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The freshwater and terrestrial turtles from Monte Pila and Fuenmayor (La Rioja, northern Spain): new data on the lower Miocene turtle diversity of the Ebro Basin

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ABSTRACT

Abundant turtle fossils from two lower Miocene localities in which this lineage had not previously been studied are described herein. The localities are Monte Pila and Fuenmayor, which are 10 km apart, both located in the Autonomous Community of La Rioja (northern Spain), in the Ebro Basin. Information about the turtles from the lower Miocene levels in this basin was until now restricted to the finds made in the MN3 biozone of the Bardenas Reales of Navarre. Several turtle taxa had been recognized there. However, the material attributed to each of them was scarce. Monte Pila and Fuenmayor are located in biozone MN2. The remains of turtles are abundant in both sites. A terrestrial lineage, recognized at Monte Pila, is not represented in the Bardenas Reales fauna of Navarre. It represents the first record of *Titanochelon* Pérez-García & Vlachos, 2014 in La Rioja and is one of the oldest member of this genus, being assigned to *Titanochelon* cf. *bolivari* (Hernández-Pacheco, 1917). The only lineage of turtles identified in Fuenmayor, and the most abundant in Monte Pila, is Ptychogasterinae. All material of this clade of freshwater turtles identified there is compatible with a single form, for which a high range of intraspecific variability is recognized. It is attributed to *Ptychogaster* (*Temnoclemmys*) cf. *bardenensis* Murelaga, Lapparent de Broin, Pereda Suberbiola & Astibia, 1999, this species having been recognized, until now, as exclusive to the Bardenas Reales of Navarre.

KEY WORDS
Turtles,
Cryptodira,
Geoemydidae,
Ptychogaster,
Testudinidae,
Titanochelon,
early Miocene,
Spanish record,
Ebro basin.

RÉSUMÉ

Tortues terrestres et d'eau douce de Monte Pila et Fuenmayor (La Rioja, nord de l'Espagne) : nouvelles données sur la diversité des tortues du Miocène inférieur du Bassin de l'Èbre.

Des restes abondants de tortues, provenant de deux localités du Miocène inférieur dans lesquelles ce groupe n'a jamais été étudié, sont présentés ici. Ces localités, Monte Pila et Fuenmayor, distantes de 10 km l'une de l'autre, sont situées dans la communauté autonome de La Rioja (nord de l'Espagne), dans le Bassin de l'Èbre. Les informations sur les tortues des niveaux du Miocène inférieur de ce bassin étaient jusqu'à présent limitées aux découvertes faites dans la biozone MN3, dans les Bardenas Reales de Navarre. Plusieurs taxons de tortues y avaient été reconnus. Cependant, le matériel attribué à chacun d'eux était très rare et parcellaire. Monte Pila et Fuenmayor sont situés dans la biozone MN2. Les restes de tortues sont abondants dans les deux sites. Un groupe de tortues terrestres, reconnu à Monte Pila, n'est pas représenté dans la faune des Bardenas Reales en Navarre. Il correspond à la première identification de *Titanochelon* Pérez-García & Vlachos, 2014 dans La Rioja et à l'un des plus anciens représentants de ce genre, attribué à *Titanochelon* cf. *bolivari* (Hernández-Pacheco, 1917). Les Ptychogasterinae constituent le seul groupe de tortues identifié à Fuenmayor et le plus abondant à Monte Pila. Tout le matériel de ce clade de tortues d'eau douce identifié dans ces deux sites n'est compatible qu'avec une seule forme, pour laquelle une grande variabilité intraspécifique est reconnue. Elle est attribuée à *Ptychogaster* (*Temnoclemmys*) cf. *bardenensis* Murelaga, Lapparent de Broin, Pereda Suberbiola & Astibia, 1999. Cette espèce a été jusqu'à présent reconnue comme exclusive des Bardenas Reales en Navarre.

MOTS CLÉS
Tortues,
Cryptodira,
Geoemydidae,
Ptychogaster,
Testudinidae,
Titanochelon,
Miocène inférieur,
registre espagnol,
Bassin de l'Èbre.

INTRODUCTION

The information about the turtles from the lower Miocene of the Iberian Peninsula is limited, compared to the knowledge about the diversity of this group in Iberian middle and upper Miocene sites (see Pérez-García 2017, and references therein). One of the locations that had provided much information about the Iberian lower Miocene turtles is the Bardenas Reales of Navarre (Autonomous Community of Navarra), a region located in the northeast of Spain, in the Ebro Basin (Murelaga *et al.* 1999, 2002; Fig. 1). Despite the relatively limited record found in that paleontological area, several taxa had been identified there, in deposits corresponding to the MN3 biozone (Burdigalian): a new chelydrid, *Chelydropsis apellanizi* Murelaga, Lapparent de Broin, Pereda Suberbiola & Astibia, 1999; a member of Ptychogasterinae tentatively attributed to the German lower Oligocene form *Ptychogaster* (?*Ptychogaster*) *ronheimensis* Groessens-Van Dyck & Schleich, 1985 (for which Murelaga *et al.* [2002] recognized that the specific attribution cannot be confirmed, but that it should belong to the same lineage, cited here as *Ptychogaster* sp.); a second species defined as a new taxon of that lineage, *Ptychogaster* (*Temnoclemmys*) *bardenensis* Murelaga, Lapparent de Broin, Pereda Suberbiola & Astibia, 1999; and an unidentified representative of Trionychidae (Murelaga *et al.* 1999, 2002). All the information so far available concerning the lower Miocene turtles from the western half of that Basin was almost exclusively limited to that provided by the remains from the Bardenas Reales of Navarre, corresponding to scarce and isolated plates, with the sole exception of the shell tentatively attributed to *Ptychogaster* (?*Ptychogaster*) *ronheimensis* (Murelaga *et al.* 1999, 2002). The representatives of Ptychogasterinae from the Bardenas Reales of Navarre are the oldest representatives of this lineage identified at a specific level in the Iberian fossil record (see Pérez-García 2017, and references therein).

Abundant remains of turtles, corresponding to both isolated plates and relatively complete shells or articulated plates, have been found in a hitherto poorly known fossiliferous locality, also located in lower Miocene levels of the western region of the Ebro Basin (but from a biozone older than that from which the turtles from the Bardenas Reales of Navarre came, being from the upper part of the MN2 biozone, corresponding to the Burdigalian): Monte Pila (Autonomous Community of La Rioja; Fig. 1). These remains of turtles, hitherto unpublished but previously cited, without justification, as attributable to *Ptychogaster* sp. and to Chelonii indet. (Hernández *et al.* 2003), are presented and analyzed in this paper. Members of two lineages are recognized there. The most abundant corresponds to Ptychogasterinae. The knowledge about the oldest representatives of this lineage in the Iberian Peninsula could be greatly increased through the study of these specimens (this paper). Some unpublished remains from the Bardenas Reales of Navarre are figured here for the first time, in order to improve the comparative study between the specimens of Ptychogasterinae from the lower Miocene of the Ebro Basin. In addition, a partial shell and several isolated plates of this lineage, from another new lower Miocene locality (also from the MN2 biozone) of the same Basin (Fuenmayor, also in the Autonomous Community of La Rioja; Fig. 1), are also presented and analyzed.

The second lineage recognized in Monte Pila does not correspond to any of those so far identified in the Bardenas Reales of Navarre. It is represented by a relatively large terrestrial turtle, this tortoise being attributable to Testudinidae. Thus, these fossils, which correspond to one of the oldest finds of large testudinids in the Spanish Neogene record, are also analyzed in this paper, expanding the knowledge about the biodiversity of turtles in the lower Miocene levels of the Iberian Peninsula.

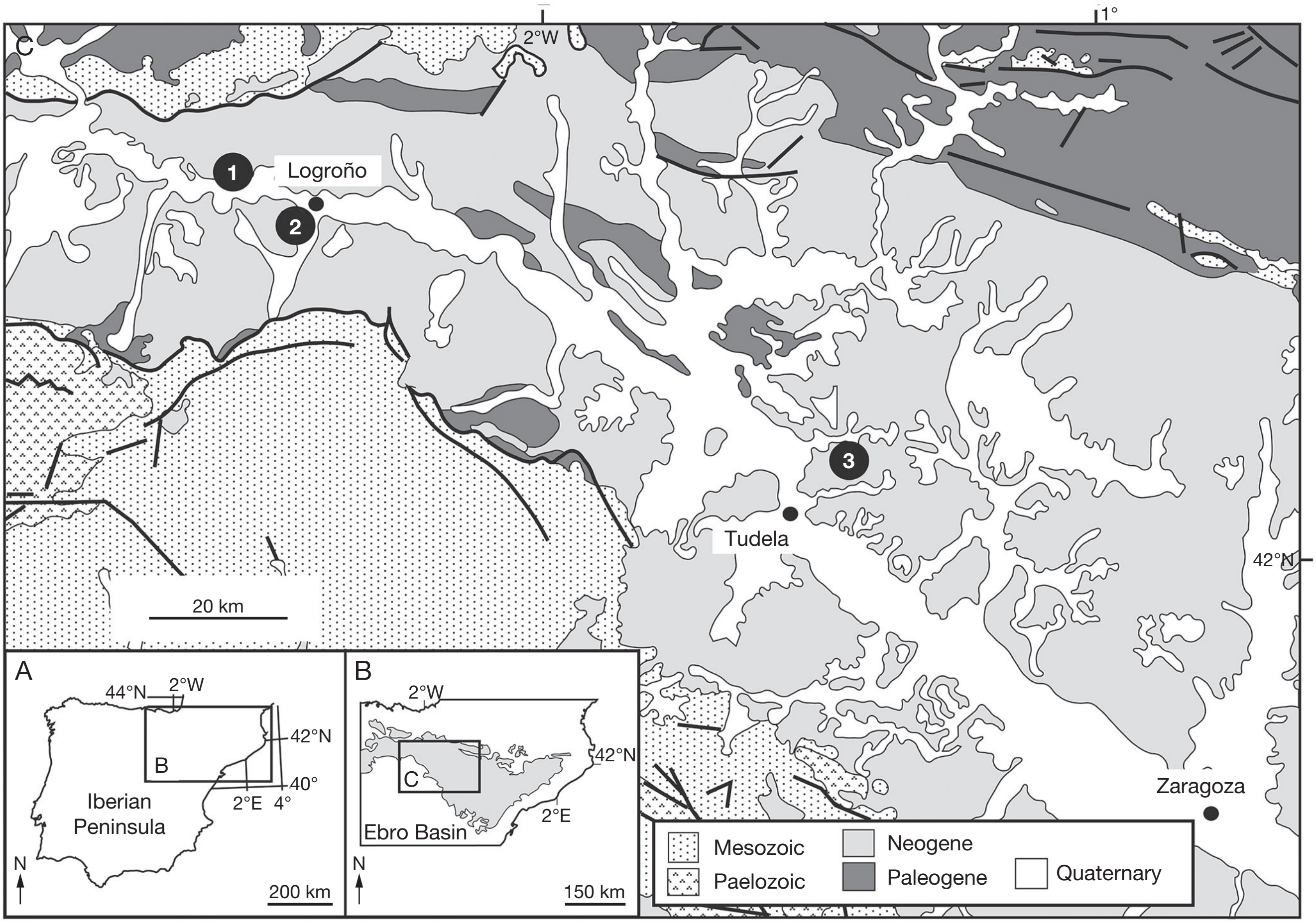


Fig. 1. — Geographic and geological position of the fossil areas from which the remains of turtles studied in this paper come. **1**, Fuenmayor (La Rioja); **2**, Monte Pila (La Rioja); **3**, the Bardenas Reales of Navarre (Navarre). All of them are located in the Spanish Ebro Basin.

Institutional and collection abbreviations

BT	Barranco de Tudela, the Bardenas Reales of Navarre collection, deposited in Dirección General de Cultura del Gobierno de Navarra, Navarra, Spain;
FM	Fuenmayor collection, deposited in the Centro Paleontológico de Enciso, La Rioja, Spain;
MCNA	Museo de Ciencias Naturales de Alava, Vitoria-Gasteiz, Spain;
MP	Monte Pila collection, deposited in the Centro Paleontológico de Enciso, La Rioja, Spain;
N	Nasa, the Bardenas Reales of Navarre collection, deposited in Dirección General de Cultura del Gobierno de Navarra, Navarra, Spain;
RB	Rincón del Bu, the Bardenas Reales of Navarre collection, deposited in Dirección General de Cultura del Gobierno de Navarra, Navarra, Spain.

GEOGRAPHIC AND GEOLOGICAL SETTING

The Ebro Basin is a triangular sedimentary basin in Spain, infilled with continental deposits, and connected to the Duero Basin in its westernmost margin (Fig. 1). The Ebro Basin was formed during the Cenozoic at the foreland of the Pyrenees, the Iberian Ranges and the Catalan Coastal Ranges fold-and-thrust belts (Muñoz *et al.* 2002; Pardo *et al.* 2004). During most of the upper Eocene and the late Miocene, the Ebro Basin was an endorheic depression (Urgeles *et al.* 2011; García-Castellanos & Larrasoaña 2015). The western part of the Ebro Basin comprises a sequence of up to 5500 metres of late Eocene, Oligocene and Miocene continental sedimentary deposits (Muñoz-Jiménez & Casas-Sainz 1997). The marginal fringes of the Basin are composed of thick conglomeratic sequences related to proximal alluvial systems. Toward the centre of the Basin, thick coarse formations grade into channelized sandstones and mudstones related to the floodplains of a distal alluvial and fluvial environment (Muñoz *et al.* 2002; Larrasoaña et al 2006). In the central sector, carbonate or shallow saline lakes were present, surrounded by palustrine areas related to the fluvial systems from the Pyrenees and the Iberian Ranges (Muñoz *et al.* 2002).

The fossil areas from which the turtle specimens studied in this paper come were formed in distal areas of these alluvial systems, where low energy materials, such as mudstones, marls, limestones and gypsum accumulations, were deposited with intercalations of sandstone-filled channels. All the deposits in the area of the Bardenas Reales of Navarre are located in the Tudela Formation, whereas the Monte Pila and Fuenmayor deposits occur in the transitional facies between the Najera and Haro formations.

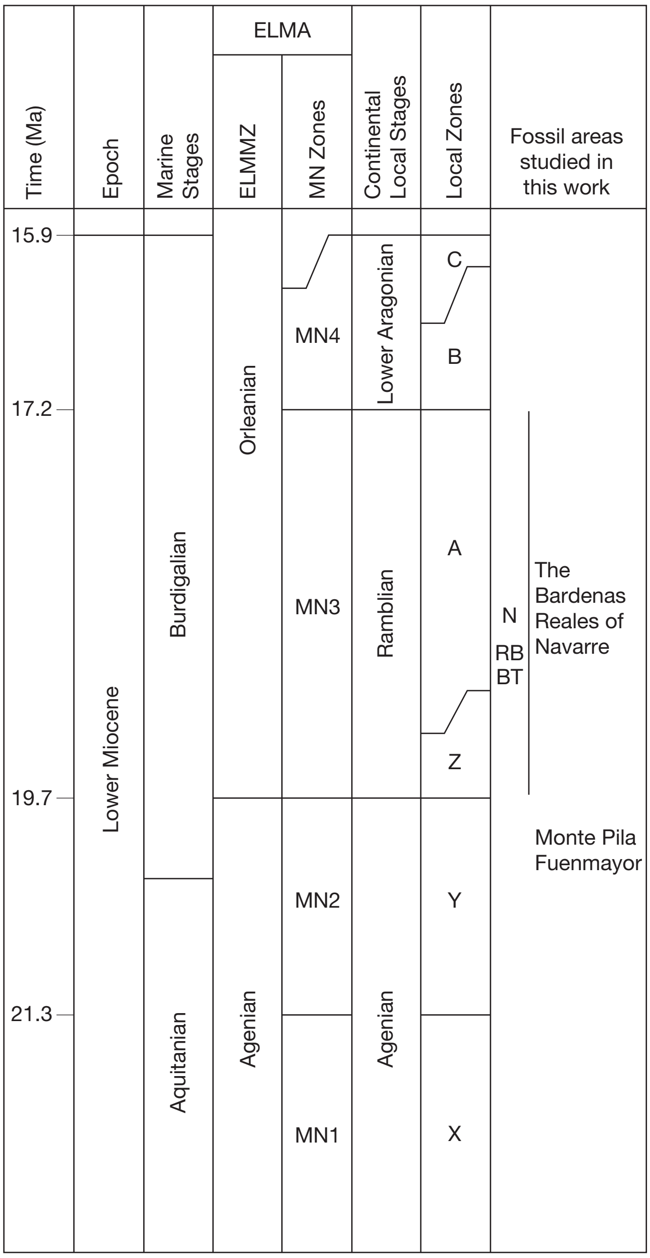


Fig. 2. — Biostratigraphic diagram with the fossil areas studied in this paper situated in a stratigraphical table. The three outcrops indicated in the Bardenas Reales of Navarre correspond to Barranco de Tudela (**BT**), Nasa (**N**) and Rincón del Bu (**RB**). The chronological data are based on Larrasoaña *et al.* (2006) and Suarez-Hernando (2017).

The fossil locality called Fuenmayor is located near the homonymous town, in La Rioja (Fig. 1). Its faunal content was described by Martínez-Salanova (1987), who not only studied several taxa of micromammals, but also recognized the presence of macrovertebrates, including remains of indeterminate turtles. Based on its stratigraphic position and on its microfaunal content, this site was positioned within the local biozone Y (Fig. 2). The outcrop was destroyed by industrial activity in the quarry. The partial shell presented here comes from a marl level located about 200 metres from the original site, at the same level (FM2). The other isolated turtle remains from this fossiliferous region were found in a position closer to that of the original outcrop, but at a slightly lower level, also belonging to the local zone Y (FM1).

The outcrops of Monte Pila are located in the municipality of Lardero, a few kilometres from Logroño (Fig. 1). In this section, three marl levels with vertebrate remains were identified (Hernández *et al.* 2003). The lower level was called MP1, the intermediate MP2 and the highest MP3. The excavations in MP1 and MP2 were carried out between the years 2000 and 2010. The macrovertebrate remains from MP3 were collected by surface prospecting. Sediment from the three levels was collected, washed and sieved. The fauna associated with the MP1 level was at first located in the local zone Z (Hernández *et al.* 2003). However, subsequent investigations at this site and the field work carried out during the following years allowed the identification of a molar of the genus *Ritteneria* between the microvertebrates from MP3. Therefore, this level is identified as placed in the local zone Y. The levels MP1 and MP2, which are below, are also recognized as located in the same local zone. Comparing the microfaunas of Fuenmayor and Monte Pila, the first one is identified as slightly older (Fig. 2).

The Bardenas Reales of Navarre is located about 10 km from the town of Tudela (Navarra; Fig. 1). The oldest locality with remains of turtles in this area is Cabezo de la Junta (local zone Z, MN3) (Murelaga 2000), and the younger is Pico del Fraile 1 (local zone A, MN3) (Suarez-Hernando 2017). Therefore, the deposits with fossil turtles of the Bardenas Reales of Navarre are more modern than those of both Fuenmayor and Monte Pila (Fig. 2).

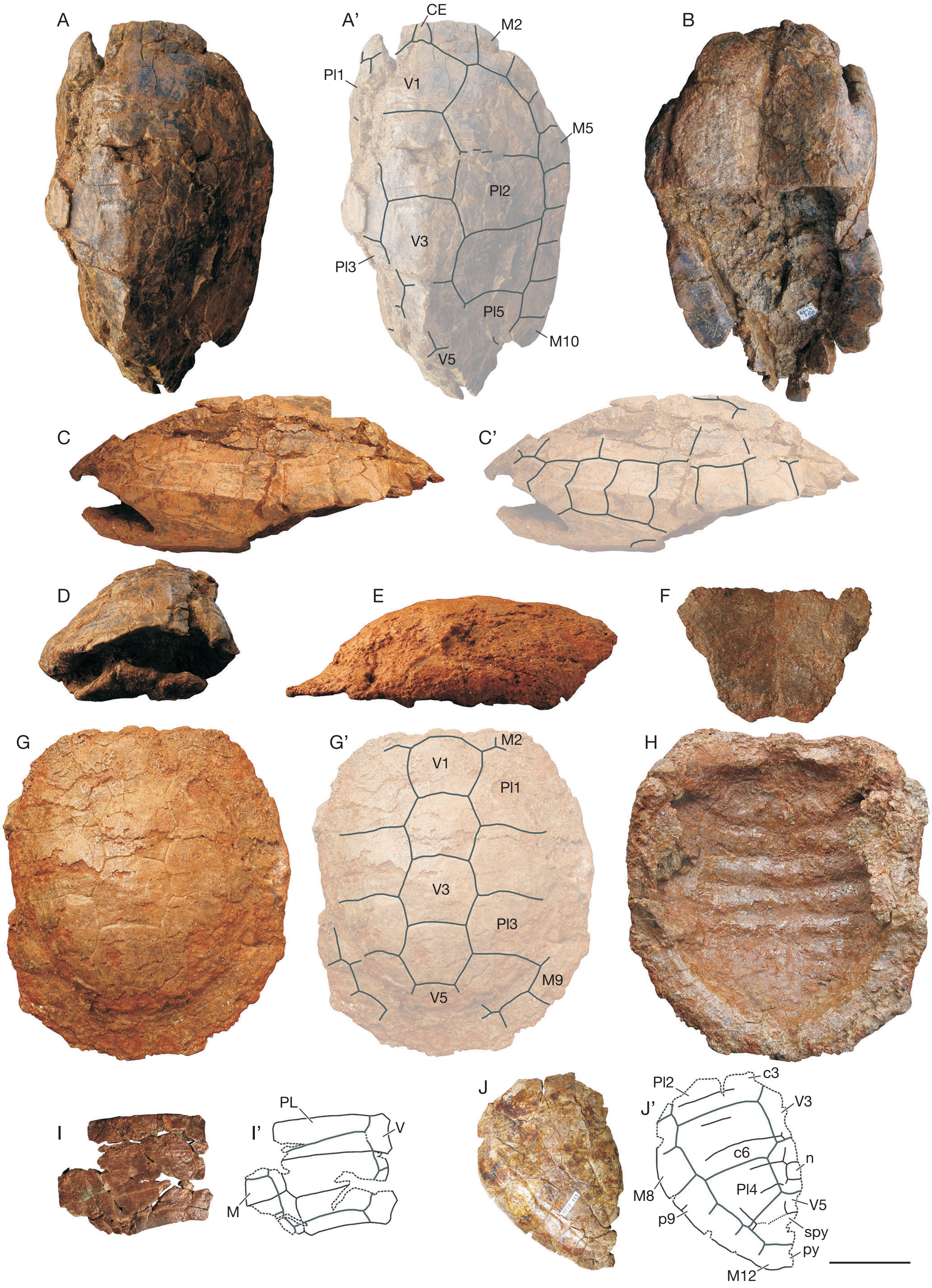
SYSTEMATIC PALAEONTOLOGY: THE MONTE PILA AND FUENMAYOR TURTLE REMAINS

Suborder CRYPTODIRA Cope, 1868
Superfamily TESTUDINOIDEA Batsch, 1788
Family GEOEMYDIDAE Theobald, 1868
Subfamily PTYCHOGASTERINAE De Stefano, 1903
Genus *Ptychogaster* Pomel, 1847
Subgenus *Ptychogaster* (*Temnoclemmys*) Bergounioux, 1958

Ptychogaster **(*Temnoclemmys*)** cf. ***bardenensis***
Murelaga, Lapparent de Broin,
Pereda Suberbiola & Astibia, 1999 (Figs 3-10)

MATERIAL EXAMINED. — Numerous disjointed and isolated plates, several partial carapace and plastra, and some relatively complete

Fig. 3. — Partial shells and carapaces of several individuals of freshwater Ptychogasterinae *Ptychogaster* (*Temnoclemmys*) cf. *bardenensis* Murelaga, Lapparent de Broin, Pereda Suberbiola & Astibia, 1999, from the lower Miocene (MN2) of Monte Pila 1 (Lardero, La Rioja, Spain): **A**-**D**, carapace and articulated anterior half of the plastron, MP1a-169, in dorsal (**A**), ventral (**B**), left lateral (**C**) and anterior (**D**) views; **E**-**H**, carapace and disjointed posterior half of the plastron, MP1a-643; **E**, **G**-**H**, carapace, in right lateral (**E**), dorsal (**G**) and ventral (**H**) views; **F**, posterior half of the plastron, in ventral view; **I**, partial carapace, MP1a-1070, in dorsal view; **J**, partial carapace, MP1b-415, in dorsal view. Abbreviations for the plates (in lower case and normal type): **c**, costal; **n**, neural; **p**, peripheral; **py**, pygal; **spy**, suprapygal. Abbreviations for the scutes (in upper case and in bold type): **CE**, cervical; **M**, marginal; **PL**, pleural; **V**, vertebral. Scale bar: 5 cm.


A
A'
CE
M2
Pl1
V1
M5
Pl2
V3
Pl3
Pl5
M10
V5
B
C
C'
D
E
F
G
G'
M2
V1
Pl1
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M9
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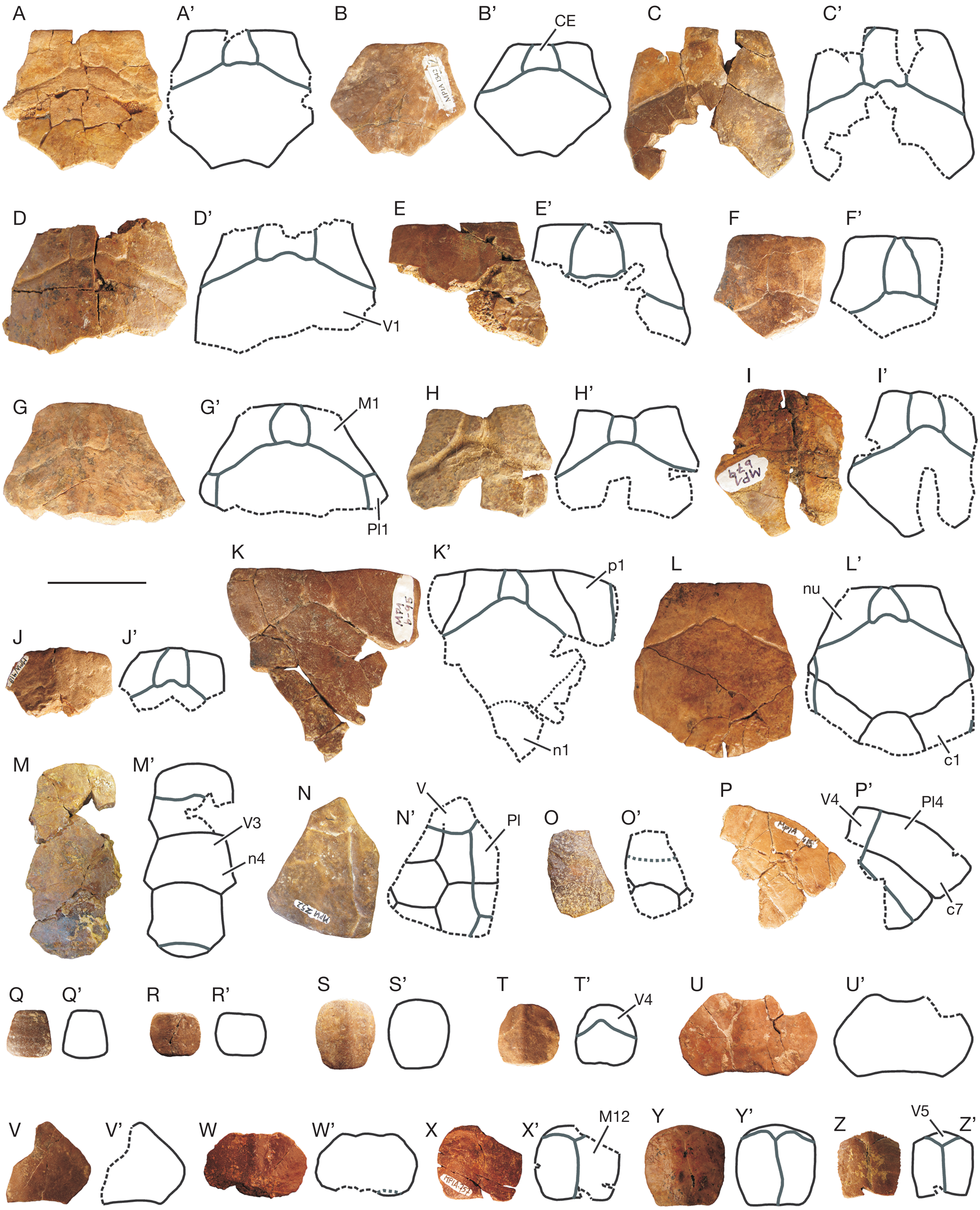

Fig. 4. — Elements of the carapace of several individuals of freshwater Ptychogasterinae *Ptychogaster* (*Temnoclemmys*) cf. *bardenensis* Murelaga, Lapparent de Broin, Pereda Suberbiola & Astibia, 1999, from the lower Miocene (MN2) of Monte Pila 1 (Lardero, La Rioja, Spain): **A**-**L**, nuchals and adjacent plates, in dorsal view; **A**, MP1a-1570; **B**, MP1a-1342; **C**, MP1a-1364; **D**, MP1a-638; **E**, MP1a-528; **F**, MP1a-228; **G**, MP1a-475; **H**, MP1a-341; **I**, MP1a-679; **J**, MP1a-918; **K**, MP1b-95; **L**, MP1a-14; **M**-**O**, neurals and adjacent plates, in dorsal view; **M**, MP1b-556; **N**, MP1a-252; **O**, MP1a-707; **P**, two articulated costals, MP1a-48, in dorsal view; **Q**-**W**, suprapygals, in dorsal view; **Q**, MP1a-1305; **R**, MP1a-1221; **S**, MP1b-369; **T**, MP1a-1066; **U**, MP1a-1350; **V**, MP1a-511; **W**, MP1a-911; **X**-**Z**, pygals, in dorsal view; **X**, MP1a-757; **Y**, MP1a-6; **Z**, MP1a-879. Abbreviations for the plates (in lower case): **c**, costal; **n**, neural; **nu**, nuchal. Abbreviations for the scutes (in upper case): **CE**, cervical; **M**, marginal; **PL**, pleural; **V**, vertebral. Scale bar: 3 cm.

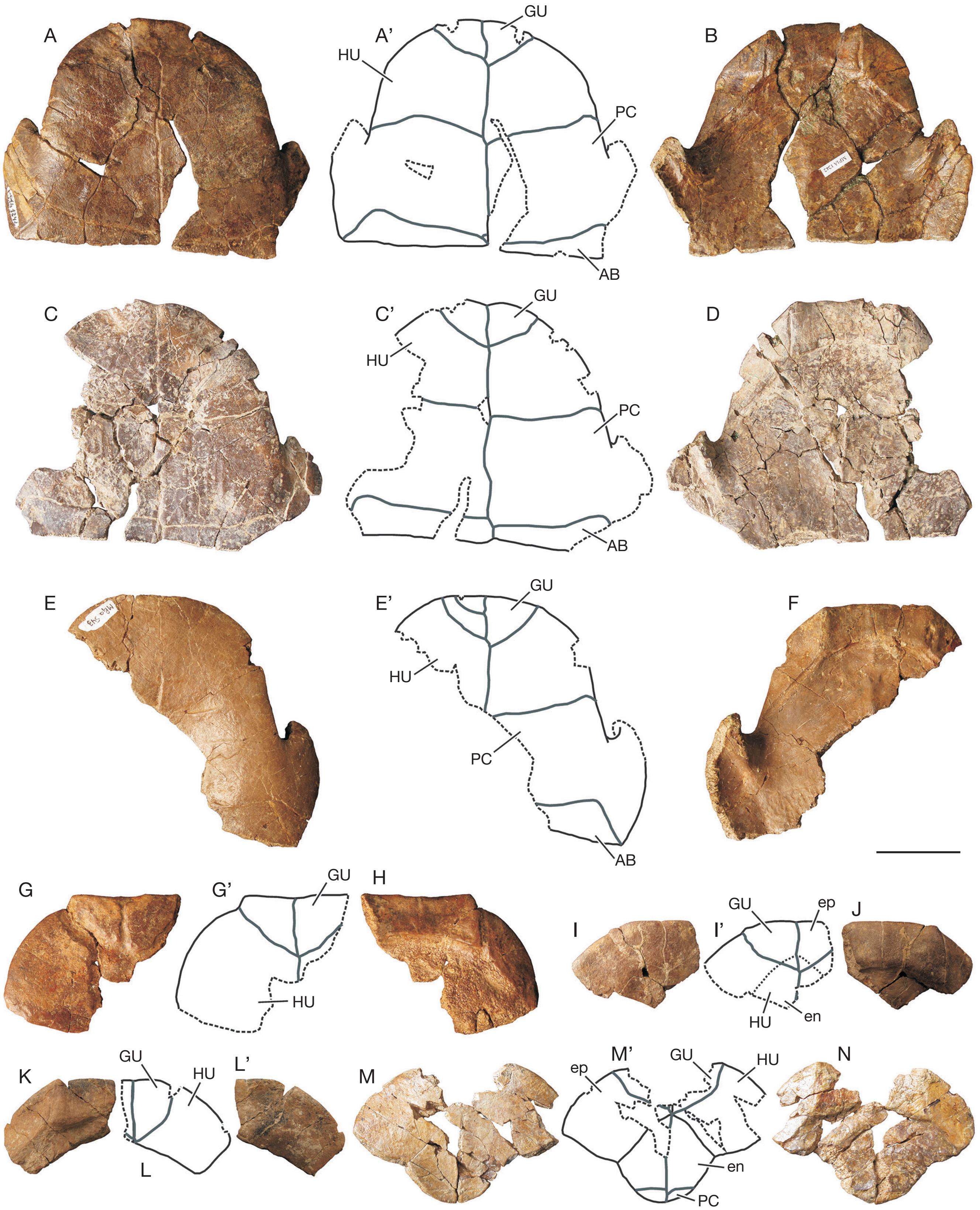

Fig. 5. — Articulated elements of the anterior plastral lobe of several individuals of freshwater Ptychogasterinae *Ptychogaster* (*Temnoclemmys*) cf. *bardenensis* Murelaga, Lapparent de Broin, Pereda Suberbiola & Astibia, 1999, from the lower Miocene (MN2) of Monte Pila 1 (Lardero, La Rioja, Spain): **A**, **B**, MP1a-1242; **C**, **D**, MP1a-1422; **E**, **F**, MP1a-543; **G**, **H**, MP1a-277a; **I**, **J**, MP1a-1594; **K**, **L**, MP1a-1417; **M**, **N**, MP1a-1724. All of them are in dorsal and ventral views. Abbreviations for the plates (in lower case): **en**, entoplastron; **ep**, epiplastron. Abbreviations for the scutes (in upper case): **AB**, abdominal; **GU**, gular; **HU**, humeral; **PC**, pectoral. Scale bar: 3 cm.

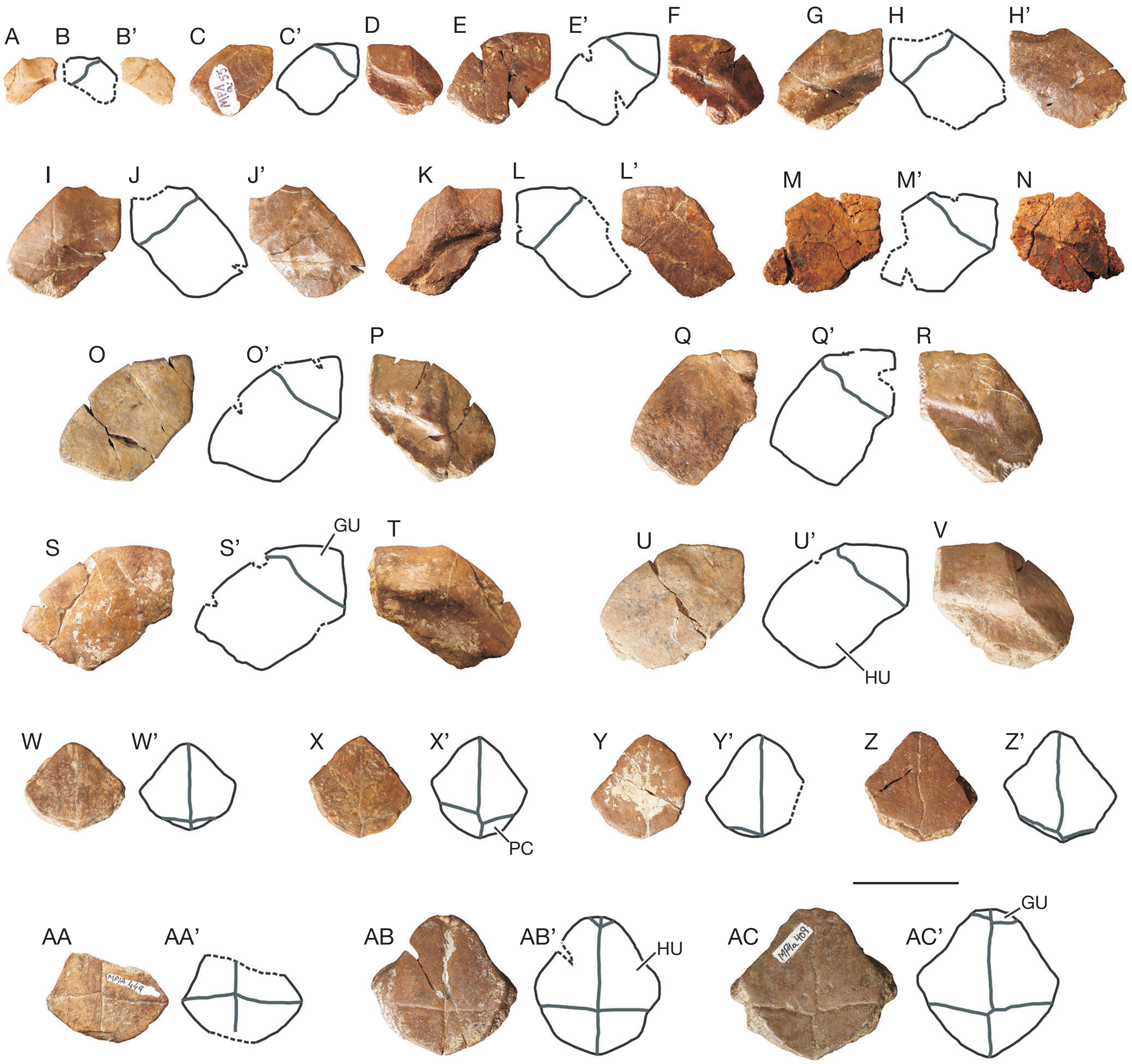

FIG. 6. — Plastral plates of several individuals of freshwater Ptychogasterinae *Ptychogaster* (*Temnoclemmys*) cf. *bardenensis* Murelaga, Lapparent de Broin, Pereda Suberbiola & Astibia, 1999, from the lower Miocene (MN2) of Monte Pila 1 (Lardero, La Rioja, Spain): **A**-**V**, epiplastra, in dorsal and ventral views; **A**, **B**, MP1b-sup1-a; **C**, **D**, MP1a-55; **E**, **F**, MP1a-1210a; **G**, **H**, MP1a-975a; **I**, **J**, MP1a-1145a; **K**, **L**, MP1a-1745; **M**, **N**, MP1b-481; **O**, **P**, MP1a-1679b; **Q**, **R**, MP1a-1189a; **S**, **T**, MP1a-1557; **U**, **V**, MP1a-529b; **W**-**AC**, entoplastral, in ventral view; **W**, MP1a-1394b; **X**, MP1b-1597a; **Y**, MP1a-347a; **Z**, MP1a-672; **AA**, MP1a-449; **AB**, MP1a-180a; **AC**, MP1a-409. Abbreviations for the scutes (in upper case): **GU**, gular; **HU**, humeral; **PC**, pectoral. Scale bar: 3 cm.

shells from Monte Pila (e.g., MP1a-6, MP1a-14, MP1a-48, MP1a-55, MP1a-56, MP1a-81, MP1a-109, MP1a-169, MP1a-180a, MP1a-228, MP1a-252, MP1a-263, MP1a-277a, MP1a-281, MP1a-341, MP1a-347a, MP1a-367, MP1b-369, MP1b-380b, MP1a-385, MP1a-409, MP1a-449, MP1a-474, MP1a-475, MP1a-511, MP1a-528, MP1a-529b, MP1a-543, MP1a-638, MP1a-643, MP1a-659, MP1a-672, MP1a-679, MP1a-681, MP1a-694, MP1a-707, MP1a-757, MP1a-865, MP1a-879, MP1a-911, MP1a-918, MP1a-975a, MP1a-1025, MP1a-1066, MP1a-1068b, MP1a-1070, MP1a-1145a, MP1a-1189a, MP1a-1194, MP1a-1210a, MP1a-1221, MP1a-1227, MP1a-1242, MP1a-1305, MP1a-1333, MP1a-1342, MP1a-1345, MP1a-1350, MP1a-1364, MP1a-1394b, MP1a-1417, MP1a-1421, MP1a-1422, MP1a-1423, MP1a-1557, MP1a-1570, MP1a-1594, MP1a-1679b, MP1a-1724, MP1a-1745, MP1b-95, MP1b-169, MP1b-415, MP1b-456, MP1b-467, MP1b-481, MP1b-556, MP1b-585, MP1b-1597a, MP1b-sup1-a, MP2-93, MP2-175, MP2-306, MP2-307, MP2-308, MP3-1; Figs 3-9) and Fuenmayor (e.g., FM1-1, FM1-2, FM1-3, FM1-4, FM2-1, MCNA 16032, MCNA 16031; Fig. 10).

LOCALITY AND HORIZON. — Most specimens come from the Monte Pila sites, municipality of Lardero, Autonomous Community of La Rioja, Spain. Levels MP1, MP2 and MP3 (Figs 3-9). Other specimens came from the site of Fuenmayor, municipality of Fuenmayor, Autonomous Community of La Rioja, Spain (Fig. 10). Western part of the Ebro Basin. Transitional facies between the Najera and Haro formations. Local zone Y, biozone MN2, lower Miocene (see Figs 1, 2 and the section Geographic and geological setting).

Fig. 7. — Plastral plates of several individuals of freshwater Ptychogasterinae *Ptychogaster* (*Temnoclemmys*) cf. *bardenensis* Murelaga, Lapparent de Broin, Pereda Suberbiola & Astibia, 1999, from the lower Miocene (MN2) of Monte Pila 1 (Lardero, La Rioja, Spain): **A**-**I**, hyoplastra, in ventral view; **A**, MP1a-694; **B**, MP1a-385; **C**, MP1a-1333; **D**, MP1a-1025; **E**, MP1a-281; **F**, MP1a-1227; **G**, MP1b-585; **H**, MP1a-109; **I**, MP1b-169; **J**-**M**, hypoplastra, in ventral view; **J**, MP1b-467; **K**, MP1a-1194; **L**, MP1b-456; **M**, MP1a-367; **N**-**U**, xiphiplastra, in ventral view; **N**, MP1a-865; **O**, MP1a-56; **P**, MP1a-659; **Q**, MP1a-681; **R**, MP1a-474; **S**, MP1b-380b; **T**, MP1a-81; **U**, MP1a-263. Abbreviations for the scutes (in upper case): **AB**, abdominal; **AN**, anal; **FE**, femoral; **HU**, humeral; **PC**, pectoral. Scale bar: 3 cm.

DESCRIPTION

The maximum length of the shells of the larger specimens of the freshwater turtles identified at both Monte Pila and Fuenmayor is close to 20 cm (Figs 3-10). However, elements corresponding to individuals of very varied sizes are identified, some of them with a length of less than half that of the largest specimens. Some of the most complete shells, as well as the articulated elements of other specimens recognized as adult individuals due

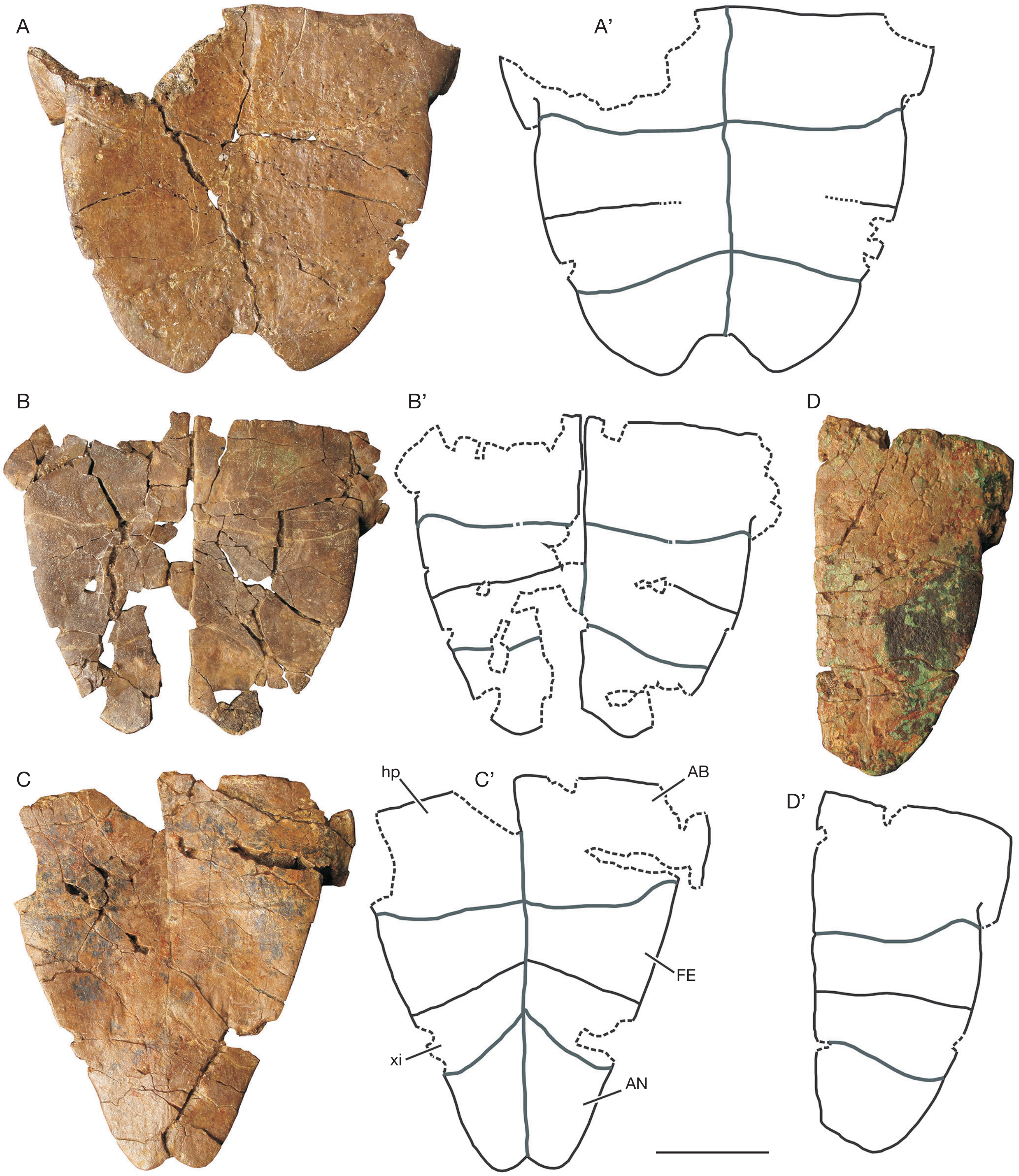

Fig. 8. — Articulated elements of the posterior plastral lobe of several individuals of freshwater Ptychogasterinae *Ptychogaster* (*Temnoclemmys*) cf. *bardenensis* Murelaga, Lapparent de Broin, Pereda Suberbiola & Astibia, 1999, from the lower Miocene (MN2) of Monte Pila 1 (Lardero, La Rioja, Spain). All of them are in ventral view: **A**, MP1a-1345; **B**, MP1a-1068b; **C**, MP1a-1423; **D**, MP1a-1421. Abbreviations for the plates (in lower case): **hp**, hypoplastron; **xi**, xiphiplastron. Abbreviations for the scutes (in upper case): **AB**, abdominal; **AN**, anal; **FE**, femoral. Scale bar: 3 cm.

to their size, show fusion of many of their sutures, so that the margins of each plate cannot be recognized in them (Figs 3; 5). The thickness of the plates is greater in the larger individuals. Although the width/length ratio of the shell is variable, this form shows a relatively wide carapace, being recognized as slightly longer than wide in some cases (Fig. 3G). The carapaces are low.

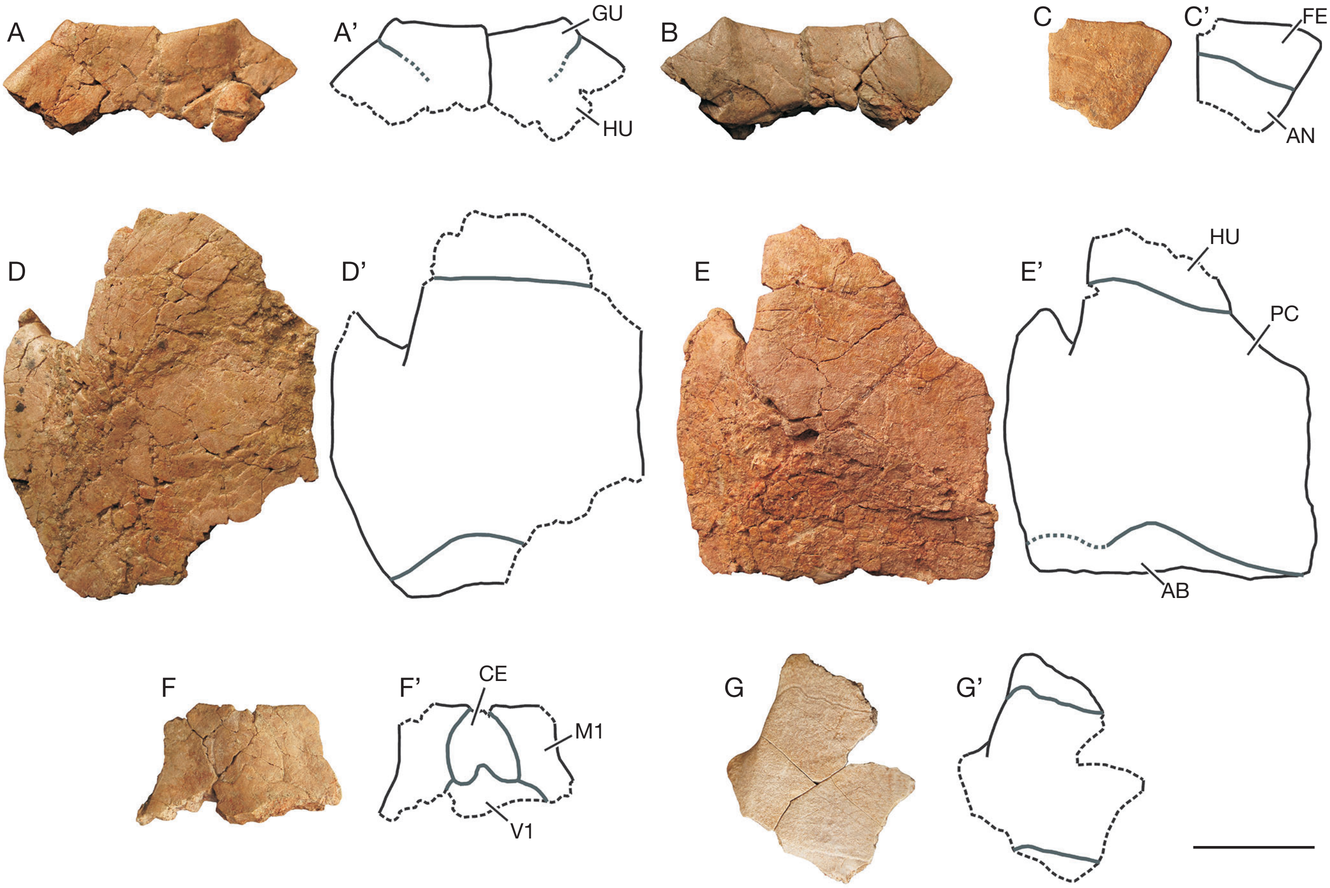

Fig. 9. — Plates of several individuals of freshwater Ptychogasterinae *Ptychogaster* (*Temnoclemmys*) cf. *bardenensis* Murelaga, Lapparent de Broin, Pereda Suberbiola & Astibia, 1999, from the lower Miocene (MN2) of Monte Pila 2 (**A**-**F**) and Monte Pila 3 (**G**) (Lardero, La Rioja, Spain): **A**, **B**, articulated epiplastra, MP2-306, in ventral (**A**) and dorsal (**B**) views; **C**, xiphiplastron, MP2-93, in ventral view; **D**, hyoplastra, MP2-308, in ventral view; **E**, hyoplastra, MP2-175, in ventral view; **F**, nuchal, MP2-307, in dorsal view; **G**, hyoplastra, MP3-1, in ventral view. Abbreviations for the scutes (in upper case): **AB**, abdominal; **AN**, anal; **CE**, cervical; **FE**, femoral; **GU**, gular; **HU**, humeral; **M**, marginal; **PC**, pectoral. Scale bar: 3 cm.

The abundance of specimens allows assessment of the variability in morphology and dimensions of several elements. For example, the relatively wide nuchal plates are almost as long as wide in some individuals, but slightly wider than long in others (Fig. 4A-L). All of them show a thickening in the visceral region. The neural series anteriorly contacts the nuchal plate, and posteriorly the suprapygals. The neurals are wide in relation to their length (Fig. 4M-O; 10C, D). The morphology of these plates is variable. However, most of them are hexagonal, with the shortest margins being postero-laterally located. Although the anterior suprapygal is subquadrangular, the posterior is hexagonal, noticeably wider than long (Fig. 4Q-W). The pygal is also subquadrangular (Fig. 4X-Z).

This taxon has a single cervical scute (Figs 3A; 4A-L; 9F). Its lateral margins are subrounded. Its width/length ratio shows a wide range of variability, being slightly wider than long in some specimens, but almost twice as long as wide in others. The overlap of the cervical on the visceral surface of the nuchal is relatively long. The vertebral scutes are hexagonal, almost as wide as they are long (Fig. 3A-G). The first and last ones are slightly wider than the second to fourth vertebrals, which are all similar in width. However, the vertebral series is narrow, the first scute being narrower than the nuchal in many cases, not overlapping the postero-lateral margins of this plate. The fifth vertebral overlaps the anterior region of the pygal plate (Fig. 4X-Z).

The contact between the hyoplastra and the hypoplastra, and that between the hypoplastra and the peripheral series, corresponds to a ligamentous junction, so that a hinge is developed between these plates, allowing mobility of the posterior plastral region (Figs 3F; 5A-F; 7B-M; 8; 9D-E; 10A, B). The lateral margins of both plastral lobes are subrounded. The anterior lobe is very wide. Its anterior margin varies from subrounded to almost straight. Although the posterior lobe is clearly expanded in some specimens, it is much narrower in others. Thus, the development of the anal notch is variable in width and length, as is the shape of its margins (Figs 3F; 7N-U; 8; 10A, B). The epiplastral lip is concave (Figs 5; 6A-V; 9A, B; 10A, B, G-L). Both the length and the thickness of this lip are observed to be highly variable. The dorsal thickening of this lip shows a pair of anterior processes, which exceed the margin of the anterior plastral lobe, at the level of the contacts between the gulars and the humerals.

The gular scutes overlap the anterior region of the entoplastron in some specimens, but not in others (Fig. 6W-AC). In the same way, the humero-pectoral sulci may be located next

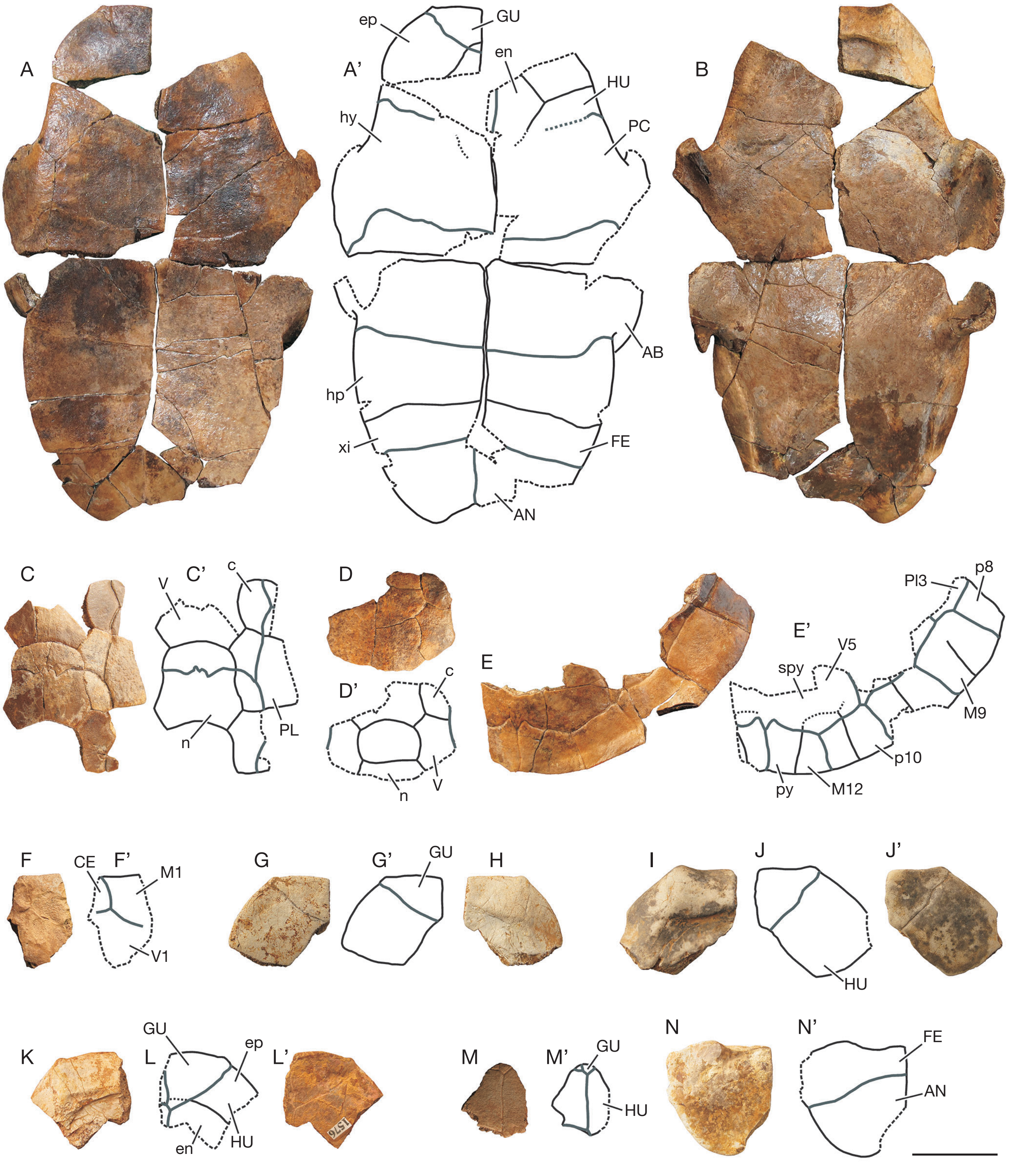

Fig. 10. — Elements of the shell of several individuals of freshwater Ptychogasterinae *Ptychogaster* (*Temnoclemmys*) cf. *bardenensis* Murelaga, Lapparent de Broin, Pereda Suberbiola & Astibia, 1999, from the lower Miocene (MN2) of Fuenmayor (La Rioja, Spain): **A**-**E**, selection of plates of the individual FM2-1; **A**, **B**, almost complete plastron, in ventral (**A**) and dorsal (**B**) views; **C**, **D**, neurals and proximal region of several adjacent costals, in dorsal view; **E**, posterior and right postero-lateral margin of the carapace, in dorsal view; **F**-**N**, disjointed and isolated plates of several individuals; **F**, partial nuchal, MCNA 16032, in dorsal view; **G**-**H**, epiplastron, FM1-2, in ventral (**G**) and dorsal (**H**) views; **I**, **J**, epiplastron, FM1-3, in dorsal (**I**) and ventral (**J**) views; **K**-**L**, anterior area of an anterior plastral lobe, FM1-4, in dorsal (**K**) and ventral (**L**) views; **M**, entoplastron, MCNA 16031, in ventral view; **N**, xiphiplastron, FM1-1, in ventral view. Abbreviations for the plates (in lower case): **c**, costal; **en**, entoplastron; **ep**, epiplastron; **hp**, hypoplastron; **hy**, hyoplastron; **n**, neural; **nu**, nuchal; **p**, peripheral; **py**, pygal; **spy**, suprapygal; **xi**, xiphiplastron. Abbreviations for the scutes (in upper case): **AB**, abdominal; **AN**, anal; **CE**, cervical; **FE**, femoral; **GU**, gular; **HU**, humeral; **M**, marginal; **PC**, pectoral; **PL**, pleural; **V**, vertebral. Scale bar: 3 cm.

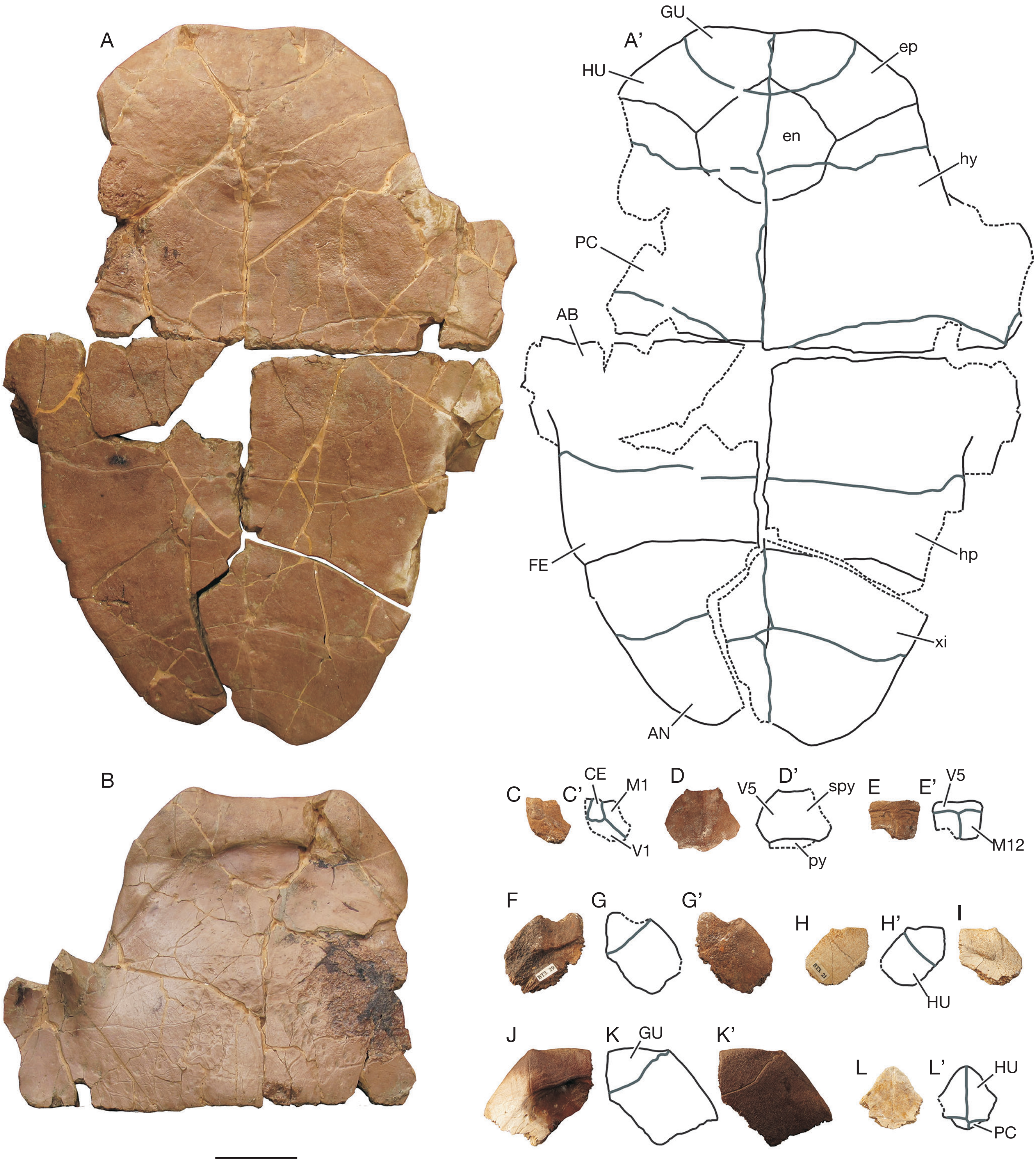

Fig. 11. — Elements of the shell of several individuals of the freshwater clade of turtles Ptychogasterinae, from the lower Miocene (MN3) of the Bardenas Reales of Navarre (Navarre, Spain): **A**, **B**, plastron of the shell of *Ptychogaster* sp. N5-28, in ventral (**A**) and dorsal (**B**) views; **C**-**L**, isolated elements of *Ptychogaster* (*Temnoclemmys*) *bardenensis* Murelaga, Lapparent de Broin, Pereda Suberbiola & Astibia, 1999, including the holotype (**H**, **I**), and several paratypes (**C**-**E**, **L**); **C**, partial nuchal, BT3-90, in dorsal view; **D**, suprapygal and articulated anterior region of the pygal, RB1-37, in dorsal view; **E**, pygal, RB1-20, in dorsal view; **F**, **G**, epiplastron, BT3-29, in dorsal (**F**) and ventral (**G**) views; **H**-**I**, epiplastron, BT3-21, in ventral (**H**) and dorsal (**I**) views; **J**, **K**, epiplastron, N2-125, in dorsal (**J**) and ventral (**K**) views; **L**, entoplastron, N1-63, in ventral view. Abbreviations for the plates (in lower case): **en**, entoplastron; **ep**, epiplastron; **hp**, hypoplastron; **hy**, hyoplastron; **py**, pygal; **spy**, suprapygal; **xi**, xiphiplastron. Abbreviations for the scutes (in upper case): **AB**, abdominal; **AN**, anal; **CE**, cervical; **FE**, femoral; **GU**, gular; **HU**, humeral; **PC**, pectoral; **V**, vertebral. Scale bar: 3 cm.

to the posterior margin of the entoplastron in some specimens, but overlap this plate in others, ranging from a very short overlap of the pectorals on the entoplastron in some individuals, to a relatively long overlap, greater than a quarter of the length of this plate, in others. The abdominal scutes overlap the posterior region of the hyoplastra (Figs 5A-F; 7B-I; 9D-E;

10A). The anal scutes are restricted to the xiphiplastra, their anterior margin being well away from the suture between those plates and the hypoplastra (Figs 7N-U; 8; 9C; 10A, N).

Family TESTUDINIDAE Batsch, 1788
Subfamily TESTUDININAE Batsch, 1788
Genus *Titanochelon* Pérez-García & Vlachos, 2014

Titanochelon cf. ***bolivari*** (Hernández-Pacheco, 1917)
(Fig. 12)

MATERIAL EXAMIED. — Several generally disjointed and isolated remains, most of them corresponding to plates (e.g., MP1b-418, MP2-39, MP2-79, MP2-309, MP2-313, MP2-2018), but with some appendicular remains (e.g., MP2-81-1, MP2-81-5, MP2-81-3, MP2-81-4) also being recognized (Fig. 12).

LOCALITY AND HORIZON. — Monte Pila, municipality of Lardero, Autonomous Community of La Rioja, Spain. Levels MP1 and MP2. Western part of the Ebro Basin. Transitional facies between the Najera and Haro formations. Local zone Y, biozone MN2, lower Miocene (see Figs 1, 2 and the section Geographic and geological setting).

DESCRIPTION

A selection of the best preserved and most informative remains is presented in Fig. 12. This taxon had a shell size of the adult individuals greater than one metre in length. The outer surface of the plates, both of the carapace elements and of those of the plastron, is granular. The carapace is interpreted as relatively low. Several costal plates are recognized. The medial margins of the costal plates indicates that this taxon showed an alternation of rectangular plates with non-rectangular ones, at least some of them probably being octagonal (Fig. 12A-C). At least some of the neurals are wider than long (Fig. 12D). The length of the first costal is interpreted as almost half of its width. Some costals were longer medially than laterally, but this condition was the reverse in others. The proximal region of the dorsal ribs was reduced. The vertebral scutes are interpreted as narrow, since they show a relatively short overlap on the costals. The sulci between the pleural and the marginal scutes were located on the contact area between the costal and the peripheral plates, which corresponded to well-developed sutures. This taxon lacked pointed tips in the region of contact of the sulci between two adjacent marginals with the lateral borders of the peripherals.

The entoplastron was noticeably wider than long (Fig. 12E). Due to its preservation, boundaries between scutes are not recognized on its ventral surface. The preserved postero-lateral area of a xiphiplastron, interpreted as belonging to a male considering the morphology of this plate in the genus *Titanochelon*, allows the identification of a well-developed ventral thickening posterior to the femoro-anal sulcus (Fig. 12F). That region shows a lateral protuberance. Ahead of this, the lateral margin of the xiphiplastron is almost straight. In fact, the posterior plastral lobe is trapezoidal, lacking a well-developed anal notch.

Several appendicular elements are recognized, including a fragment of the diaphysis of a robust femur, some elements of the carpal complex, and several phalanges. A medial fused with a lateral centrale is identified among the elements of the carpal complex (Fig. 12G-J). Among the preserved phalanges, several distal ones are recognized (Fig. 12K-S).

DISCUSSION

IDENTIFICATION OF THE FRESHWATER GENUS *PTYCHOGASTER* IN MONTE PILA AND FUENMAYOR

The most common turtle taxon at Monte Pila (abundant in MP1, but also recorded in MP2 and MP3; Figs 3-9) can be attributed to the freshwater lineage Ptychogasterinae considering the presence of characters such as, among others: irregular neural series, the shortest margins of some hexagonal neurals being postero-laterally located; thickened visceral surface of the nuchal; relatively narrow first vertebral scute in relation to the width of the nuchal plate, not overlapping the postero-lateral margins of this plate in some specimens; relatively long overlap of the cervical scute and the first pair of marginals on the visceral surface of the carapace; subrounded lateral margins of the plastral lobes; dorsal thickening of the moderately elongated epiplastral lips at the level of the contacts between the gulars and the humerals, generating a pair of 'ptychogasterid spikes' (*sensu* Hervet 2004); humero-pectoral sulci located next to the posterior margin of the entoplastron or on this plate (Lapparent de Broin 2000; Murelaga *et al.* 2002; Hervet 2004).

Ptychogasterinae is a relatively diverse lineage of freshwater cryptodiran turtles recognized in the Spanish Cenozoic record (Pérez-García 2017). Although this lineage is known in other European countries since the early Eocene (Hervet 2006), the oldest Spanish finds so far known came from the lower Miocene of the Ebro Basin, but from levels slightly younger than those of Monte Pila and Fuenmayor, in the Bardenas Reales of Navarre (Murelaga *et al.* 2002; Fig. 2). Members of two genera of Ptychogasterinae have been identified in Spain: the poorly represented *Clemmydopsis* Boda, 1927, and the more abundant and diverse *Ptychogaster* (see Pérez-García 2017, and references therein).

The material from Monte Pila differs from the genus *Clemmydopsis* in several character states that, however, are shared with the members of *Ptychogaster*, such as the presence of rounded lateral margins of the cervical scute, absence of fusion between the vertebrals and the anterior pleural scutes, posterior vertebrals at least as narrow as the adjacent pleurals, and fifth vertebral reaching the anterior region of the pygal plate. In fact, the specimens from Monte Pila show an exclusive condition for the members of *Ptychogaster* that allows their attribution to this genus within Ptychogasterinae: presence of a plastral hinge between the hyoplastra and the hypoplastra, both in males and in females, with a ligamentous junction between the hypoplastra and the peripheral plates, that allowed the mobility of the posterior region of the plastron (Murelaga *et al.* 1999, 2002; Lapparent de Broin 2000; Luján *et al.* 2014).

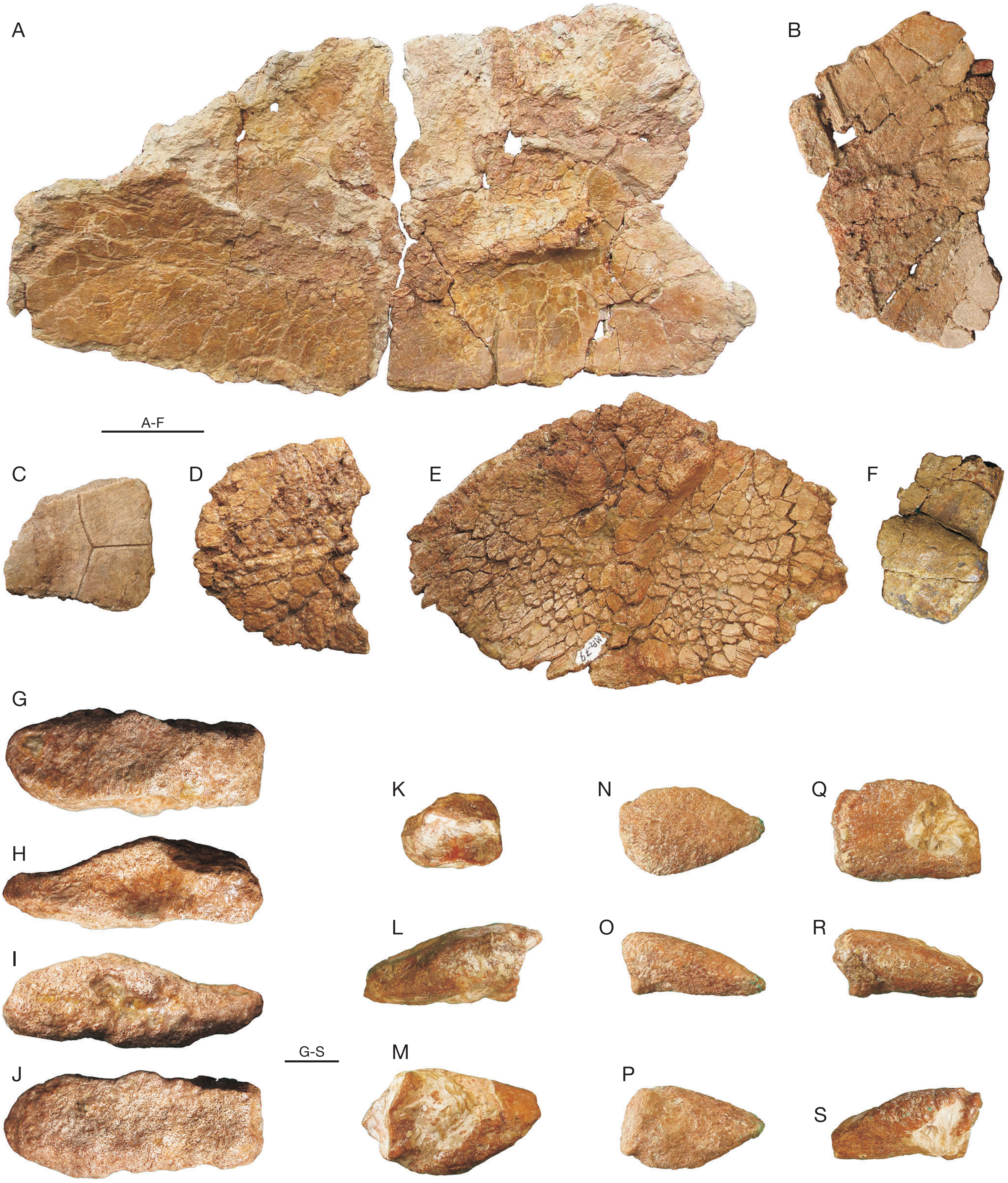

FIG. 12. — Several postcranial elements of the large tortoise *Titanochelon* cf. *bolivari* (Hernández-Pacheco, 1917) (Testudinidae), from the lower Miocene (MN2) of Monte Pila (Lardero, La Rioja, Spain): **A**, visceral view of a first right costal, MP2-313; **B**, dorsal view of the proximal region of a costal corresponding to an odd position in the costal series, MP2-309; **C**, dorsal view of the proximal region of a costal corresponding to an odd position, MP2-2018; **D**, lateral half of a third or fifth neural, MP2-39; **E**, visceral view of an entoplastron, MP2-79; **F**, ventral view of the latero-posterior region of a left xiphiplastron, MP1b-418; **G**-**J**, fused medial and lateral centrale, MP2-81-1, in proximal (**G**), anterior (**H**), posterior (**I**) and distal (**J**) views; **K**-**M**, distal phalanx, MP2-81-4, in proximal (**K**), lateral (**L**) and ventral (**M**) views; **N**-**P**, distal phalanx, MP2-81-5, in dorsal (**N**), lateral (**O**) and ventral (**P**) views; **Q**-**S**, distal phalanx, MP2-81-3, in dorsal (**Q**) and lateral (**R**, **S**) views. All of them come from the level MP2 except the partial xiphiplastron (**F**), from MP1. Scale bars: A-F, 5 cm; G-S, 1 cm.

In the Iberian record, *Ptychogaster* has been recognized as probably represented by the two subgenera that compose its lineage: *Ptychogaster* (*Ptychogaster*) and *Ptychogaster* (*Temnoclemmys*). Thus, the species *Ptychogaster* (?*Ptychogaster*) *ronheimensis*, defined in the lower Oligocene (MP 22) record of Ronheim (Germany), was tentatively recognized in younger levels, in the lower Miocene (MN3) of the Bardenas Reales of Navarre, by the partial carapace and the almost complete plastron of a single individual (Murelaga *et al.* 1999, 2002). Its attribution to that subgenus should be considered with caution, since, as Murelaga *et al.* (2002) indicated, the German species cannot be robustly attributed to it. The Spanish specimen is here referred as *Ptychogaster* sp. Fragmentary remains attributed to indeterminate members of the subgenus *Ptychogaster* have been recorded in other Spanish regions (see Pérez-García 2017, and references therein). In addition to the identification of representatives of this subgenus in Spain, members of the other subgenus, *Temnoclemmys*, are recognized in this country (see Pérez-García 2017, and references therein). In fact, its presence is also known in the Bardenas Reales of Navarre, where a new species was defined, *Ptychogaster* (*Temnoclemmys*) *bardenensis* (Murelaga *et al.* 1999). The information about this form was limited, being exclusively restricted to that provided by scarce and isolated plates, from the lower Miocene (MN3) of its type locality. A second representative of this subgenus was much better represented in the Spanish record, corresponding to the younger form *Ptychogaster* (*Temnoclemmys*) *batalleri* (Bergounioux 1931). This species was defined in the late Miocene (MN10) of the Vallès-Penedès Basin, being identified in that Basin from the uppermost middle Miocene (MN7/8), not only by abundant isolated elements, but also by several complete and partial shells (Bataller 1926; Bergounioux 1957, 1958; Luján *et al.* 2014). *Ptychogaster* (*Temnoclemmys*) *batalleri* is also recognized in the French fossil record (see Lapparent de Broin 2001).

All turtle material found so far in Fuenmayor can be attributed to Ptychogasterinae (Fig. 10), considering several of the previously indicated characters. The taxon from this locality is compatible with *Ptychogaster*, showing the above-mentioned exclusive condition for the representatives of this genus.

ON THE SYSTEMATIC POSITION OF THE *PTYCHOGASTER* REPRESENTATIVE FROM MONTE PILA AND FUENMAYOR

All freshwater turtle elements from Monte Pila are compatible with a single form, of which the plates belong to individuals of different sizes (due to different ontogenetic stages and, in the case of adult individuals, possibly to sexual dimorphism). The presence of abundant specimens (several of them shown in Figs 3-9), allows us to recognize characters subject to intraspecific variability not only related to the ontogeny or dimorphism, but also to individually variation.

The availability of characters in the collection from Monte Pila allows us to recognize the states for all the characters used in the diagnosis of the subgenus *Temnoclemmys* as opposed to those of the subgenus *Ptychogaster* (see Murelaga *et al.* 1999, 2002; Luján *et al.* 2014; and references therein). In addition, the character states in the specimens from Monte Pila can be compared in detail with those present in the Iberian specimens hitherto recognized at a specific level, that is, with the type species of the subgenus *Temnoclemmys* (i.e., *Ptychogaster* (*Temnoclemmys*) *batalleri*), with the other species of this subgenus identified in the Spanish fossil record (i.e., *Ptychogaster* (*Temnoclemmys*) *bardenensis*), and with the specimen of *Ptychogaster* sp. from the Bardenas Reales of Navarre (i.e. the specimen identified as *Ptychogaster* (?*Ptychogaster*) *ronheimensis* by Murelaga *et al.* 2002).

The shell size of the adult specimens of the members of the subgenus *Temnoclemmys* is known to be smaller than those of the subgenus *Ptychogaster*, those of *Temnoclemmys* being between 10 and 16 cm, whilst those of the other subgenus are between 20 and 30 cm. The carapaces of the two articulated and almost complete shells from Monte Pila, recognized as adults due to the fusion of many sutures, is about 20 cm, being compatible with the estimated size of other specimens from the site, preserved as isolated plates. Therefore, the taxon recorded in Monte Pila is compatible with the size recognized for the smaller forms of the subgenus *Ptychogaster*, but it cannot be ruled out that it corresponded to a species of the subgenus *Temnoclemmys* of slightly larger dimensions (approximately 20% larger) than the largest representatives of this subgenus so far identified, including those of *Ptychogaster* (*Temnoclemmys*) *batalleri*. The estimated size of the shell of the specimen of *Ptychogaster* sp. from the Bardenas Reales of Navarre previously recognized as *Ptychogaster* (?*Ptychogaster*) *ronheimensis* is close to 27 cm (Murelaga *et al.* 2002; Fig. 11A, B). By contrast, the scarce isolated plates that were attributed to *Ptychogaster* (*Temnoclemmys*) *bardenensis* correspond to specimens with a shell length estimated at about 12 cm (Murelaga *et al.* 2002), unpublished isolated plates attributable to *Ptychogaster* from that locality, corresponding to specimens of almost twice the size of the holotype in this species, having subsequently been found in that region (e.g., Fig. 11J, K). As usual, a larger shell size usually involves the development of thicker plates. Thus, the thickness of the Monte Pila plates is proportionally greater when larger plates are considered. Therefore, the characterization of the subgenus *Ptychogaster* as a form with thicker plates than those of the subgenus *Temnoclemmys* is considered here as a feature closely related to the size.

The almost complete and undeformed carapace from Monte Pila (Fig. 3E, G, H) is wide in relation to its length (i.e., slightly longer than wide), being relatively low. Although the shell of the males of Ptychogasterinae has been recognized as narrower than that of the females, the carapace of the subgenus *Ptychogaster* is considered as being narrower than that of *Temnoclemmys* (Murelaga *et al.* 2002). Therefore, the morphology of that shell is compatible with members of the subgenus *Temnoclemmys* but differs from that which characterizes the subgenus *Ptychogaster*. In fact, the carapace of the subgenus *Ptychogaster* was considered to be taller than that of *Temnoclemmys* (Murelaga *et al.* 2002). The width of the carapace of the specimen of *Ptychogaster* sp. from the Bardenas Reales of Navarre was interpreted as three quarters of its length (Murelaga *et al.* 2002). The width/length ratio recorded in both the aforementioned specimens from Monte Pila and the Bardenas Reales of Navarre are part of the known variability range for the type species of the subgenus *Temnoclemmys* (i.e., *Ptychogaster* (*Temnoclemmys*) *batalleri*).

The nuchal plate of the subgenus *Temnoclemmys* is short, being shorter than wide in relation to that of *Ptychogaster*, a subgenus in which it is elongated in most forms (Murelaga *et al.* 2002; Luján *et al.* 2014). The nuchals from Monte Pila are not elongated, but they are almost as long as wide in some cases, or wider than long in others. Therefore, they correspond to the condition defined for the subgenus *Temnoclemmys*. However, this character must be taken with caution. Thus, the width of the nuchal plate of the specimen of *Ptychogaster* sp. from the Bardenas Reales of Navarre is more than a third greater than its width, this condition being compatible with that known for other specimens of the species *Ptychogaster* (?*Ptychogaster*) *ronheimensis* (see Groessens-Van Dyck & Schleich 1985), with that defined for the subgenus *Temnoclemmys*, and also with that identified in some specimens from Monte Pila and the type locality of *Ptychogaster* (*Temnoclemmys*) *batalleri*. Therefore, this character does not allow a clear attribution of the material from Monte Pila to either of these two subgenera, nor does the characterization of the nuchal of the subgenus *Ptychogaster* as more concave ventrally than that of *Temnoclemmys* (Murelaga *et al.* 2002), since this character is also recognized as being highly variable due to the relative high availability of material from Monte Pila analyzed here.

The neural series of the subgenus *Ptychogaster* has often been considered as composed of quadrate and octagonal elements, the presence of hexagonal plates, with the shortest margins postero-laterally directed, being recognized as more characteristic of *Temnoclemmys* (Murelaga *et al.* 2002). Following these ideas, the neurals from Monte Pila would support the presence of the subgenus *Temnoclemmys* at this locality. However, observation of the specimen of *Ptychogaster* sp. from the Bardenas Reales of Navarre shows that it also has several hexagonal neurals, with the short sides being posteriorly located.

The most anterior peripherals of the subgenus *Temnoclemmys* have been characterized as shorter than those of the subgenus *Ptychogaster*, lacking marked anterior expansions (Luján *et al.* 2014). The condition observed in the Monte Pila material does not differ from that known for *Ptychogaster* (*Temnoclemmys*) *batalleri*. The preserved region of the most anterior peripherals of the specimen of *Ptychogaster* sp. from the Bardenas Reales of Navarre is also compatible. The cervical scute of the subgenus *Ptychogaster* has been considered to be wider than that of *Temnoclemmys*, which is shorter in relation to the length of this plate (Murelaga *et al.* 2002; Luján *et al.* 2014). A high variability in the morphology, width/length ratio, and length of this scute relative to the total length of the nuchal is observed in the Monte Pila material. Thus, some cervicals are slightly wider than long or are as wide as long, but others are longer than wide, becoming almost twice as long as wide in some cases. In addition, some are shorter than a quarter of the total length of this plate, but the length of others is slightly greater than one third of the length of the nuchal. The cervical scute of the specimen of *Ptychogaster* sp. from the Bardenas Reales of Navarre is as long as it is wide, and its length is slightly greater than one third of the length of the nuchal. Therefore, it is compatible with the ranges of variability in both width and length of this scute observed in Monte Pila. Variability in this scute is also recognized for *Ptychogaster* (*Temnoclemmys*) *batalleri*, although the range of variability is smaller than that recognized for the Monte Pila material, probably because far fewer cervical scutes are known. The width/length ratio of the only cervical scute that was known for *Ptychogaster* (*Temnoclemmys*) *bardenensis*, which is relatively narrow, is also located within the range of variability identified by the Monte Pila material.

The anterior lobe of the subgenus *Temnoclemmys* was defined as being trapezoidal, with a transverse epiplastral border, the anterior margin in the subgenus *Ptychogaster* being subrounded (Murelaga *et al.* 1999, 2002; Luján *et al.* 2014). The availability of several articulated anterior plastral lobes from Monte Pila, as well as that of numerous disjointed epiplastra, allows recognition of the variability in this character, the anterior margin being clearly perpendicular to the axial plane in some specimens, but subrounded in others, intermediate shapes also being recognized. A similar variability can be observed in *Ptychogaster* (*Temnoclemmys*) *batalleri*. The morphology of this region in the holotype and so far only known epiplastron of *Ptychogaster* (*Temnoclemmys*) *bardenensis* is located within that range of variability, but also that of the specimen of *Ptychogaster* sp. from the Bardenas Reales of Navarre, both being more trapezoidal than subrounded.

Although both the subgenus *Ptychogaster* and the subgenus *Temnoclemmys* have a concave dorsal epiplastral lip, that of the subgenus *Temnoclemmys* has been defined as thicker but shorter (Murelaga *et al.* 1999, 2002; Luján *et al.* 2014). Both the length and the thickness of the epiplastral lip are recognized as being highly variable considering the abundant material from Monte Pila. Specimens in which the length of the epiplastral lip is less than half that of the epiplastral symphysis are identified (e.g., Fig. 6D), but also others where it reaches the posterior region of the symphysis (e.g., Fig. 6R), with numerous intermediate stages being recognized. This variability is recognized as being independent of the thickness of that structure, which is also not closely related to ontogeny. Thus, for example, specimens with a long epiplastral lip, some of them much thicker than others (e.g., being very thick in Fig. 6K, but not in Fig. 4P, despite the larger dimensions of the latter) are recognized. The length and thickness identified in the holotype of *Ptychogaster* (*Temnoclemmys*) *bardenensis* fall within the range of variability recognized in the Monte Pila material. The thickness of the epiplastral lip of the specimen of *Ptychogaster* sp. from the Bardenas Reales of Navarre is not less than that of the subgenus *Temnoclemmys*. Given the wide range of variability observed in the abundant material from Monte Pila, the morphology of this region so far known for the specimens of *Ptychogaster* (*Temnoclemmys*) *batalleri* cannot be clearly characterized as differing from that of the form present in this site.

The posterior plastral lobe of the subgenus *Ptychogaster* was characterized as wider than the more tapering lobe in the subgenus *Temnoclemmys* (Murelaga *et al.* 2002; Luján *et al.* 2014). Clearly expanded posterior lobes, with rounded lateral margins, are recognized among the adult individuals from Monte Pila (e.g., Fig. 3F; 8A, B), but there are also much narrower ones, with almost straight lateral margins (e.g., Fig. 8C). As previously interpreted, the shell of the males of the genus *Ptychogaster* should be narrower than those of the females (Lapparent de Broin 2000; Murelaga *et al.* 2002). Therefore, the two morphologies recorded in the Monte Pila material are interpreted to correspond to sexual dimorphism within a single taxon. The posterior plastral lobe of the specimen of *Ptychogaster* sp. from the Bardenas Reales of Navarre is not wider than that of some specimens of Monte Pila. The morphological variability recognized in the specimens of *Ptychogaster* (*Temnoclemmys*) *batalleri* is also compatible with that identified in this locality. The morphology of the lateral margin of the partial xiphiplastron of *Ptychogaster* (*Temnoclemmys*) *bardenensis* is also compatible with the range of variability in the shape of the Monte Pila specimens.

The anal notch of the subgenus *Temnoclemmys* was recognized as being shorter than that of the subgenus *Ptychogaster* (Murelaga *et al.* 2002). Some degree of variability is identified in the Monte Pila material, the notch being very narrow and shallow in some specimens (e.g., Fig. 8C) but relatively long in others (Fig. 8A). In fact, the length is greater than that observed in the type species of the subgenus (i.e., *Ptychogaster* (*Temnoclemmys*) *batalleri*), reaching a development compatible with that used to characterize the subgenus *Ptychogaster*. Thus, it is much deeper than that of the specimen of *Ptychogaster* sp. from the Bardenas Reales of Navarre in some individuals, showing a morphology and arrangement compatible with that of *Ptychogaster* (*Temnoclemmys*) *batalleri*. In addition, although the lateral margins of the anal notch of the subgenus *Temnoclemmys* were defined as straight, a condition opposed to that proposed for the subgenus *Ptychogaster* (Murelaga *et al.* 2002), this character is also recognized as being subject to variability in the abundant material from Monte Pila (e.g., being rounded in specimen in Fig. 8A, but straight in that in Fig. 8D).

The characters observed in the specimens from Fuenmayor are compatible with the range of variability identified in the Monte Pila material. In fact, the great variability recognized in Monte Pila, due to the availability of abundant specimens, does not distinguish the form present there from that of *Ptychogaster* (*Temnoclemmys*) *batalleri* or of *Ptychogaster* (*Temnoclemmys*) *bardenensis* by any of the previously proposed characters. Thus, although the difference between *Ptychogaster* (*Temnoclemmys*) *batalleri* and *Ptychogaster* (*Temnoclemmys*) *bardenensis* were recently established based on the presence of a medially less concave and much thicker dorsal epiplastral lip throughout its width in the Catalan species (Luján *et al.* 2014), this character is observed to be highly variable in the Monte Pila material analyzed here. Since the material from Monte Pila and Fuenmayor is temporally and geographically close to the poorly known *Ptychogaster* (*Temnoclemmys*) *bardenensis*, its attribution to that form cannot be ruled out. However, a detailed review of all members of this subgenus, as well as that of the subgenus *Ptychogaster*, especially taking into account intraspecific variability, is required in order to improve knowledge about the diversity of this lineage. Many forms have been defined by extremely scarce material, so their diagnoses are problematic, not only due to the very limited availability of characters but, especially, because many of them could be problematic since their potential variability could not be taken into account. The validity and, in this case, the proposal for a new diagnosis for *Ptychogaster* (*Temnoclemmys*) *bardenensis*, cannot be done without carrying out that detailed study. In fact, its identification as belonging to a different taxon to which the specimen of that locality here attributed to *Ptychogaster* sp. (i.e., *Ptychogaster* (?*Ptychogaster*) *ronheimensis* sensu Murelaga *et al.* 2002) belongs should be re-evaluated.

Analysis of the tortoise from Monte Pila

The presence of a second lineage of turtles is recognized in Monte Pila, both in MP1 and in MP2. It is represented by a much larger form than the specimens of this locality attributed to Ptychogasterinae. The presence of characters such as a granular outer surface of the shell; alternating medially long but laterally short costals and medially short but laterally long ones; alternating rectangular and non-rectangular neurals; reduced proximal region of the ribs; and overlap of the sulci between the pleural and the marginal scutes on the sutures between the costal and the peripheral plates; allows us to attribute it to a terrestrial form, corresponding to the Testudinidae clade (Pérez-García & Vlachos 2014). No specimen belonging to this lineage is identified among the material from Fuenmayor, nor is it present, so far, in the Bardenas Reales of Navarre (Murelaga *et al.* 1999, 2002). Remains of several individuals of Testudinidae are identified in each of the two mentioned levels of Monte Pila (i.e. MP1 and MP2), all of them being attributable to one form but, probably, representing different ontogenetic stages based on the differences in size which are observed. For example, the length of the proximal region of some costals from MP2 (Fig. 12A, B) is more than twice that of others coming from the same level (Fig. 12C). The testudinid from Monte Pila corresponds to a large form, the width of the entoplastron from MP2 being close to 22 cm (Fig. 12E), and that of the preserved region of the first costal from the same level of about 36 cm (Fig. 12A). Therefore, the shell length of adult specimens was greater than one metre.

All species of large testudinids so far identified in the European Neogene record are attributable to the genus *Titanochelon* (Pérez-García & Vlachos 2014). In fact, this genus is identified from the lower Miocene to the lower

Pleistocene, being represented by about ten named species (Pérez-García & Vlachos 2014; Pérez-García *et al.* 2017a). In addition to the information concerning size, characters such as relatively low carapace interpreted from the preserved costal plates; the absence of pointed tips in the carapacial rim, in the region of contact of the sulci between the marginal scutes and the lateral border of the peripherals; and the identification of a ventral thickening in the area covered by the anal scutes of the males; allow us to attribute these remains from Monte Pila to *Titanochelon*, being located within the known biostratigraphic and biogeographic ranges of distribution in this genus (Pérez-García & Vlachos 2014). A single valid species of this genus is currently identified in the Iberian record, *Titanochelon bolivari*, its presence having been confirmed between the Aragonian and the lower Vallesian (Langhian to early Tortonian, MN5 to MN10) (Pérez-García & Vlachos 2014; Pérez-García *et al.* 2017b). Although scarce, some remains of *Titanochelon*, with an uncertain specific attribution, had previously been identified in the MN2 biozone of the Spanish fossil record (see Pérez-García & Vlachos 2014, and references therein). The males of *Titanochelon bolivari* were characterized by the presence of a trapezoidal posterior lobe, showing a wide and very shallow anal notch, and with a pair of latero-posterior protuberances (Pérez-García & Vlachos 2014). These characters, until now exclusive to the Iberian species, are recognized in the material presented here (Fig. 12F). Considering the limited information provided by the relatively scarce material of *Titanochelon* from Monte Pila, so that most of the characters of the diagnosis of *Titanochelon bolivari* cannot be evaluated, the testudinid from this site is assigned to *Titanochelon* cf. *bolivari*. This represents both the first identification of this genus in the Autonomous Community of La Rioja and the oldest record of the possible presence of the species *Titanochelon bolivari*.

IMPLICATIONS AND CONCLUSIONS

The information concerning the turtles from the lower Miocene of the Iberian Peninsula is limited. It was almost restricted to that provided by the study of the specimens found in the Bardenas Reales of Navarre (Ebro Basin; biozone MN3). Several forms of freshwater turtles were recognized there, from scarce material. The best represented lineage was Ptychogasterinae, the putative presence of two forms having been cited there: the first record of the lower Oligocene form from Germany *Ptychogaster* (?*Ptychogaster*) *ronheimensis* in the Iberian Peninsula, represented by a single relatively complete shell (identified here as *Ptychogaster* sp.); and a new taxon, *Ptychogaster* (*Temnoclemmys*) *bardenensis*, poorly defined, known by very scarce isolated and disarticulated remains. *Ptychogaster* (*Temnoclemmys*) *bardenensis* had not been recognized until now outside its type locality. Thus, the representatives of Ptychogasterinae from the Bardenas Reales of Navarre were the oldest representatives of this lineage identified at a specific level in the Iberian fossil record.

The presence of turtles was recorded in another location in the lower Miocene of the Ebro basin, in Monte Pila (La Rioja). The material from that locality is older than that from the Bardenas Reales of Navarre (biozone MN2). It is still unpublished, having been cited, without justification, as *Ptychogaster* sp. and Chelonii indet. The remains of turtles from this locality are abundant, and have been prepared for study, which is done in this paper. In addition, turtle remains are recognized, for the first time, in another nearby location, also corresponding to the MN2 biozone: Fuenmayor (La Rioja).

One of the taxa recognized here through the analysis of the Monte Pila material allows an increase in knowledge about the diversity of turtles in the lower Miocene of the Ebro Basin, since it corresponds to a lineage unknown in the Bardenas Reales of Navarre. In fact, unlike all the turtles from that area, it represents a terrestrial form. It is a large testudinid, attributed to the genus *Titanochelon*. Therefore, it is one of the oldest records of this genus. This find represents both the first identification of *Titanochelon* in the Autonomous Community of La Rioja and the oldest of the possible presence of the species *Titanochelon bolivari*.

The most abundant turtles in Monte Pila are not terrestrial forms, but are aquatic ones. Thus, Ptychogasterinae is well represented. This clade is also identified in Fuenmayor. The remains of Ptychogasterinae from both locations are the oldest known in the Iberian Peninsula. The abundance of material of this clade in both localities allows the recognition of a high range of intraspecific variability, related to ontogeny and dimorphism, but also individual variation. Many of the species of that lineage are known from scarce material, meaning that their diagnoses incorporate very few characters. In fact, many of the characters traditionally used for the distinction of their representatives are here recognized as subject to variability, at least for the form recorded in these Spanish sites. The material from Monte Pila and Fuenmayor is tentatively attributed to *Ptychogaster* (*Temnoclemmys*) cf. *bardenensis*. However, redefinition of many of the species of this lineage is necessary, as well as analysis of the validity of many of them, in order to confirm this attribution and that of the forms present in many other European locations, as well as to know the diversity represented by the fossils of Ptychogasterinae hitherto known.

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