3A).

The pores of *Bairdemys* have a diameter ranging from 170 to 200 μm; those of *Podocnemis unifilis* are *c.* 27·7 μm wide, which is 6·1–7·2 times smaller than those of *Bairdemys*. *Chelus fimbriatus*, a recent chelid, possesses pores with a diameter of around 55 μm, and eggshell pores of the geoemydid *Cuora amboinensis* measure 10–200 μm in diameter (Schleich and Kästle 1988). The large pore diameter might be associated with the great total thickness of the eggshell. The distance between the pores ranges from 235 to 670 μm.

The fine morphology/ultrastructure of radial fractures also exhibit a typical testudine form. On magnification (100×) of the shell units, the crystalline layer of the eggshell can be clearly identified as being of turtle origin, as they show regular growing crystals projecting radially from a centre ('radial aragonite structure' *sensu* Mikhaïlov 1991) to the external zone (Text-fig. 2C). Following Mikhaïlov (1991) the centre or organic core on the base of a shell unit provides taxonomic information; in the case of the specimen under description the centre is of fairly undifferentiated form and gives little evidence of organic structures. However, the shape and structure of the shell units contain sufficient diagnostic information to assign the fragments to a turtle independent of the carapace association discussed above. Text-figure 2D shows the base of shell units. The horizontal fraction of the eggshell in the region of the columns' bases brings the symmetrically structured organic cores to light, where the regular spherulitic growth of aragonite crystals originates.

The height of the shell units ranges from 565 to 730 μm, resulting in a relatively thick eggshell. The thickest eggshell reported in the literature that we know of is that of *Chelonoidis denticulata* (Testudinidae), at 570 μm. In *Chelonoidis*, the range of thickness of the calcareous layer is between 150 and 535 μm (Schleich and Kästle 1988). The width of the columns closest to the organic cover or tegmentum is around 440 μm, so the columns are 0·6 times wider than high. This identifies the specimen as being of 'spherurigidis morphotype' *sensu* Hirsch (1996), which specifies eggshells of testudoid basic type with interlocking shell units (causing rigidity) that are higher than wide. This applies to all rigid-shelled eggs.

The interlocking shell units of *Podocnemis unifilis* are *c.* 205·6 μm in height and *c.* 96·3–120·4 μm in width, so the columns are 0·5–0·6 times wider than they are high. In comparison with the difference between total height and width of the shell units in *Bairdemys* and *P. unifilis*, this ratio is only slightly different from that of *Bairdemys* (0·6).

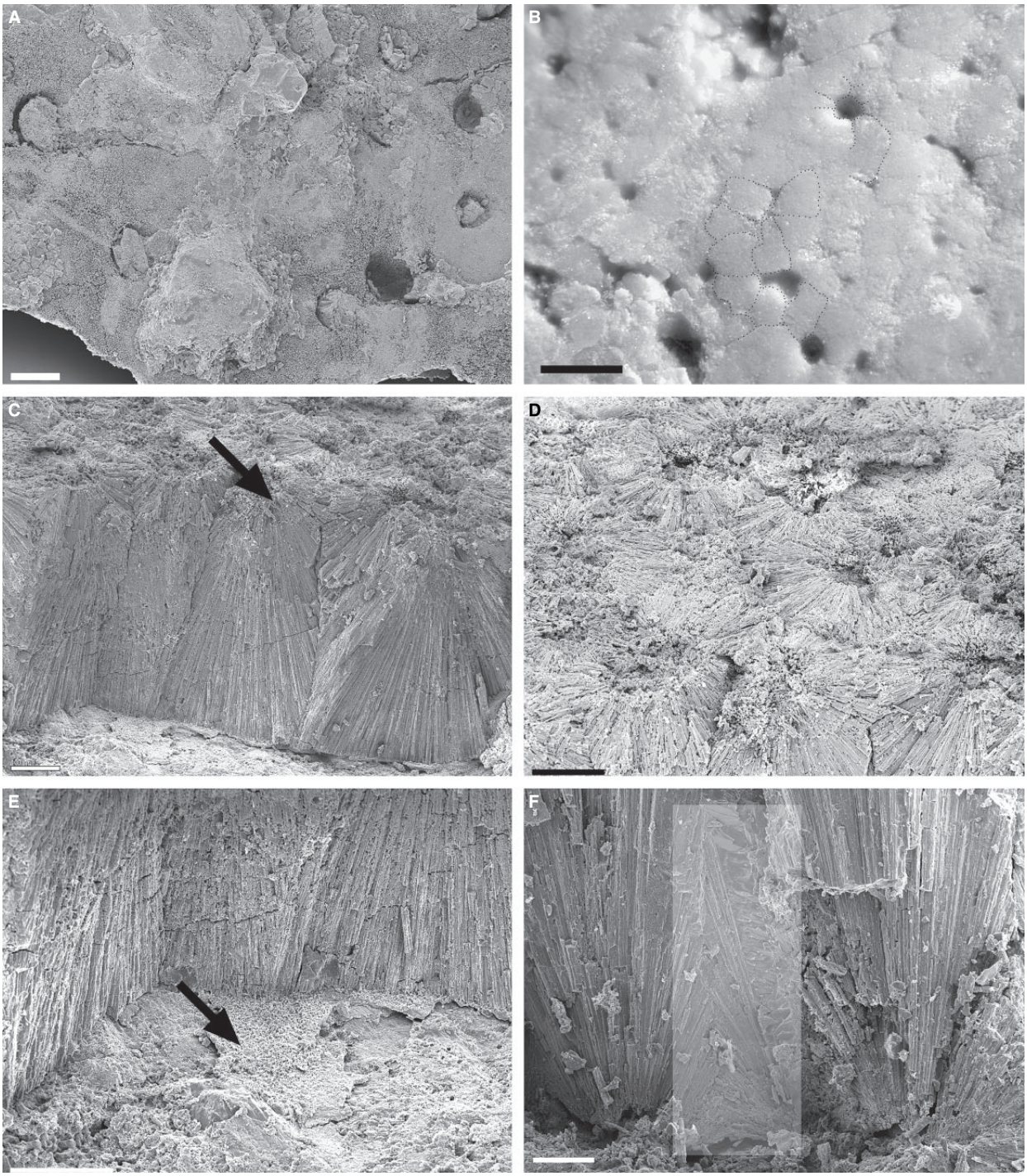
The cylindrical shell units contact each other closely without visible caverns in between (Text-fig. 2F, lightened rectangle). In *Podocnemis unifilis* different fractions show different patterns: in some photographs no caverns can be recognized as in *Bairdemys*, whereas in others they are apparent (Text-fig. 3B–D, lightened rectangles).

In *Bairdemys* a visible boundary between the columns and the organic cover, consisting of fibrous material, can be recognized under the SEM. This boundary is approximately 22 μm thick (Text-fig. 2E).

The shell membrane with inner and outer boundaries on the inner side of the eggshell can be described as a composition of fibrous layers (Text-fig. 2E), but its total thickness cannot be estimated owing to difficulties in recognizing the inner boundary. There are no globules in the shell membrane, in contrast to shell membranes of *Podocnemis unifilis* and numerous other testudines (e.g. *Mauremys caspica*, *Cuora amboinensis*; Schleich and Kästle 1988). The eggshells of *P. unifilis* we studied lack globules (Text-fig. 3B), contrasting with the structure that Schleich and Kästle (1988, p. 30, pl. 6) depicted for this species.

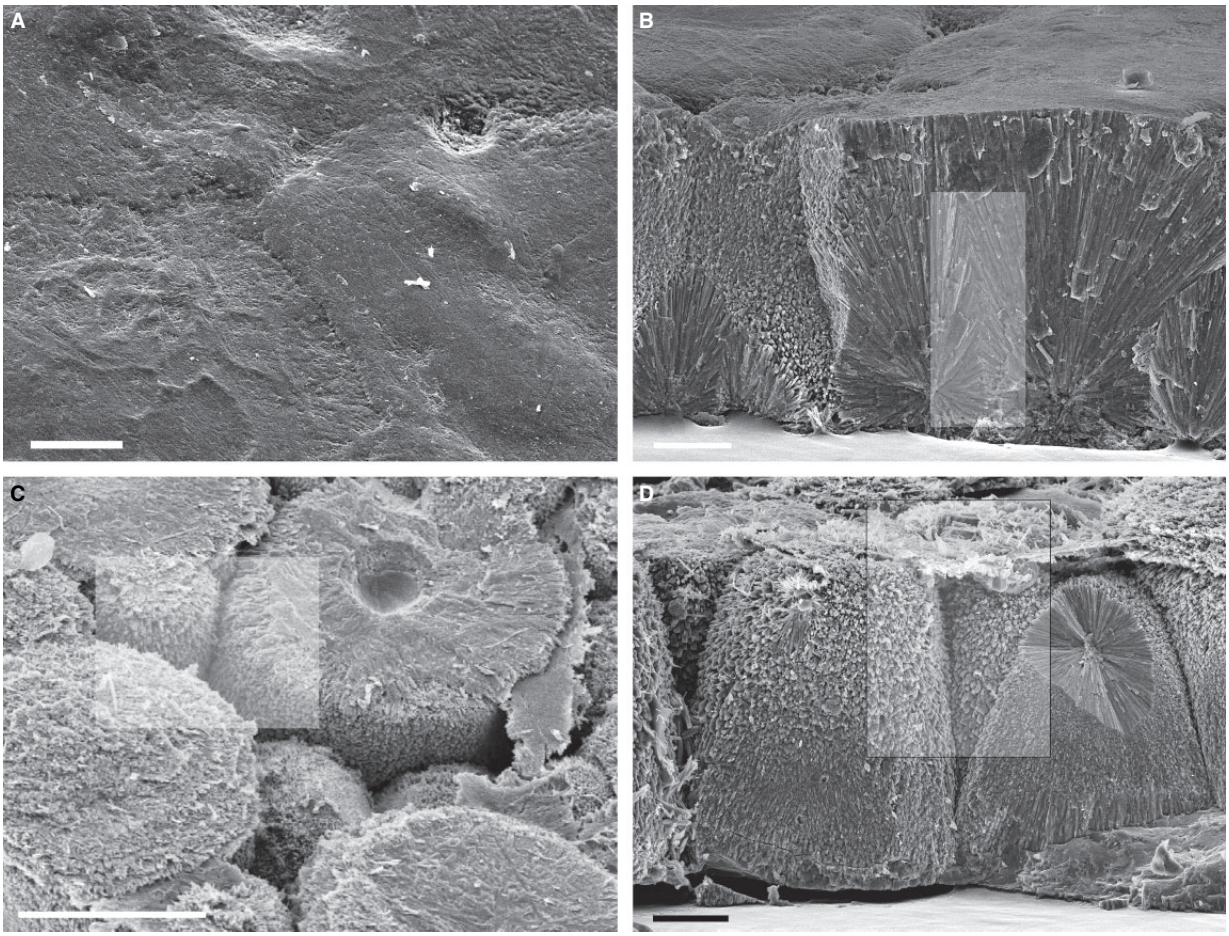
DISCUSSION

The evidence presented in this paper suggests that *Bairdemys venezuelensis* was probably a colonial nester, which laid its eggs in beaches and lived in a marine or nearshore marine environment. Associating a marine nesting site with *Bairdemys* is significant because it provides the first direct evidence of the palaeoecology of these Miocene turtles. All living Pelomedusoides are freshwater forms. There is indirect evidence, however, that many late Mesozoic and early Cenozoic Pelomedusoides were adapted to marine environments (Lapparent de Broin and Werner 1998; Wood 2003). Most representatives of the Pelomedusoides clade to which *Bairdemys* belongs (Gaffney *et al.* 1996) occur in sediments that could be of nearshore or fluvio-lacustrine origin, but none is known from clearly offshore marine sediments. Although no studies of the palaeobiology of *Bairdemys* have been made, all findings suggest that these turtles lived in marine or brackish waters (Sánchez-Villagra *et al.* 2000, 2004; Gaffney and Wood 2002). *Bairdemys* has been found in nearshore marine associations, and not in clearly offshore marine sediments.



TEXT-FIG. 2. *Bairdemys venezuelensis*, UNEFM-1500. A, exterior of eggshell; note the pores (SEM). B, exterior of eggshell; note the column pattern (dotted lines) (SM). C, shell units in cross-section, showing regular growing crystals projecting radially from the centre (arrow) to the external zone (SEM). D, base of shell units in a horizontal fracture of the eggshell (SEM). E, shell membrane with inner and outer boundaries on the inner side of the eggshell. The inner boundary consists of fibrous layers (arrow) (SEM). F, shell units in cross-section, showing the lack of caverns between the units (lightened rectangle) (SEM). Scale bars represent 200 μm in A, 1 mm in B, 100 μm in C–E, 50 μm in F.

The inferred general features of the nesting behaviour of *Bairdemys venezuelensis* (colonial, in a beach) are not unique among Pelomedusoides, although there is great variation in nesting strategies within the group. Among *Podocnemis* species, *P. expansa*, *P. sextuberculata* and *P. unifilis* nest only on exposed river sand beaches



TEXT-FIG. 3. *Podocnemis unifilis*, NHM 1961.360 (SEM). A, exterior of eggshell; note the sparse distribution of pores. B, shell units in cross-section, showing regular growing crystals and the lack of caverns between shell units (lightened rectangle). C, base of shell units, showing the outline of the columns and the presence of caverns between shell units (lightened rectangle). D, shell units in cross-section, showing the presence of caverns (lightened rectangle). Scale bars represent 50 μm.

(Pritchard and Trebbau 1984; Pezzuti and Vogt 1999), *P. erythrocephala* nests in beaches, seasonally flooded savannas and forests (Castaño-Mora *et al.* 2003), *P. vogli* makes major overland migrations to lay its eggs (Pritchard and Trebbau 1984) and *Peltocephalus dumerilianus* wanders into the forest to nest on patches of high ground rather than use sandbanks and beaches (Pritchard and Trebbau 1984).

The elliptical shape of the eggs reported here is not unexpected. Among pleurodires, eggs are also elliptical in all the Pelomedusoides for which information is available to us, including *Podocnemis sextuberculata* (Pezzuti and Vogt 1999), *P. erythrocephala* (Castaño-Mora *et al.* 2003), *P. unifilis* (Pritchard and Trebbau 1984), *P. vogli* (Pritchard and Trebbau 1984), *Peltocephalus dumerilianus* (Pritchard and Trebbau 1984), *Pelomedusa subrufa* (Loveridge 1941) and *Pelusios castanoides* (Spawls *et al.* 2002). Some chelid species produce oval eggs, others spherical ones (Pritchard and Trebbau 1984; Cann 1998; Souza 2004).

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